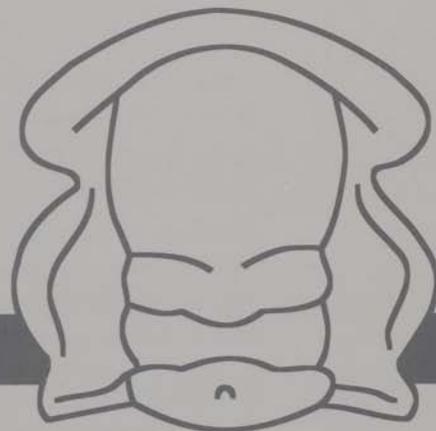


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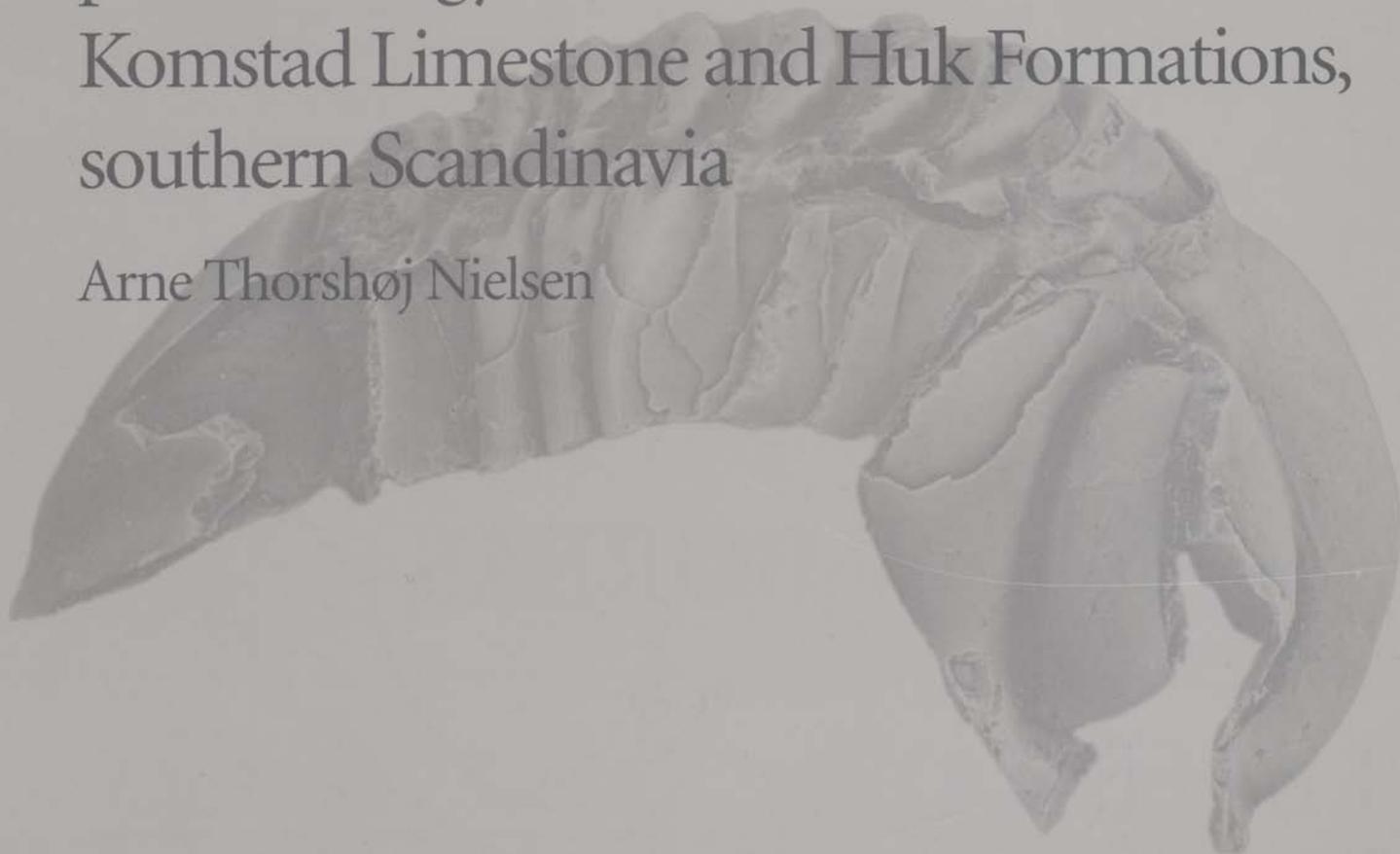
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Trilobite systematics, biostratigraphy and
palaeoecology of the Lower Ordovician
Komstad Limestone and Huk Formations,
southern Scandinavia

Arne Thorshøj Nielsen



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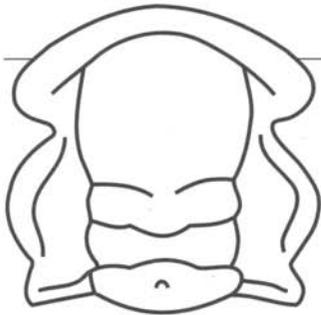
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Trilobite systematics, biostratigraphy and palaeoecology of the Lower Ordovician Komstad Limestone and Huk Formations, southern Scandinavia

ARNE THORSHØJ NIELSEN

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The upper Arenigian to lower Llanvirnian Komstad Limestone Formation is a tongue of the Baltoscandian 'Orthoceratite limestone', intercalated in the predominantly shaly Ordovician succession of Scania–Bornholm, southernmost Scandinavia. The Formation is 2–5 m thick on Bornholm, 10 to more than 15 m in southeastern Scania, 3 to more than 4.5 m in central western Scania, and from there thins towards northwestern Scania, where it wedges out. The stratigraphically equivalent Huk Formation of the Oslo area has been studied only at Slemmestad, where it comprises the 1.5 m thick Hukodden Limestone Member ('*Megistaspis* Limestone'), the 4.4 m thick Lysaker Member ('*Asaphus* Shale'), and the 2.6 m thick Svartodden Limestone Member ('*Endoceras* Limestone'). The 'Skelbro Limestone Formation' of Bornholm is abandoned and merged with the Komstad Limestone Formation. The Killeröd quarry is proposed as a paratype section for the Komstad Limestone Formation. Based on collections of about 8000 trilobites, the Komstad Limestone and Huk Formations are assigned to the Zones of *Megistaspis polyphemus* (former *M. lata*), *M. simon*, *M. limbata*, *Asaphus expansus*, and *A. 'raniceps'* of the Volkhov and Kunda Stages. The Komstad Limestone Formation is diachronous. The correlation of trilobite and graptolite zones is briefly discussed. The Yapeenian–Darrwilian boundary approximates the *M. simon*–*M. limbata* zonal boundary. The Arenig–Llanvirn boundary corresponds to a level slightly above base of the *A. 'raniceps'* Zone. Inferences on the autecology of the most common trilobite groups are summarised. Five recurrent trilobite biofacies are defined: the benthic assemblage succession *Nileus*→*Geragnostus*→*Symphysurus*→*Megistaspis* represents a depth transect, whereas the *Cyclopyge* assemblage was pelagic. The correlation of palaeoenvironmental changes as revealed by the alternation of biofacies, i.e. ecostratigraphy, improves stratigraphical resolution significantly. A relative-sea-level curve is reconstructed on this basis. The deposition of the Komstad Limestone and Huk Formations was connected to a series of sea-level falls, shifting the limestone deposition stepwise into the western facies belts. Systematic descriptions are presented of *Ampyx*, *Asaphus*, *Cnemidopyge*, *Dysplanus*, *Globampyx*, *Hallanta*, *Illaeus*, *Lonchodomas*, *Megistaspis*, *Nileus*, *Niobe*, *Ottenbyaspis*, *Panderia*, *Parillaenus*, *Raymondaspis*, and *Stygina*, including eighteen new species and subspecies, viz. *Megistaspis* (*Megistaspis*) *geminus* n.sp., *Nileus depressus schranki* n.subsp., *N. d. serotinus* n.subsp., *N. d. parvus* n.subsp., *N. planiceps* n.sp., *N. latifrons* n.sp., *N. implexus* n.sp., *Niobe* (*Niobe*) *tjernviki* n.sp., *Lonchodomas volborthi schmidti* n.subsp., *Dysplanus acutigenia vetustus* n.subsp., *Illaeus fornicatus* n.sp., *I. schuberti* n.sp., *Lonchodomas tenuis* n.sp., *Rhombampyx frater* n.sp., *Raymondaspis* (*Turgicephalus*) *whittingtoni* n.sp., *R. (T.) neglecta* n.sp., *R. (Raymondaspis) scitula* n.sp., and *R. (R.) insignis* n.sp. Nineteen forms, including several new species, are treated under open nomenclature. □ Trilobites, asaphids, niobinids, nileids, styginids, illaeids, raphiophorids, ontogeny, ecophenotypes, biostratigraphy, palaeoecology, ecostratigraphy, sea-level changes, Lower Ordovician, Arenig, Scania, Bornholm, Oslo.

Arne Thorshøj Nielsen, Geological Museum, Øster Voldgade 5–7, DK–1350 København K, Denmark; 6th June, 1993; revised 5th April, 1995.

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Introduction

The rich Lower Ordovician trilobite faunas of Baltoscandia have attracted the attention of palaeontologists for almost two centuries (e.g., Dalman 1827; Angelin 1851–1878; Balashova 1953–1976; Brögger 1882; Eichwald 1825–1869; Hoffman 1858; Holm 1883, 1886; Jaanusson 1953a, b, 1957; Lamansky 1905; Moberg & Segerberg 1906; Nieszkowski 1857; Pander 1830; Pompecki 1890; Schmidt 1881–1907; Steinhardt 1874; Tjernvik 1956; Törnquist 1884). The first regional chronostratigraphical schemes were based almost exclusively on trilobites (Angelin 1854; Schmidt 1881; Moberg 1890; Lamansky 1905), and for this historical reason the trilobite zonation is still the standard frame of reference within the post-Tremadocian Early Ordovician of Baltoscandia. However, the majority of the monographs listed above are comparatively old, and virtually all of them are based on material of which the provenance is known only in general terms from a modern biostratigraphic point of view. A notable exception is Tjernvik (1956), who revised the Early Arenigian trilobites of Scandinavia. Little modern systematic work has been undertaken, however, on the late Arenigian and earliest Llanvirnian faunas (Volkhov–Kunda Stages). For the same reason the trilobite biostratigraphy of the Volkhov Stage within Scandinavia is currently known only in broad outline (Tjernvik 1980).

The primary aim of the present work is to establish a trilobite biozonation for the Komstad Limestone Formation of Scania–Bornholm, and the equivalent Huk Formation of the Oslo Region (Fig. 1). A secondary aim is to explore the palaeoenvironmental conditions responsible for this ‘anomalous’ period of sedimentation. The roughly coeval Komstad Limestone and Huk Formations, which are a western tongue of the central Baltoscandian ‘*Orthoceras* limestone’ facies, constitute the only major limestone intercalation in the Scanian and Oslo Ordovician confacies belts, which otherwise are dominated by graptolite mudstones (Fig. 40).

The stratigraphy of the Komstad Limestone and the Huk Formation has been dealt with by many authors (e.g., Brögger 1882; Tullberg 1883a, b; Grönwall 1916; Funkquist 1919; C. Poulsen 1936; Ekström 1937; and V. Poulsen 1965, 1966), but mostly based on ‘bag-stratigraphical’ material (*sensu* Jaanusson 1976, p. 302). In order to make new headway, systematic fossil-sampling was carried out in 1981–83 and

1986–87 at a number of localities in Scania, on Bornholm and south of Oslo. The assembled material contains more than 8000 trilobite specimens, of which ca. 40% belong to groups revised in the present paper. The selection of taxa for revision was guided by the assumed stratigraphical significance of particular groups, based mainly on Tjernvik (1980). The systematic descriptions comprise analyses of variation ranges, ontogeny and gradual morphologic shifts in time and space. It appears that a number of trilobites were morphologically rather ‘plastic’, and that expression of the phenotype was controlled by the environment.

The quantity of material allows the ecology to be investigated, and four depth-related trilobite biofacies are recognized. The correlation of palaeoenvironmental oscillations, as reflected by the alternation of trilobite biofacies, produces a far higher stratigraphical resolution than conventional biostratigraphy, and this ecostratigraphical aspect, although still in its initial phase, may be the most interesting result of the present work.

Acknowledgements. – During the preparation of this thesis I have been helped by many persons and institutions. I want to express my sincere gratitude to the Carlsberg Foundation for financial support during the final phases of my work, including the costs of travels and fieldwork (scholarship 1984–287; grants 1985/86: 221a/VI, 1986/87: 298/VI, 1987: 289/20, 1988: 587/20). Professor Valdemar Poulsen, University of Copenhagen, initially encouraged me to undertake this study and has offered much helpful advice throughout the period of work. Dr. Richard Fortey, Museum of Natural History, London, and Dr. Nigel Hughes, Cincinnati Museum of Natural History, reviewed the manuscript and made a number of suggestions towards its improvement. Professor Jan Bergström, Stockholm, has in a most friendly way helped me on several occasions, e.g., by arranging permission to excavate the protected quarries at Fågelsång and by providing access to the collections at the Swedish Museum of Natural History, Stockholm. My sincere thanks to these persons. Furthermore, I wish to extend my thanks to Dr. David Bruton, Oslo, for kind help when I visited the Paleontological Museum, to the late Dr. Torsten Tjernvik, Lindesberg, who generously provided information about his unpublished research on the trilobite fauna of the Volkhov Stage, to Mr. Sten L. Jacobsen, Geological Museum, Copenhagen, for skilfully doing the photographic work, and to Mr. Thomas Bredsdorff and Cand. scient Lene Clausen for the drawings. The Swedish authority Länsstyrelsen i Malmöhus län (Naturvårdsenheten) is thanked for the permission to excavate the protected quarries at Fågelsång.

Finishing this thesis has required a laborious effort. No words can cover the gratitude I feel towards my companion Lene Clausen, who patiently has supported me and assisted whenever possible.

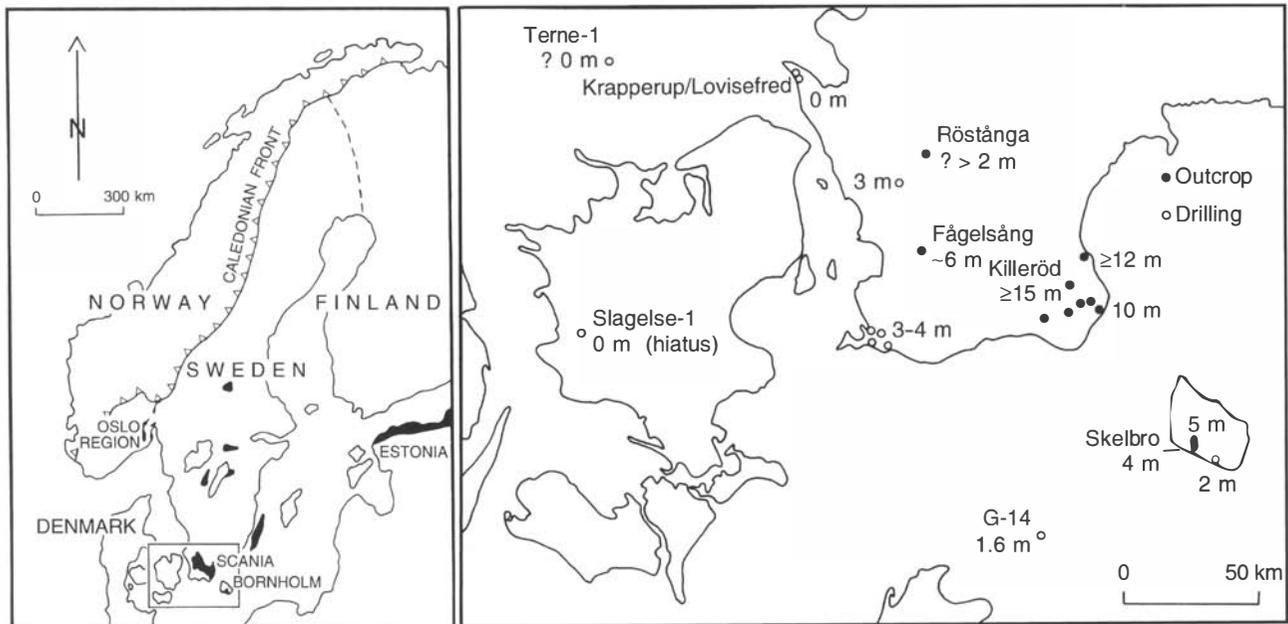


Fig. 1. Location map of study area showing distribution and thickness variations of the Komstad Limestone. The most important localities and drill holes referred to are indicated.

Methods and material

The Komstad Limestone was investigated at most localities reported from Bornholm (Denmark) and Scania (Sweden), but fossils were sampled systematically only at Skelbro, Kille-röd, and Fågelsång. The Hukodden Limestone and Lysaker Members of the Huk Formation were sampled at Slemmestad (Norway). The levels of fossils collected from the Komstad and Hukodden Limestones are generally known with an accuracy of ± 5 mm. Material sampled from the Lysaker Member is specified only to bed, as a precise intrabed assignment is not possible because of the irregular boundaries of the nodular limestone.

The normal procedure of sampling was to collect all fossils encountered during crushing of the limestone (i.e. bulk sampling from hard rock *sensu* Jaanusson 1979). Fossils were collected only from strata *in situ*, which were crushed down to about walnut size. An area of approximately $\frac{1}{2}$ m² of each bed was sampled at Skelbro, whereas ca. $\frac{1}{8}$ to $\frac{1}{4}$ m² were sampled of each bed in the remaining sections, sometimes less; a total of about 6 m³ of limestone has been investigated.

The material collected includes 4593 samples, containing a total of 8034 trilobite skeletal parts (6367 from the Komstad Limestone and 1667 from the Slemmestad section) in addition to thousands of brachiopods, ostracodes and other fossil groups. The brachiopods and ostracodes in the Norwegian material have not been registered. Selected well-preserved specimens from various museums and private collections have been included in the taxonomical descriptions. The exact provenance of the latter material is as a rule unknown,

but the stratigraphical level is assessed whenever possible, based on the lithology of the samples and the associated fossils. This can often be done with a high degree of precision. The prefixes of the sample numbers and repositories are listed in Table 1.

The remaining non-revised material (ca. 60% of the collection) has been determined at the genus or family level only and have not been subjected to detailed studies as yet. It is

Table 1. Prefixes of sample numbers and repositories. Except for Ar, LO, PMO and MGUH numbers, the number refers to the sample. Individual samples often contain several fossil specimens, which therefore carry the same number. When two or more specimens belonging to the same genus are present within a single sample, a suffix is added to the number (a, b, c, etc.). Fossiliferous larger samples, e.g., no. S 70, comprising several limestone pieces, are usually cited as S 70-1, -2 etc., referring to a numbered slab, which eases the retrieval of particular specimens.

A-numbers:	Slemmestad
F-numbers:	Fågelsång
K-numbers:	SE Scania
S-numbers:	Skelbro
Ar-numbers:	Swedish Museum of Nat. Hist., Stockholm
PMO-numbers:	Paleontological Museum, Oslo
LO- & LU-numbers:	University of Lund
MGUH- & GM-numbers:	Geological Museum, Copenhagen
IK-numbers:	Coll. Mrs. Inga Krause, Germany
DGU-numbers:	Geological Survey of Denmark

dominated by *Symphysurus*, agnostids, ptychopygids, *Cyclopyge* and *Cyrtometopus*; no other group is represented by more than 30 specimens.

Sections have been measured at many localities, but it is not possible to evaluate the lithology without actually crushing the rock, as the appearance on surface is much dependent upon the level of weathering. Hence two types of logs are presented, a simplified version for localities not studied in greater detail and itemized logs from localities where fossils have been sampled. It is hazardous to base a lithological correlation on matching series of discontinuity surfaces, except between close localities. Discontinuity surfaces abound, and their expression in different sections is much dependent upon the level of surface weathering.

Description of localities

Bornholm

The Komstad Limestone was in the past worked in nine small quarries in the Læså area of southern Bornholm (Fig. 2), but when the industry ceased all but two quarries became filled

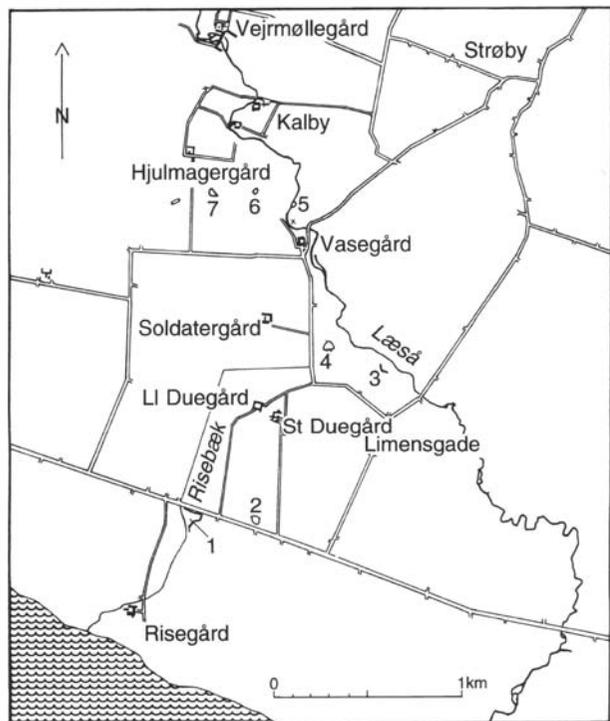


Fig. 2. Map of the Læså area, southern Bornholm, showing location of abandoned Komstad Limestone quarries. 1: Skelbro; 2: Duegård; 3: Limensgade; 4: Soldatergård; 5: Vasegård; 6: Quarry 400 m northwest of Vasegård; 7: Hjulmagergård. Another two quarries, situated 150 m NE of the Limensgade quarry and 200 m due west of the Hjulmagergård quarry, respectively, are now obliterated by infilling. The Vasegård-1 shallow drill-hole is marked by an x, just south of 5.



Fig. 3. Map of the Pedersker area, southern Bornholm, showing wells penetrating the Komstad Limestone and its thickness, calculated from gamma- and electrical logs (K. Klitten, personal communication, 1989). Billegrav Gd.-1 did not reach the Komstad Limestone (see Pedersen 1989). Sømarken 3 was referred to as the Bavnegård well by V. Poulsen (1978).

with water. Since the turn of the century, only the Skelbro, Limensgade and northernmost Vasegård quarries have been accessible for study, but no continuous complete section is exposed today on the island, despite the limited thickness of the Komstad Limestone. The formation is 4 m thick at Skelbro, 4.7 m in a new drilling at Vasegård, and probably about 5 m at Hjulmagergård (cf. Grönwall 1916, pp. 72–75). It appears that the limestone is somewhat thinner in drill-holes on southeastern Bornholm (Fig. 3). Systematic studies were undertaken only in the Skelbro quarry.

Skelbro quarry

The abandoned but dry quarry has for long been the most important exposure of Komstad Limestone on Bornholm (Grönwall 1916; Nørregaard 1907; C. Poulsen 1936; V. Poulsen 1965; Stouge 1974, 1975). The lower boundary and basal conglomerate of the limestone are exposed in Risenbæk just north of the road (Fig. 2). The subjacent Alum Shale can be followed for about 600 m further north in the bottom and banks of the ditch. Up to 2.5 m of limestone is exposed in the eastern and south-eastern quarry faces of the Skelbro quarry itself. The strata dip gently southwards; the orientation aver-



Fig. 4. Section excavated in northern part of the Skelbro quarry. The middle interval containing numerous thin shale beds represents the *M. simon* Zone, the more massive limestones below and above belong to the *M. polyphemus* and *M. limbata* Zones, respectively.

ages 81°/4° S. An excavation reaching the lower boundary of the limestone was made in the northeastern corner of the quarry (Fig. 4). Further excavations in the southwestern-most part of the quarry failed to locate the upper boundary of the limestone, but another 0.15 m of black limestone was added to the section exposed within the main quarry. This black interval constitutes the top part of the Komstad limestone at Soldatergård and Vasegård (Grönwall 1916), and the section measured at Skelbro (Fig. 5) thus appears to be complete (at the most 0.1 m may be missing).

The limestone beds are numbered counting from a n easily recognizable shale level, with a 'negative series' down to bed -21 and a 'positive series' up to bed +14 (Fig. 5). The sample volume was continuously recorded for palaeoecological purposes; on average an area of 0.5 m² was sampled, but up to 1 m² has been processed in some intervals. The section represents the *M. polyphemus*, *M. simon*, *M. limbata*, and basal part of the *A. expansus* Zones.

Ice-polished orthocone cephalopods are exposed on the scour-marked upper limestone surface in the southern part of the quarry, representing the *A. expansus* Zone interval (Fig. 6).

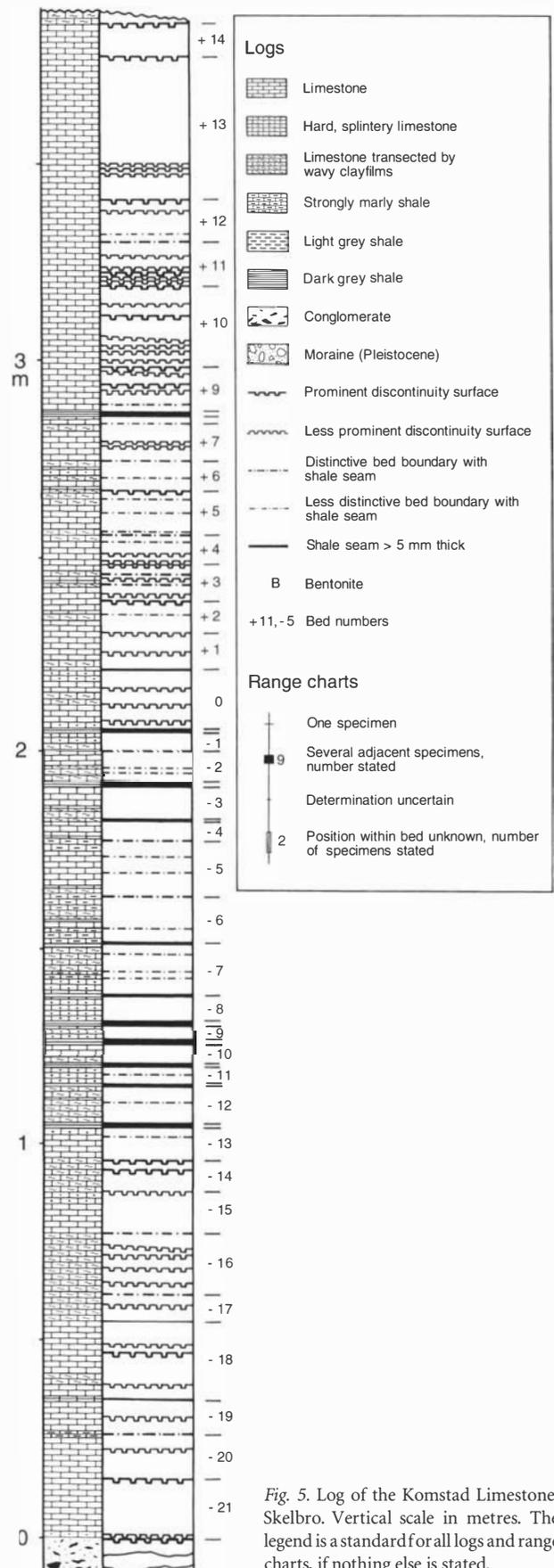


Fig. 5. Log of the Komstad Limestone, Skelbro. Vertical scale in metres. The legend is a standard for all logs and range charts, if nothing else is stated.

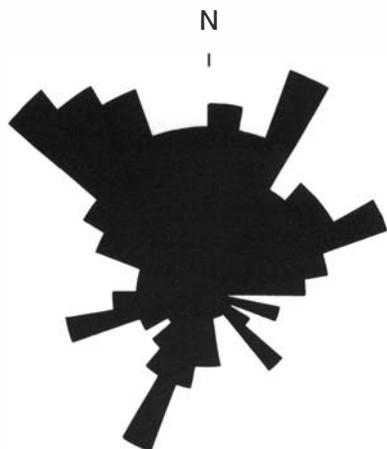


Fig. 6. Orientation of orthocone cephalopods, Skelbro ($N = 173$). The direction is measured from apex towards aperture. All specimens are from the boundary between beds +13 and +14 (± 6 cm), i.e. base of the *A. expansus* Zone. Detailed studies suggest that no significant change of orientation takes place within this interval. The cephalopods indicate a mainly northerly palaeoflow direction.

Southeastern Scania

The Komstad Limestone has been quarried at numerous sites within the region since the early Middle Ages, but the opencast mining gradually dwindled during this century and was finally suspended in 1986. At the few sites with existing outcrops, limestone is typically exposed in steep walls, from which it is impossible to obtain sufficiently large samples for systematic fossil collection.

The locations of the best known Komstad Limestone localities within SE Scania are shown in Fig. 7; see Moberg (1911), Funkquist (1919), the map sheet descriptions (e.g., Holst 1892), and Bergström & Shaikh (1980) for a listing of other sites. The present study focuses on the outcrops in the vicinity of Komstad, but the exposures at Gislövshammar and Kivik are also briefly dealt with.

In SE Scania the quarrymen distinguished between a lower light coloured unit ('Undre ljust') and an upper dark unit ('Övre grå'), which actually correspond rather precisely to



Fig. 7. Key map of Scania, showing positions of localities. Outcrops indicated by black stars, well-sections by white stars.

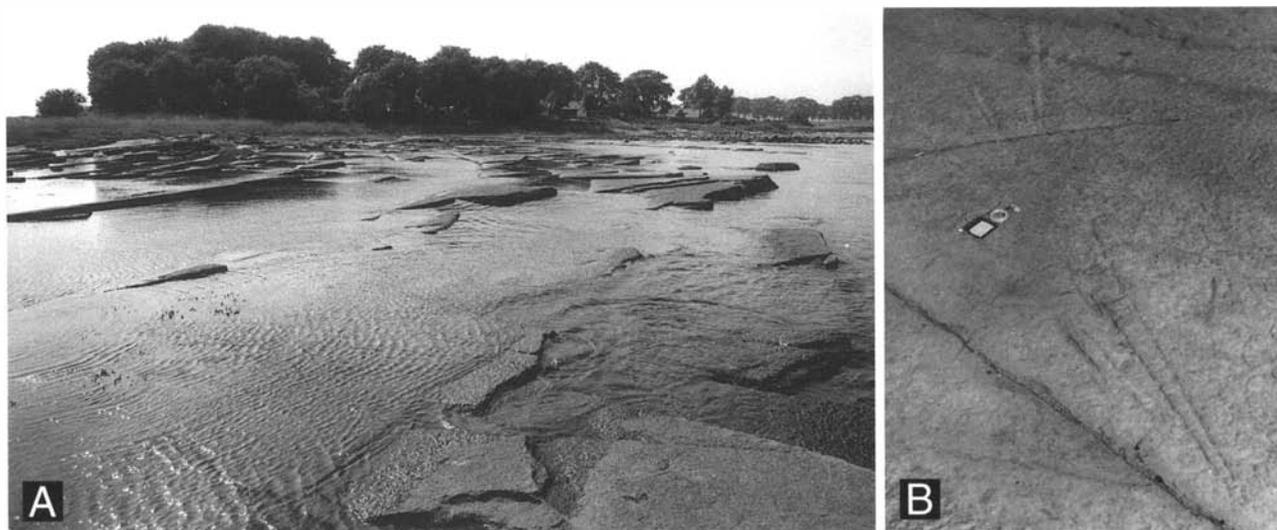


Fig. 8. □A. Gislövshammar, view towards southwest. □B. Orthocone cephalopods on bedding surface at 4.84 m, Gislövshammar. The compass mirror is pointing towards the north. The specimens exhibit a preferred orientation towards SSE (cf. Fig. 10).

the *M. simon* and the *M. limbata* Zone intervals, respectively. The 'Övre grå' unit was preferred for quarrying, whereas the lower part of the limestone generally was not worked, and, consequently, is not exposed in the old quarries. For this reason about 4 m of the *M. simon* Zone remain to be studied. The overlying thin-bedded impure limestone of the *A. expansus* and *A. 'raniceps'* Zones was technically useless ('Skit sten'), and so the *A. 'raniceps'* Zone is not exposed in any quarry and its thickness is unknown.

Gislövshammar

Komstad Limestone is exposed on the north-eastern beach of the small headland; this is the only site in SE Scania where a complete section of the formation is more or less accessible. The degree of exposure is variable, though, depending upon the wind direction: nearly no limestone is visible at high-water-level. The orientation of the limestone changes from 43°/5° SE near the beach to 124°/11° SW in the NE corner adjacent to the water front. This curving of the strata (Fig. 8A) is caused by drag from a nearby fault to the south (Lindström 1960).

Nine and a half metres of limestone were logged (Fig. 9), with a measuring error estimated to be within ± 0.25 m. The lowermost two metres of the section form a submarine cliff, which was measured by means of scuba-diving. The subjacent Tøyen Shale is exposed at the base of the submarine wall, at a water depth of 2–3 m. The shale immediately below the limestone is greenish grey and bioturbated. The first graptolites were encountered 0.5 m below the limestone. The upper bedding surface of the basal limestone bed is impregnated by glauconite and pyrite. The bed itself contains small-scale stromatolites; however, no algal filaments have been

identified in thin sections. Orthocone cephalopods occur abundantly on some bedding planes in the upper part of the limestone (Figs. 8B, 10), of which the uppermost part is calcarenitic. The top bed is extremely hard and splintery, and appears to be silicified; it is dark-coloured, concealing that it actually is quite rich in glauconite.

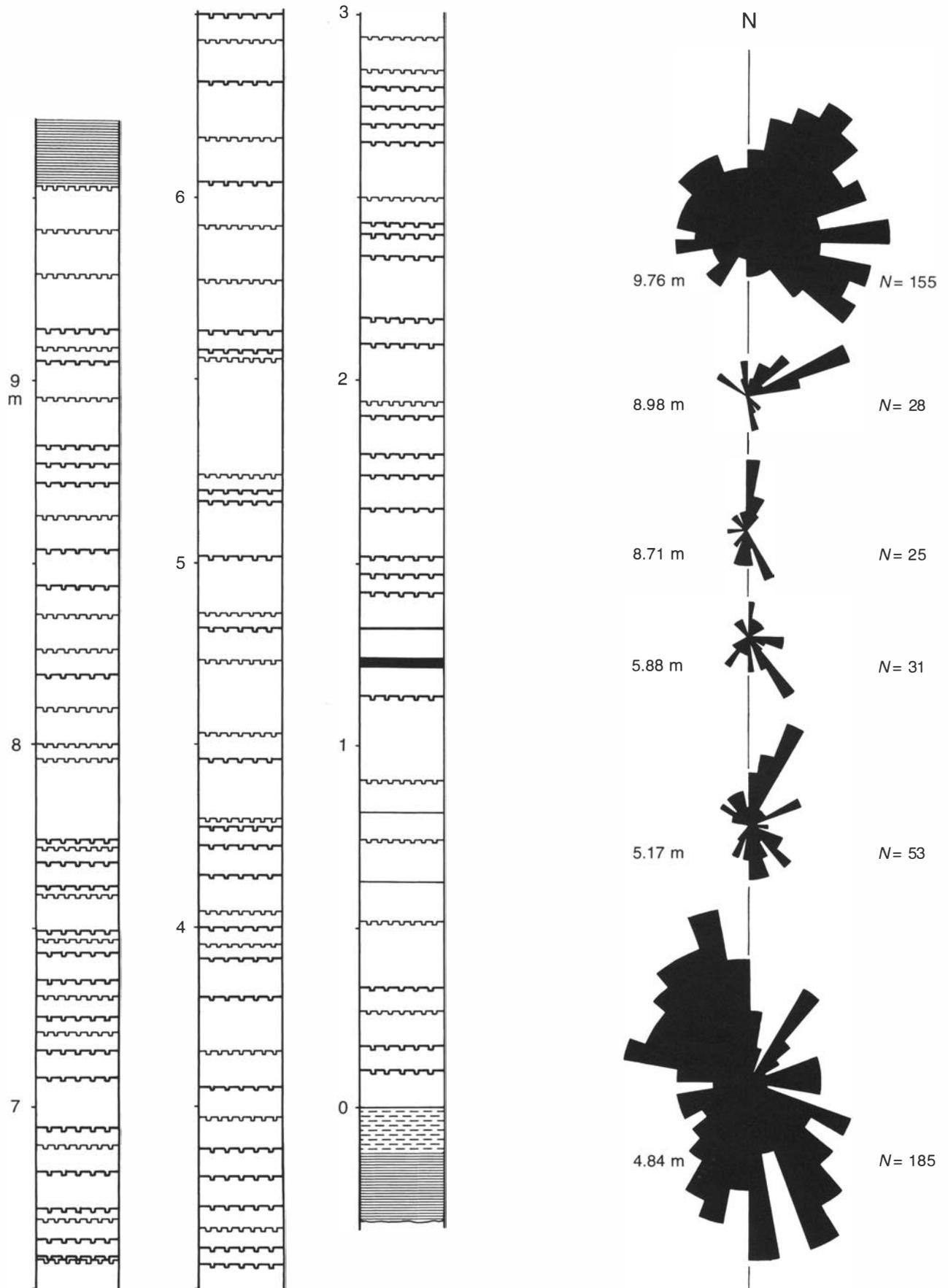
The section represents at least the *M. simon* to *A. expansus* Zones, but the base may be within the upper part of the *M. polyphemus* Zone. A few beds of the Killeröd Formation overlie the Komstad Limestone to the south, but may be difficult to locate among the many erratic boulders.

Kivik

Steeply dipping, overturned limestone is exposed in the small stream Hjerteäckan ('Heart Stream') in the garden and mill-race of the former water mill, situated in central Kivik (see also De Geer 1889, p. 16). Southwestwards, short of the house, a stone fence across the stream hides the bedrock, but further downstream several steeply dipping limestone beds crop out in the stream bed and the northern bluff. These beds may at a first glance be taken for Komstad

Fig. 9 (opposite page, left). Log of the Komstad Limestone exposed at Gislövshammar. The lower two metres were measured below sea-level by means of scuba-diving. This is the only site within Scania where a complete section of Komstad Limestone is outcropping; the Formation is bounded by the Tøyen Shale below and the Killeröd Formation above.

Fig. 10 (opposite page, right). Orientation of orthocone cephalopods, Gislövshammar. The direction is measured from apex towards aperture. Three general palaeocurrent directions are apparent: towards NW, NE and SE. The levels refer to Fig. 9.



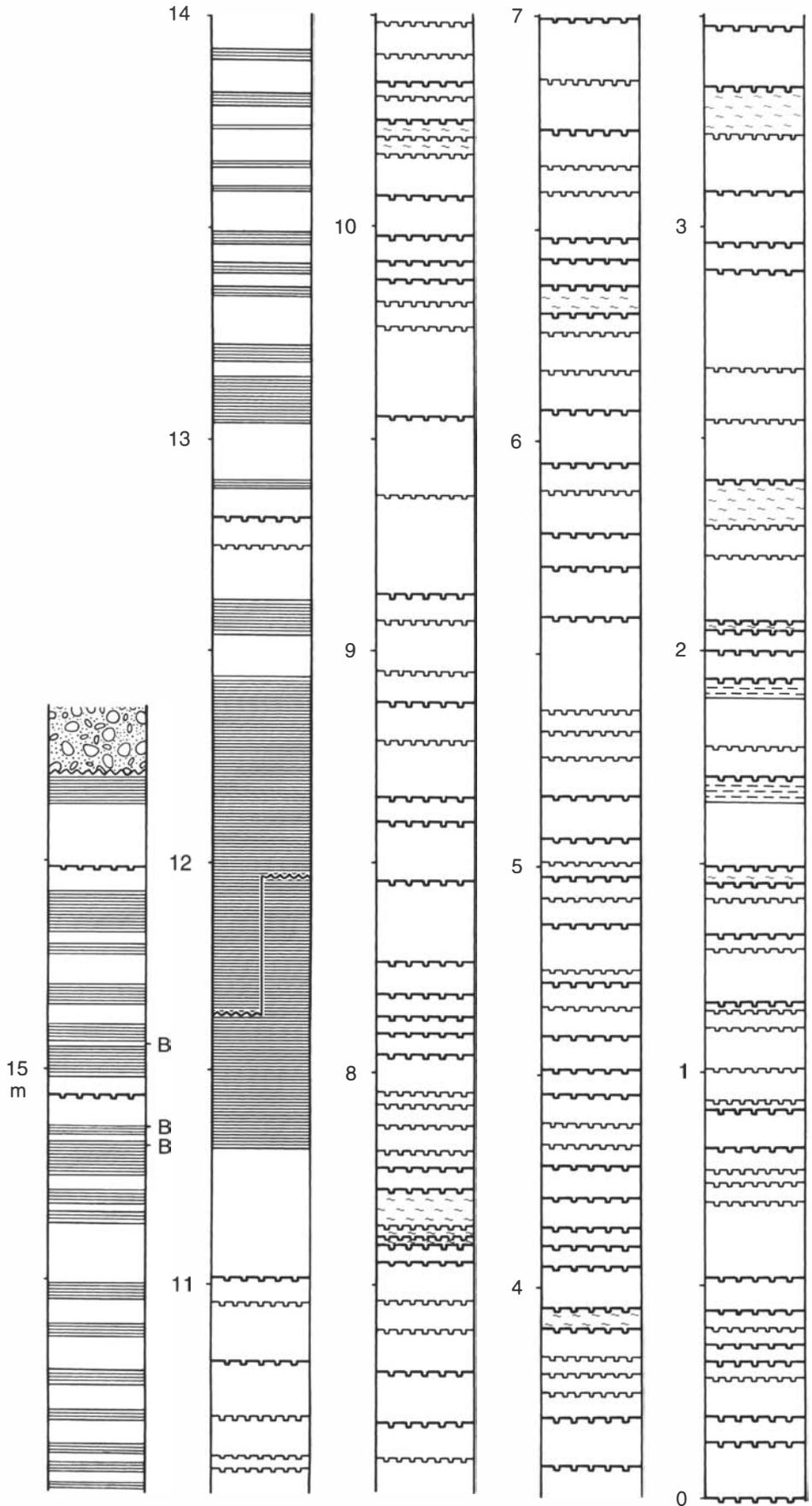


Fig. 11. Composite log from Hjertabäcken, Kivik. The two sections measured, exposed upstream and downstream of the stone fence, overlap between 11.5 and 12 m (cf. text). The strata are overturned, which is corrected for in the log. The contact between shale and limestone is slightly tectonized and a portion of shale may conceivably be smeared out of section, although this is not believed to be the case. Legend as for Fig. 5.

Limestone (cf. De Geer 1889), but they are intercalated by shale and represent the Upper *Didymograptus* Shale. An interval of about 1.1 m (± 0.1 m) of dark shale separates the limestone/shale interval from the compact Komstad Limestone (Fig. 11). The strata are oriented at $120^\circ/67^\circ$ SW on the upstream side of the stone fence, and at $125^\circ/64^\circ$ SW on the downstream side, but are overturned. The sections on either side of the fence were correlated by levelling and comprise 16 m of strata, of which 11.3 m is Komstad Limestone (Fig. 11). The total thickness may significantly exceed this figure; however, the 18 m reported by De Geer (1889, p. 16) include Upper *Didymograptus* Shale.

The sharp boundary between the shale and the Komstad Limestone is slightly tectonized, but it is unlikely that much shale or limestone, if any, is faulted out. The lower boundary (apparent top) of the limestone towards the west could not be located. According to De Geer (1889, p. 16), two additional metres of limestone are present towards SE from the main outcrop.

The exposure in the mill-race is the thickest continuous section of Komstad Limestone exposed at one and the same site in SE Scania, but the conditions do not permit large-scale sampling, and no trilobites have been collected as yet. The conodont content of a sample from the lower part of the overlying shale is listed in Table 2. The age is surprisingly young and may indicate that the Komstad Limestone at this locality ranges to the very top of the Kunda Stage.

Table 2. Conodont content of sample from lowermost limestone bed of the Upper *Didymograptus* Shale, Kivik. The fauna is indicative of the *Pygodus serra* Zone, but the subzone cannot be determined as *Eoplacognathus* has not been found. Determinations by J.A. Rasmussen, Copenhagen.

<i>Drepanodus arcuatus</i>	1 specimen
<i>Cornuodus longibasis</i>	1 specimen
<i>Pygodus serra</i>	3 specimens
<i>Baltonioidus</i> sp.	4 specimens
<i>Walliserodus?</i> sp.	1 specimen
<i>Protopanderodus</i> cf. <i>varicostatus</i>	3 specimens
<i>Periodon</i> sp.	1 specimen
<i>Drepanodus planus</i> (reworked)	3 specimens
In total	17 specimens

Komstad

Two large limestone quarries situated at Komstad (Fig. 12) represent the type locality of the Komstad Limestone Formation (Jaanusson 1960). The quarries, which have been referred to by several authors (e.g., Funkquist 1919; Regnéll 1960; Jaanusson 1960), have been abandoned since 1986 and are now flooded. Hence they are inaccessible for large-scale systematic sampling. The strata strike at about $52^\circ/4^\circ$ SE, changing to $59^\circ/5^\circ$ SE in the westernmost part. Weverinck (1936, p. 37) reported an orientation of $70^\circ/5^\circ$ S in the largest

quarry and $85^\circ/8^\circ$ S in the eastern one. Minor faults and joints are probably responsible for these variations.

Approximately 6 m of limestone are exposed in the steep southern walls of the quarries, representing the 'Övre grå' unit (upper dark unit, i.e. the *M. limbata* Zone) and the base of the *A. expansus* Zone. The characteristic shaly top of the 'Undre ljus' unit (lower light unit, i.e. the *M. simon* Zone) outcrops in the NE wall of the eastern quarry.

Gårdlösa

A number of old quarries and natural outcrops are situated roughly 500 m south of Killeröd (Fig. 12). The area is not close to any village, but the quarries belong to the Gårdlösa land register, and that name is used here. They have previously been referred to as the southernmost quarries at Killeröd (Moberg 1892a; Weverinck 1936). Despite the fact that quarrying stopped fairly recently (quarries nos. 5 and 6), around 1980 according to local information, the outcrops are now in a poor state.

Gårdlösa-1. – This outcrop was described by Regnéll (1960, loc. 3 on the map, p. 35) and Moberg (1892a), who measured 1.8 m of shale below the limestone; a photograph of the site is shown by Weverinck (1936, Textfig. 7), demonstrating that the exposure was in much better shape at that time (compare Fig. 13).

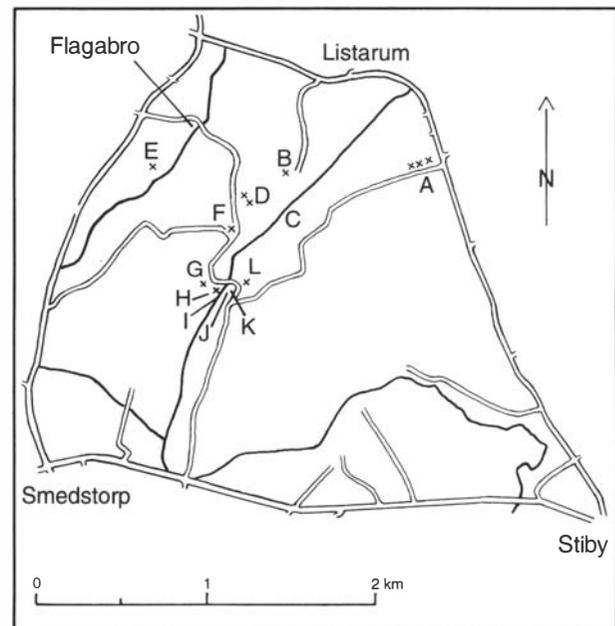


Fig. 12. Sketch map of the Komstad-Killeröd area, SE Scania, pinpointing the position of various outcrops. A: Komstad quarries; B: Listarum quarry; C: Killeröd Canal; D: Killeröd quarries; E: Flagabro quarry; F: unnamed small quarry; G: Gårdlösa-5 quarry; H: Gårdlösa-6 quarry; I: Gårdlösa-2, outcrop in the canal; J: Gårdlösa-1; K: Gårdlösa-3; L: Gårdlösa-4 quarry.



Fig. 13. Section excavated at Gårdlösa-1, representing the basal 1 m of the Komstad Limestone and the very top of the Tøyen Shale.

Limestone is now exposed in a low section, and 1 m of limestone, overlying 0.35 m of Tøyen Shale, was logged (Fig. 14). The individual beds are labelled A to N from below. The top of the basal limestone bed is impregnated by glauconite and pyrite. The first graptolites were encountered 0.18 m below the limestone. Trilobites were collected systematically from the section. The lower 0.40 m may belong to the *M. polyphemus* Zone, while the upper part represents the *M. simon* Zone.

The limestone is oriented at $103^{\circ}/5^{\circ}$ N, but the strike and dip apparently increase westwards (cf. Weverinck 1936, who reported $126^{\circ}/9^{\circ}$ N), which is believed to be due to a minor fault situated between this outcrop and site 2 in the stream; the fault probably strikes at about 160° .

Gårdlösa-2 and -3. – Site 2 is an exposure in the rivulet west of sites 1 and 3 (Fig. 12). The subjacent shale is not exposed, and the correlation of the limestone interval, 1.6 m thick, is difficult. It belongs to the *M. simon* Zone.

Site 3a is an exposure of 1.2 m of limestone 20 m north of site 1 (Figs. 12, 14). The limestone strikes at $98^{\circ}/5^{\circ}$ N. Site 3b is closer to the lane, 13 m NE of site a; 0.6 m of limestone is exposed. No fossils were collected.

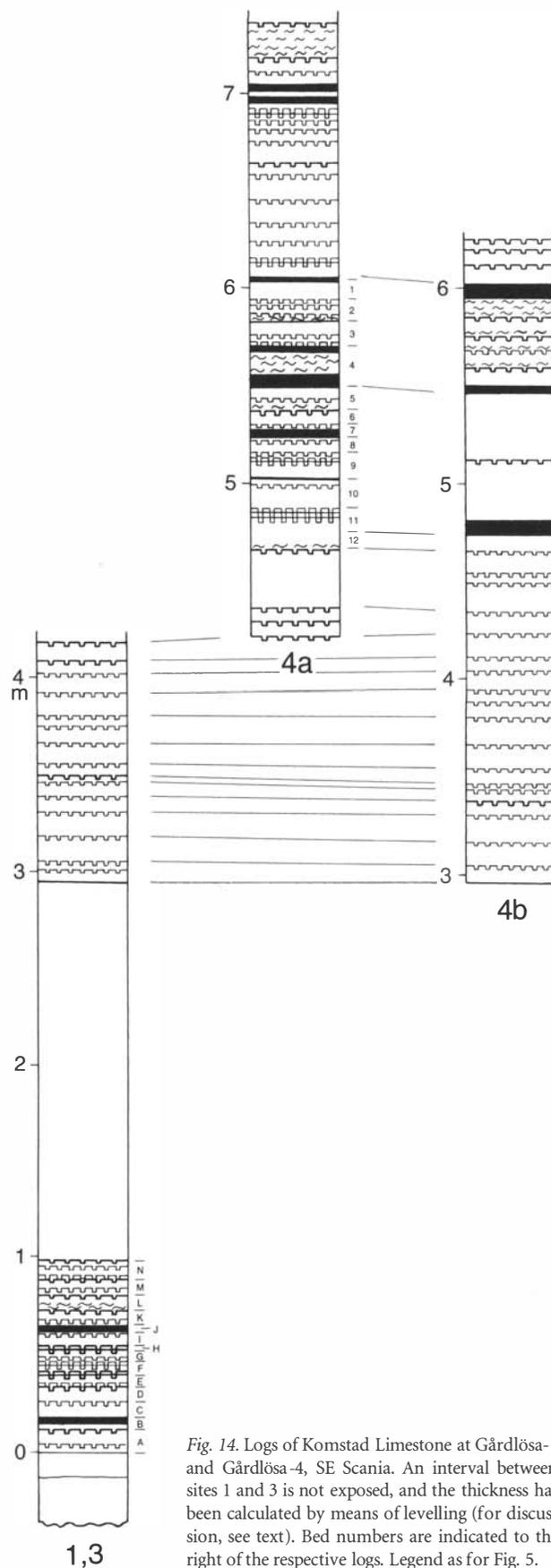


Fig. 14. Logs of Komstad Limestone at Gårdlösa-1 and Gårdlösa-4, SE Scania. An interval between sites 1 and 3 is not exposed, and the thickness has been calculated by means of levelling (for discussion, see text). Bed numbers are indicated to the right of the respective logs. Legend as for Fig. 5.

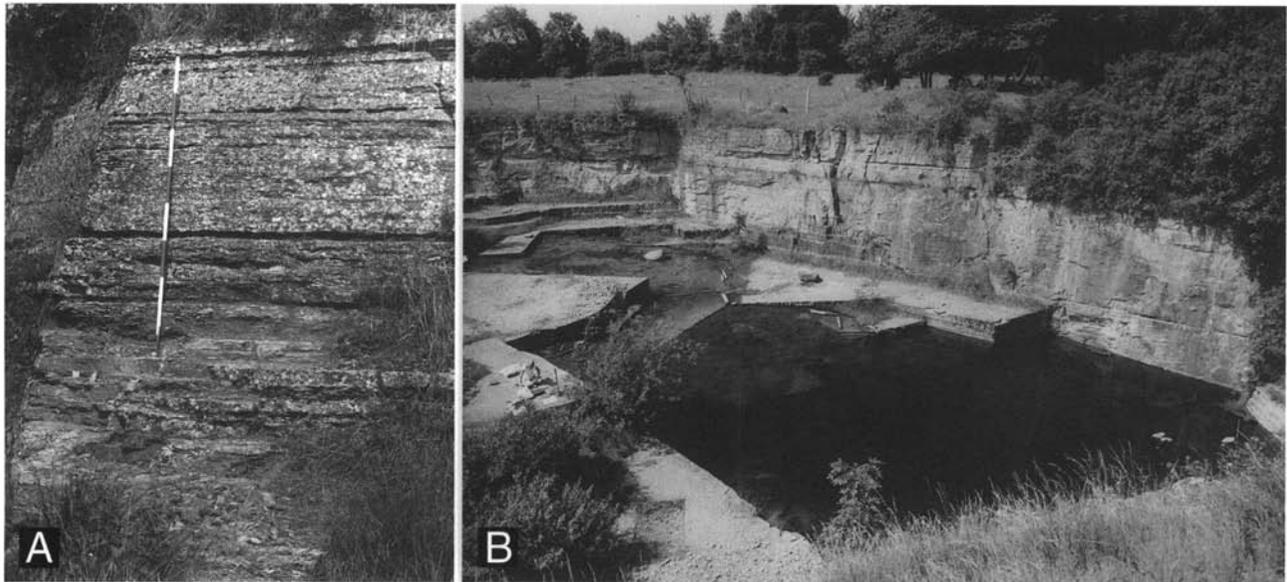


Fig. 15. □A. Northern quarry face, Gårdlösa-4a, SE Scania, anno 1986. The shaly interval at the foot of the wall represents the top of the *M. simon* Zone, the upper more massive interval represents the lower part of the *M. limbata* Zone. □B. View of the Killeröd quarry towards SW, anno 1982. The steep walls in the background represent fault planes (cf. text). For scale: In A, the black or white bands of the staff are 20 cm long; in B, note sitting person on top of bed +1 to the left.

Gårdlösa-4. – An old, waterlogged quarry with limestone exposures along the northern and eastern quarry faces (Fig. 15A), referred to as sections *a* and *b*, respectively (Fig. 14). These sections were correlated on site by tracing bedding planes along the quarry walls. The limestone is oriented at $72\text{--}87^\circ/5\text{--}6^\circ$ N in the northern quarry face, and at $136\text{--}191^\circ/2\text{--}3^\circ$ E in the eastern. Together the partly overlapping exposures represent 4.4 m of limestone. The beds in the lower main part of section *a* were numbered 1–12, and fossils have been collected systematically from them. Sections *a* and *b* represent the upper part of the *M. simon* Zone and the lower part of the *M. limbata* Zone.

Gårdlösa-5 and -6. – Abandoned quarries, partly water-filled, partly filled with waste. Three metres of limestone were logged at site 5; the orientation of strata is here $153^\circ/3^\circ$ E. A few fossils were encountered, mostly ptychopygids, and the limestone at site 5 presumably represents the *M. limbata* Zone.

Killeröd

The locality is an abandoned, partly water-filled quarry (Figs. 15B, 16) previously referred to as the ‘Large old quarry at Killeröd’ (Weverinck 1936), or the ‘Old quarry at Killeröd’ (Nilsson 1951); for location, see Fig. 12. The quarry has not become completely flooded, because of drainage through the dump wagon track to the east, and the locality is presently the most important exposure of Komstad Limestone in SE Scania. It is therefore proposed to regard the Killeröd quarry

as a paratype section of the Komstad Limestone (the type locality, the Komstad quarries, is situated about 1 km to the NE; cf. Fig. 12).

The strata dip gently to the south, and the lowermost accessible levels are in the northern part of the quarry (Fig. 16). The orientation of strata is typically about $52\text{--}58^\circ/5^\circ$ SE but varies somewhat (see also Weverinck 1936, p. 37). A total of 9.6 m of limestone was logged (Fig. 17), including 1.7 m below the water table, measured by means of scuba-diving. The thickness of individual limestone beds is mostly constant within the quarry, wherefore a single log of the entire succession is considered to suffice; individual parts were measured at different places.

The western quarry face is a fault plane, striking approximately N–S (Fig. 16), with slickensides and calcite veins; the movement was largely horizontal. An associated fault, striking NW–SE in the southwest corner, shows a net downthrow to the southwest of about 1.3 m; the beds are disturbed and strongly weathered close to the fault. A thin dolerite dyke, 0.10–0.15 m thick, strikes at about 135° in the north-eastern part of the quarry. A thicker dyke, striking at about 120° , is obliquely transversed by the dump wagon track; the dyke thickness is about 23 m.

Fossils were collected bed by bed, which were numbered counting from an easily recognizable shale level. Downwards the beds are numbered in a negative series to –9 and upwards in a positive series to +35. The section represents the upper part of the *M. simon* Zone, the *M. limbata* Zone and most of the *A. expansus* Zone.

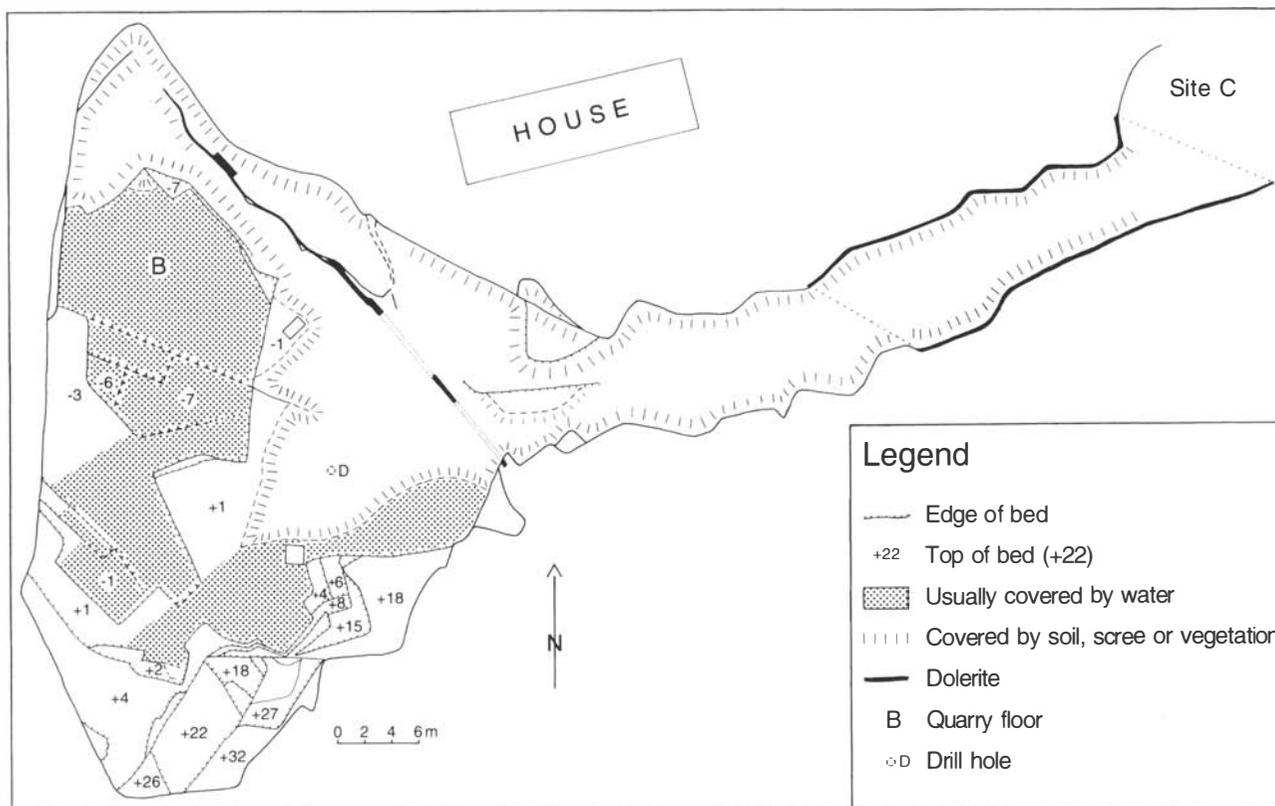


Fig. 16. Map of the Killeröd quarry, measured 1982. Within recent years the water-level has increased by more than 0.5 m, but the quarry will probably remain the best exposure of Komstad Limestone in the type area for a considerable period onwards. Easily recognizable major bedding surfaces are indicated in order to ease future identification of the bed-numbering system (Fig. 17). The position of the drilling discussed in the text is indicated in the eastern part of the quarry on top of bed +1 (midway between easternmost bed indications -1 and +18). The hole is a spring and is usually hidden by water-logged moss.

Killeröd site b

A second, but water-filled quarry is situated 60 m ESE of the main quarry. Between the flooded quarry and the entrance to the dump waggon track is a small hill with a core of limestone *in situ*. A total of 5.3 m of limestone was measured between the water table in the quarry and the top of the hill (Fig. 18). This section, Killeröd site b, can be tied to the main quarry by identification of several marker levels. There is a large overlap between the two sections, and only the upper 1.8 m at Killeröd site b extend above the limestone exposed within the main quarry. Accordingly, the combined sections represent 11.4 m of strata.

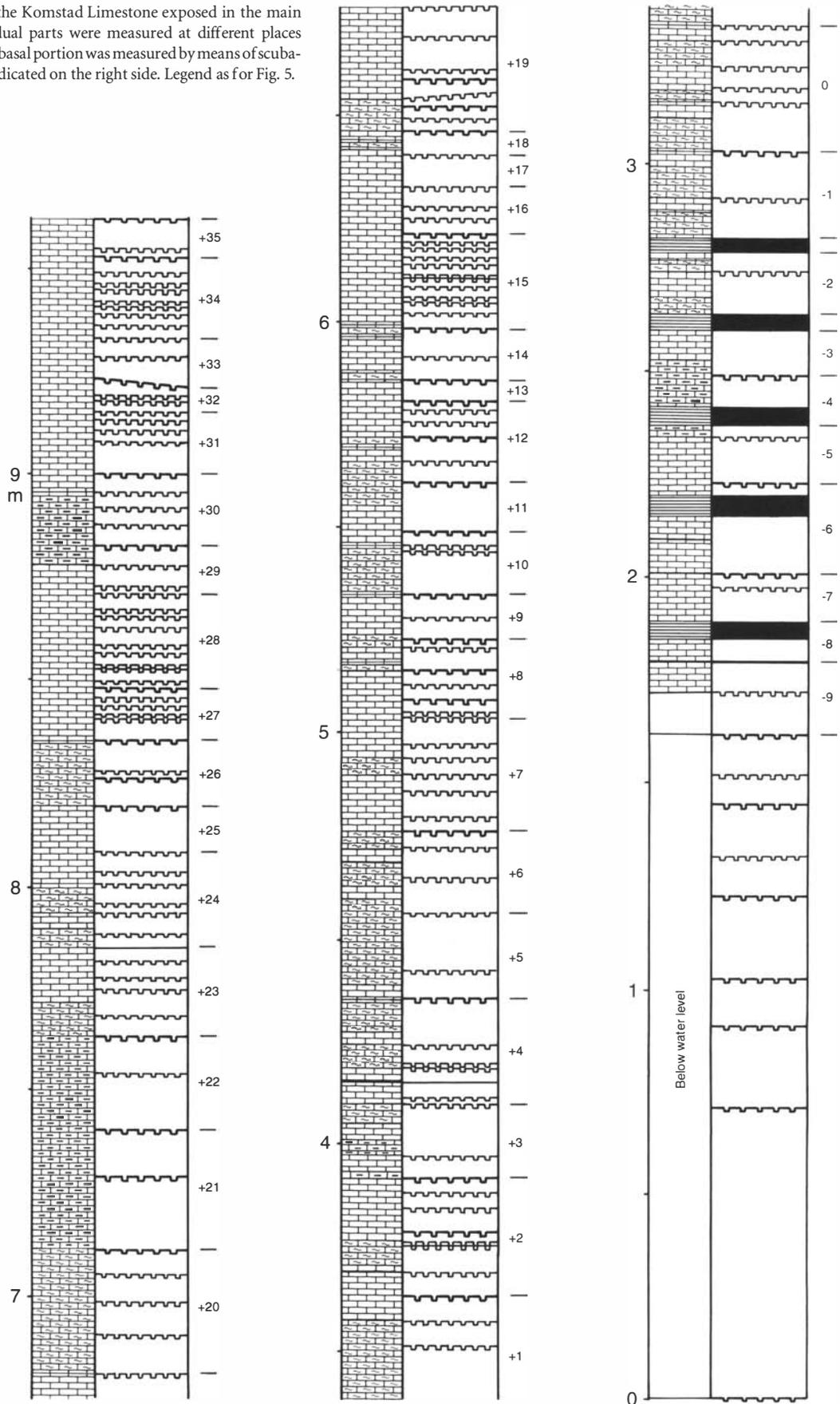
The limestone beds at Killeröd site b were numbered 0 to 20, counting from above, and fossils were collected bed by bed. A fairly large amount of stone was crushed, and it is evident that the sparsity of fossils in the *A. expansus* Zone is real (cf. Fig. 34) and not due to insufficient sampling. The section at Killeröd site b represents the *A. expansus* and the basal part of the *A. 'raniceps'* Zones.

Killeröd site c

An exposure of shale with intercalated limestone beds at the eastern entrance of the dump waggon track at Killeröd has been known for long (Weverinck 1936; Nilsson 1951; S. Bergström 1973). The outcrop is here referred to as Killeröd site c (Fig. 16). The hitherto known section represents 1.2 m of Upper *Didymograptus* Shale, 0.15 m of *Dicellograptus* Shale and 0.7 m of 'Bronni beds' (= 'Coscinorhinus beds'). J. Bergström (1982a) referred to the latter unit as the Killeröd Formation.

An excavation was made at this site. The section measured by Nilsson (1951) was readily recognized with only a few deviations (unit c was measured to 0.56 m), but below bed 'b' *sensu* Nilsson was encountered 1.3 m of shale, i.e. the Upper *Didymograptus* Shale is almost 2.9 m thick, in turn underlain by 0.65 m of marly clay with limestone nodules (Fig. 19). The clay represents dissolved Komstad Limestone, containing ghosts of orthocone cephalopods as well as trilobite fragments, none of which were determinable (asaphids). The

Fig. 17. Composite log of the Komstad Limestone exposed in the main quarry at Killeröd. Individual parts were measured at different places within the small quarry; the basal portion was measured by means of scuba-diving. Bed numbers are indicated on the right side. Legend as for Fig. 5.



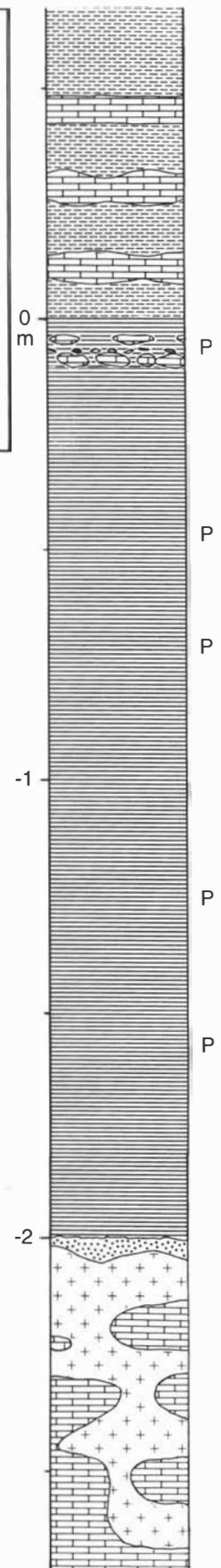
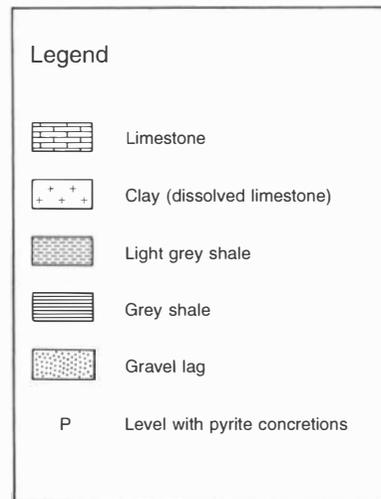
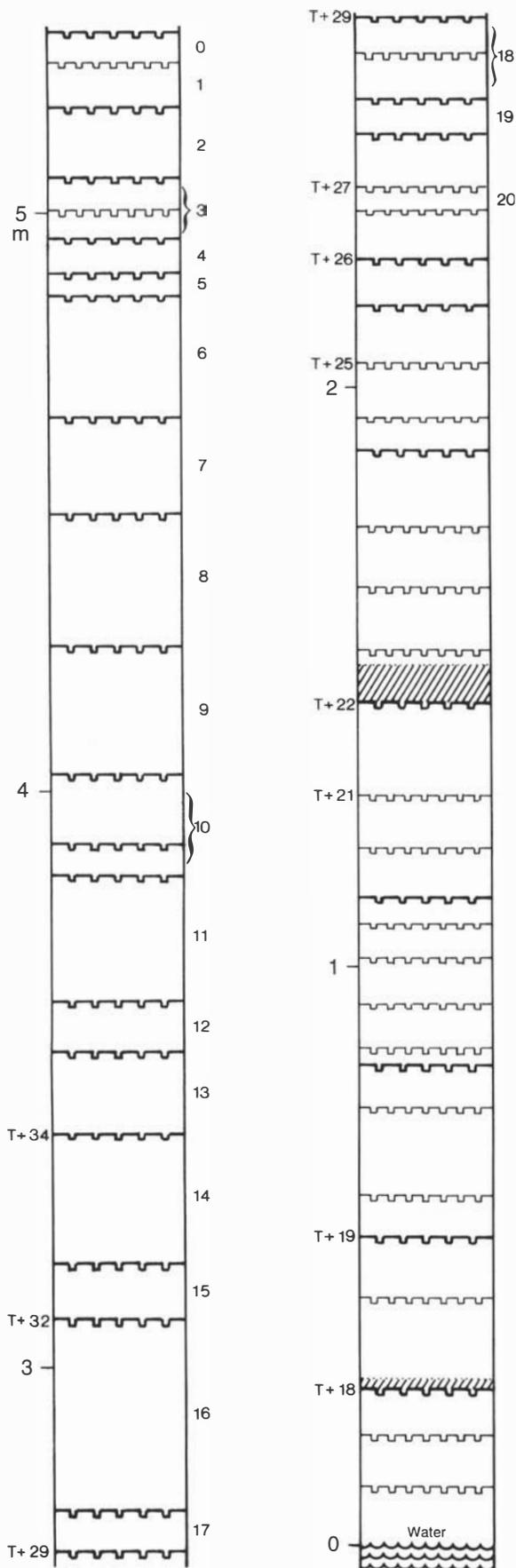


Fig. 18 (left). Composite log of the Komstad Limestone exposed at Killeröd site b. Bed numbers are shown on the right side; the equivalent numbers of selected keylevels from the adjacent Killeröd main quarry are indicated on the left side (T = top of bed; cf. Fig. 17). Base of section is at the water-surface in the quarry at site b; more limestone is exposed below water-level but is much easier to access in the main quarry. Shading indicates intervals with easily weathering lithology (caving). Legend otherwise as for Fig. 5.

Fig. 19 (right). Log of the strata exposed by excavation at Killeröd site c (for location, see Fig. 16). The top of the Komstad Limestone is dissolved and appears to represent a karst ground, succeeded by Upper *Didymograptus* Shale. The top part of the section was described in detail by Nilsson (1951).

nodules represent unweathered or less altered limestone. The clayey habitus decreases downwards, and the excavation terminated in hard limestone, which could not be penetrated. No fossils were found in the fine-grained, rather splintery, light grey limestone 'nodules'. It appears that the dissolution occurred before deposition of the Upper *Didymograptus* Shale, in which case it is the first Ordovician soil encountered in Scandinavia. There is a fairly considerable hiatus between the limestone and the succeeding shales, and the depositional break was most likely due to isostatic uplift and emergence of the area.

The Komstad Limestone at this site appears to represent a high level within the *A. 'raniceps'* Zone, judging from conodont dating (see p. 42; Table 4).

Killeröd Canal

A small stream runs to the east of the Killeröd quarries (Fig. 12). To avoid floodings it was deepened and made into a canal in 1925. Thereby the Tøyen Shale became exposed east of the quarries at Listarum (Weverinck 1936, p. 37), and the Komstad Limestone was excavated by blasting ESE of the Killeröd quarries. Most of the agnostids described by Ahlberg (1989b) originate from the canal and were probably sampled during the construction work. For lithological reasons the material is surmised to derive from the upper part of bed A (Fig. 20).

The meadow slopes gently from Killeröd site b towards the canal, roughly reflecting the bedrock gradient. Limestone, 1.2 m thick, is exposed within the canal (Fig. 20), representing the *A. 'raniceps'* Zone. None of the marker beds present in the section at Killeröd site b can be recognized in the canal

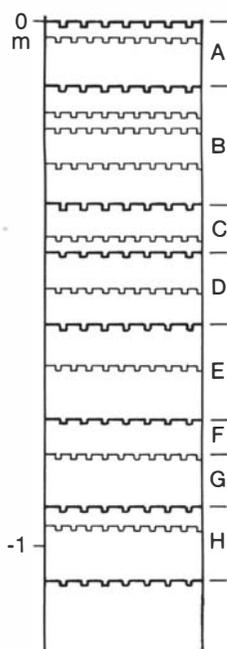


Fig. 20. Preliminary log of the Komstad Limestone exposed within the Killeröd Canal. The lower half of the section is normally below water-level.

section, but the conditions are, admittedly, difficult, as the lower half of the exposure is below water table. Hence it appears that the section represents a level in between the limestone exposed at Killeröd sites b and c. As a control, a levelling was carried out between the two exposures across the meadow. The distance is 140 m, which leaves a considerable latitude for interpretation, depending on the bedrock inclination, but a plausible estimate arrives at a thickness of the hidden interval between 2.5 and 5 m; the minimum figure is deemed most realistic.

Total thickness of the Komstad Limestone in the type area

The exposures at Gårdlösa sites 1, 3 and 4 were correlated by levelling. Provided that no faults are present, the top of section 3a is positioned 3.3–3.4 m above the top of section 1, leaving a gap of about 2 m of unexposed limestone in between (Fig. 14). Considering that the two sites are very close and that the measured orientations are basically identical, the correlation appears trustworthy. The limestone exposed at site 3a in turn overlaps the lower part of the 4b section (cf. Fig. 14).

The strata at Gårdlösa-4 are tied to the Killeröd section by correlation of the shale interval (beds –8 to –1), the marker level at the base of bed 0 and the double marker level within bed +3 (bed numbers refer to the Killeröd section). Especially the thin shale seam at the base of bed 0 is readily identified in weathered sections and is followed by a compact interval, approximately 1.15 m thick, interrupted by two thin shale levels within bed +3 (cf. Fig. 15A). The lithologically based correlation was confirmed by the biostratigraphy.

This correlation entails that 3.1 m of limestone is present below the floor of the Killeröd quarry. A more than 100 m deep drill-hole spudded on top of bed +1 within the Killeröd quarry (see map, Fig. 16) is said to have penetrated 7 m of Komstad Limestone (Nils Håkansson, Killeröd, personal communication, 1987). The drilling was performed by the Geological Survey of Sweden, but unfortunately the relevant core interval and all files appear to be lost (Lars Karis, Uppsala, personal communication, 1989), so the oral information cannot be verified. However, if 3.1 m of limestone is present below the quarry floor, as inferred from the correlation with Gårdlösa, then 6.75 m should be present below the top of bed +1, a figure which for all practical purposes is identical to that stated by Nils Håkansson. This agreement suggests that a minimum of 14.5 m of limestone is present in the Killeröd area, but the thickness of the *A. 'raniceps'* Zone is not constrained.

The topmost 0.65 m of limestone below the Upper *Didymograptus* Shale at Killeröd site c certainly does not overlap the section at Killeröd site b, and, accordingly, at least 15 m of Komstad Limestone are definitely present. Besides, the limestone exposed within the Killeröd Canal apparently overlaps neither the section at Killeröd site b nor that at site c, possibly

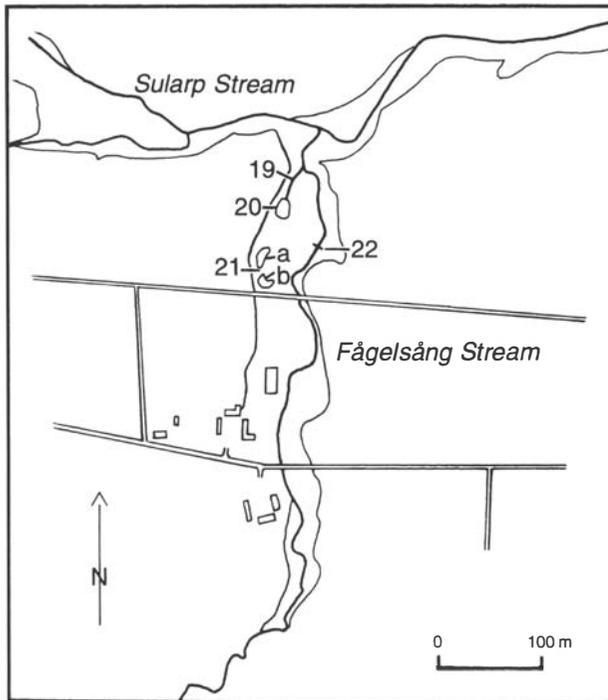


Fig. 21. Map of the Fågelsång area, central western Scania, pinpointing the positions of localities E19 to E22. (Simplified after Moberg 1911.)

adding a further 1.2 m to the minimum figure of 15 m. Quarrymen claimed 18 m of limestone to be present in the area (Nils Håkansson, personal communication, 1987), and this may very well prove correct.

The established minimum thickness of 15 m of Komstad Limestone in the type area significantly exceeds the 10 m suggested by Regnéll (1960) and the 5–6 m estimated by Hadding (1958).

Western Scania

The Komstad Limestone was quarried in this region only at Fågelsång, 8 km east of Lund, but a small outcrop in Kvarnbäcken ('Mill Brook') at Röstånga has been known for a long time. These localities are described below (for location, see Fig. 7).

Fågelsång

Three abandoned, flooded limestone quarries are situated about 50 m to the west of the Fågelsång rivulet (Fig. 21), but the entire area between the quarries and the rivulet in fact consists of refilled quarries.



Fig. 22. Fågelsång locality E21b during excavation in August, 1983. The low wall in the middle is a fault plane with two bentonite layers (cf. Figs. 23–24).

Moberg (1896) published a detailed guide of the Fågelsång area, including a numbering system of the individual outcrops. His numbers, permanent as well as temporary, have been retained by subsequent authors (see Fig. 21). The limestone quarry E21 was subdivided into E21a and E21b on the geological map, although this was not emphasized in the text (cf. Moberg 1896). Moberg (1907) referred to the southern quarry as E21a, but he subsequently exchanged the numbers and referred to the southern quarry as E21b and to the middle one as E21a (Moberg 1911). These designations were adopted by Ekström (1937). As the majority of publications refer to the southern quarry as E21b and to the larger middle quarry as E21a, it seems reasonable to stick to these labels. However, in order to eliminate misunderstandings, the phrases 'middle quarry' and 'southern quarry' are often used in the present context instead of E21a and E21b.

Southern quarry, locality E21b. – Limestone, 1.5 m thick, is exposed in a steep fault-plane in the southern part of this small quarry (Figs. 22, 23A–B); the fault strikes at 120° with a net downthrow to the north of 0.16–0.18 m. The footwall section (profile A, Fig. 24), from which it was difficult to obtain samples, includes two comparatively thick bentonite beds. The upper bedding surface of the limestone was traced to the low western quarry face, where the lower 1.2 m of the overlying Upper *Didymograptus* Shale was excavated (profile B, Fig. 24). The shale is intercalated by limestone beds and four bentonite levels. Profile B is closely comparable to section II (loc. E21b) of Ekström (1937, p. 14).

Limestone also crops out just south of (above) the fault-plane (Figs. 23A–B) but is not *in situ*. Excavations revealed a huge displaced limestone plate, embedded in till. The unit represents the upper 0.65 m of the Komstad Limestone (Fågelsång C of Fig. 24), and the first bentonite level below the top of the formation apparently acted as decollement level during the Quaternary glaciation.

A low hanging-wall section was measured in the central part of the quarry, that is, north of the fault plane (Fågelsång A' of Fig. 24). The fossils described by Moberg (1907) originate from this level, and so does the majority of the rich fauna described by Angelin (1851–1878). The lithology resembles the Lysaker Member of the Oslo region.

The limestone is oriented at $164^\circ/10^\circ$ W in the northern hanging-wall block, and at $150^\circ/5^\circ$ W in the southern foot-wall block. The limestone represents the *A. expansus* Zone (lower 0.9 m) and the *A. raniceps*' Zone (upper 0.5 m).

Middle quarry, locality E21a. – The site was described in detail by Ekström (1937), but the abandoned quarry is now (as then) completely flooded. After draining the quarry the section measured by Ekström (1937, redrawn as D' in Fig. 24) was readily recognized, but a column of limestone, 0.7 m high, was discovered on top, and a total of 2 m of limestone was measured and sampled at this site (profile D, Fig. 24). However, bed interval 11–17 yielded only a very small sample quantity (area of 0.2×0.3 m), and the rock was

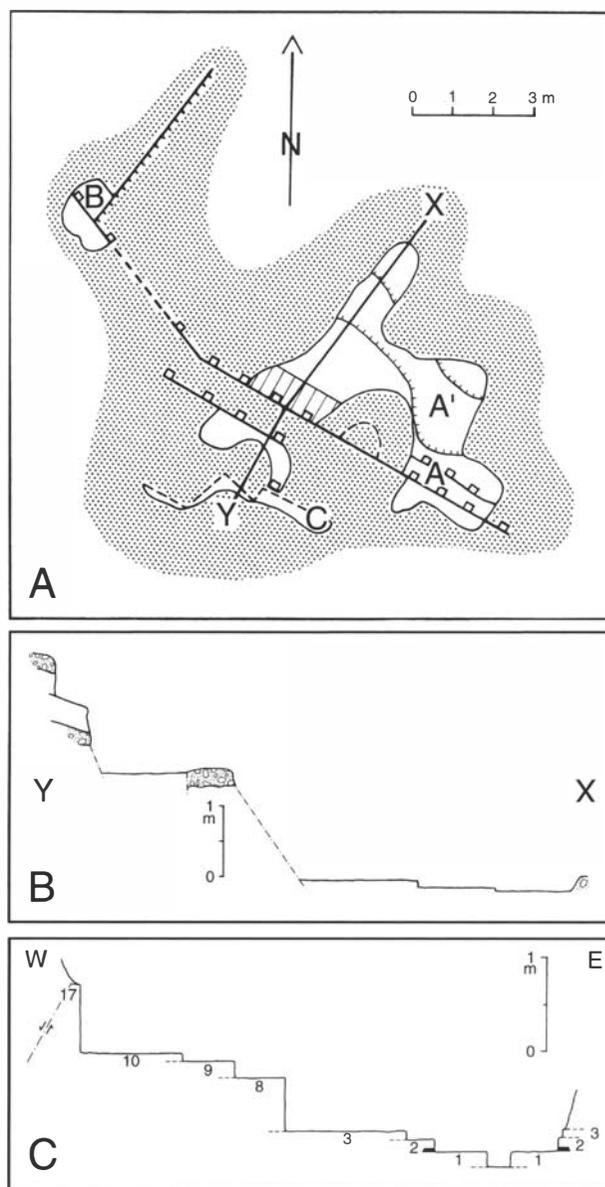


Fig. 23. Fågelsång, localities E21a–b. □A. Locality E21b. Sketch map showing extent of excavation in 1983 and position of the measured sections (A, B, C, cf. Fig. 24). □B. Locality E21b. Cross-section of line X–Y (see Fig. 24). □C. Locality E21a (middle quarry). Cross-section of the southern part of the quarry during excavation in 1983 (cf. Ekström 1937, Fig. 3). Bed numbers as in Fig. 24.

furthermore rather brecciated, because of the proximity of the N–S striking fault, bounding the limestone to the west (Fig. 23C), and a systematic search for fossils could not be undertaken. The fault strikes at about 12 – 17° and has a net downthrow to the west in the size order of 3–5 m.

A drilling spudded within the quarry (see Ekström 1937) penetrated 1 m of limestone below the quarry floor, without reaching the Tøyen Shale (section D' of Fig. 24).

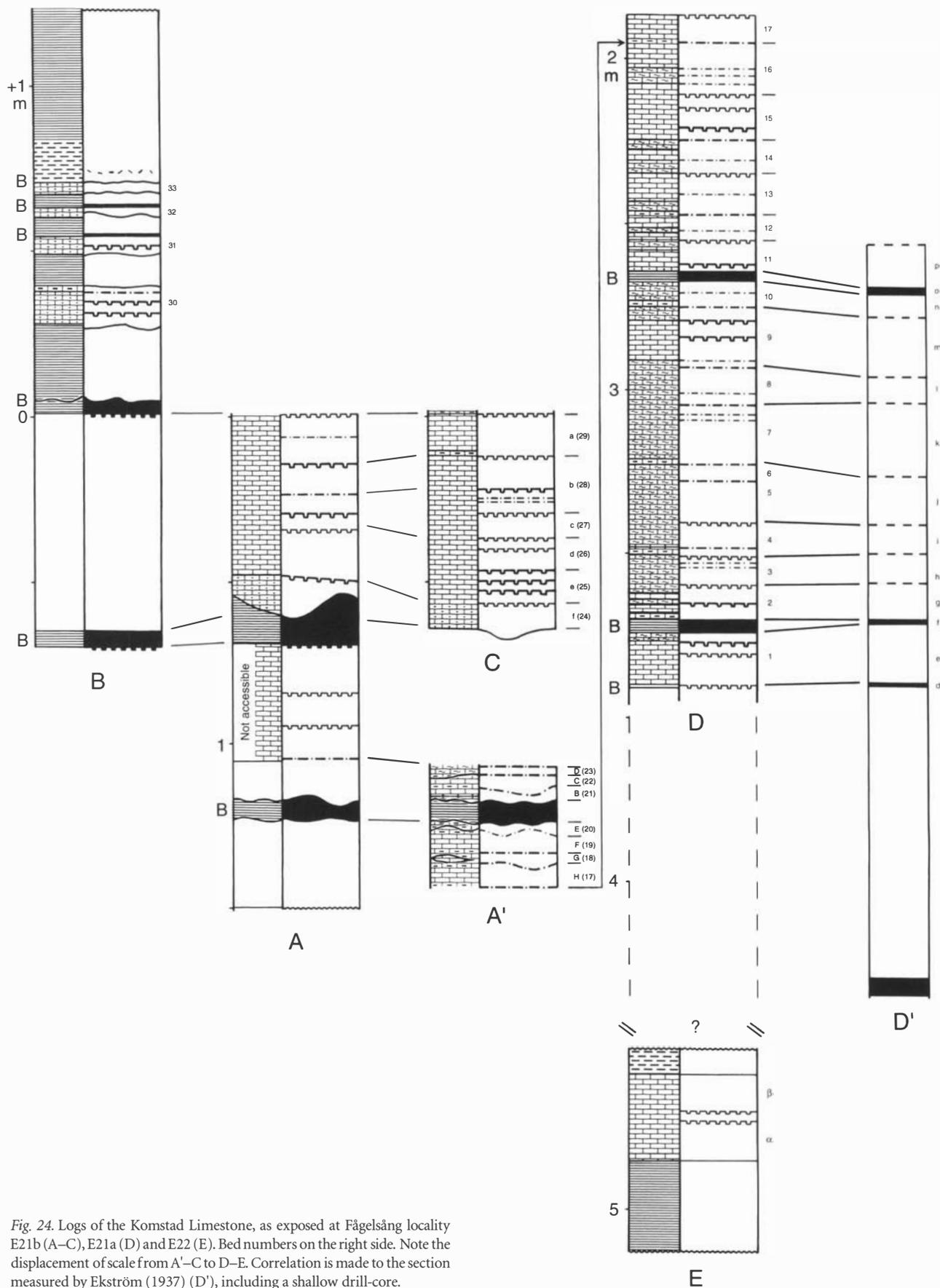


Fig. 24. Logs of the Komstad Limestone, as exposed at Fågelsång locality E21b (A-C), E21a (D) and E22 (E). Bed numbers on the right side. Note the displacement of scale from A'-C to D-E. Correlation is made to the section measured by Ekström (1937) (D'), including a shallow drill-core.

Ekström recorded a narrow fault block in the western part of the quarry (Ekström 1937, section II, Textfig. 3). The vertical displacement between sections I and II of Ekström can be calculated to roughly 2 m, and the fault between sections II and III probably has a similar or slightly smaller westward downthrow. This intermediate fault block is not present in the southernmost part of the quarry, where only a single fault separates the limestone from a western footwall fault block with Upper *Didymograptus* Shale. The single fault presumably represents the two faults recorded by Ekström united into one.

The limestone is oriented at about 190°/4° W in the middle of the quarry, but the orientation becomes unstable close to the fault. The limestone at site E21a represents the upper part of the *M. limbata* Zone.

Northern quarry, locality E20. – This is the largest of the quarries at Fågelsång. Limestone is nowadays exposed at a few places in the walls of the flooded quarry; at least 2 m of limestone are present. A levelling indicates that one or more faults is present between localities E21a and E20.

'*Dictyonema* Shale' occurs at site E19 in the drainage canal just north of the quarry (Moberg 1896; Nilsson & Tellander 1900). Another fault is obviously located between this outcrop and site E20.

Fågelsång rivulet, locality E22. – The exposure in the eastern bluff of the Fågelsång rivulet was described by Strandmark (1902); the graptolite fauna has recently been revised by Cooper & Lindholm (1985). The site was excavated and reinvestigated in 1983 (section E, Fig. 24). Two limestone beds, oriented at 115–120°/7.5–8° SW and altogether 0.24 m thick, are underlain by dark shale and overlain by light coloured shale. The fine-grained limestone is extremely splintery, and no trilobites survived extraction from the rock. The conodont content (Table 3) indicates that the limestone represents a horizon near the top of the *M. simon* Zone.

A levelling indicated that one or more faults probably are present between sites E21 and E22; alternatively the Komstad Limestone is about 10 m thick in the area. A minor fault is seen in the northern part of loc. E22; net displacement is 0.2–0.3 m to the north.

Table 3. Conodont content of sample from bed β at loc. E22, Fågelsång. Determinations by S. Stouge, Copenhagen.

<i>Baltoniodus</i> cf. <i>navis</i>	22 specimens
<i>Cornuodus longibasis</i>	2 specimens
<i>Drepanoistodus basiovalis</i>	3 specimens
<i>Drepanoistodus</i> cf. <i>venustus</i>	12 specimens
<i>Microzarkodina</i> cf. <i>parva</i>	25 specimens
<i>Protopanderodus rectus</i>	9 specimens
<i>Scalpellodus</i> cf. <i>gracilis</i>	4 specimens
In total	80 specimens

Total thickness of the Komstad Limestone in the Fågelsång area

It is obvious that the limestone at loc. E21b, representing the *M. limbata* Zone, underlies the limestone at site E21b, representing the *A. expansus* and *A. 'raniceps'* Zones. A levelling between these sites, situated less than 25 m apart, indicated that bed 17 at loc. E21a corresponds to bed H of section A' at loc. E21b (Fig. 24A), if no faults are present. It follows that at least 4.4 m of limestone is present at Fågelsång, and, even more importantly, that the succession in the middle quarry is not separated just by a thin 'transition interval' from the Upper *Didymograptus* Shale, as supposed by Ekström (1937). Hence, the confusing report of *M. limbata* immediately below the *D. 'bifidus'* graptolite Zone is in error. In this context it is also relevant to point out that the interval with abundant *Cyclopyge*, described by Moberg (1907), does not represent the basal part of the limestone at Fågelsång as assumed by some authors (cf. C. Poulsen 1936; Regnéll 1960).

Ekström (1937) cited, but chose to disregard, information about a boring from the bottom of loc. E21b encountering 4.2 m of limestone, but without reaching its base. If the information is correct, at least 5.7 m of limestone is present at Fågelsång. It has not been possible to obtain any further data on this drill-hole, but the thickness appears plausible, taking the fairly extensive quarrying in the area into account. The thickness of 2 m estimated by Ekström (1947), and cited by subsequent authors, thus seems too low.

Röstånga

'Pale grey' limestone was mentioned from the area already in 1823 by Nilsson (Angelin 1877, p. 24). It was at first believed to be Middle Cambrian Andrarum Limestone (Tullberg 1880) but was reinterpreted as '*Orthoceras* limestone' by Tullberg (1883a, b), who in some detail described the outcrop in Kvarnbäckan at locality b, section IV *sensu* Moberg (1911) (Fig. 25). The limestone was claimed to be only 1 m thick, dark, with a sparse fossil content resembling the *Orthoceras* Limestone at Fågelsång, and *Asaphus acuminatus*, *Aeglina* [= *Cyclopyge*] *umbonata* and *Iliaenus Esmarki* [= *I. cf. sarsi*] were listed by Tullberg (1883a, b). This information was reiterated by Moberg (1911) and Regnéll (1960). Ekström (1937) concluded that the limestone in all probability is a large boulder embedded in till.

The outcrop in Kvarnbäckan was re-excavated in 1984. As indicated by Ekström (1937), the limestone is not *in situ*, but represents a boulder with the minimum dimensions 1×4×2 m, although it may be considerably larger. The rock, which is unusually rich in crinoids (cf. Hadding 1958, pp. 179–181), is of Komstad Limestone type and may very well be of local origin, but obviously this occurrence of limestone does not prove the presence of Komstad Limestone in the Röstånga area, as hitherto assumed.

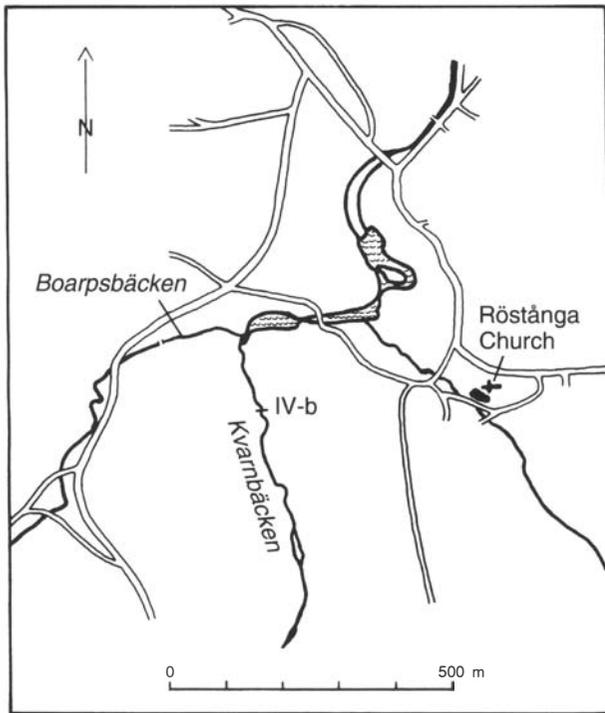


Fig. 25. Sketch map of the Röstånga area, northern Scania, showing the position of locality IV-b, where steeply dipping Komstad Limestone is exposed in the stream bed. The limestone represents, however, a huge block embedded in moraine, and it may or may not be of local origin. (Modified from Moberg 1911.)

The upper bed represents the lower part of the *A. expansus* Zone, as also indicated by the trilobites listed by Tullberg (1883a, b), whose material, kept at the Geological Survey of Sweden, Uppsala, has been examined.

Well-sections in northwestern Scania

A cable-tool drilling was made in the Stabbarb coal mine during 1879–1881 (Tullberg 1883b, p. 243; Nathorst 1885, pp. 16–18; Erdmann 1915, pp. 427–429); for location, see Fig. 7. The interval 86–92 m below surface was assigned to the *Chasmops* limestone by Nathorst (1885, p. 24), whereas the interval from about 93 m to 141.5 m predominantly consists of dark shale, according to Erdmann (1915), of which the level 100–103 m was thought to represent the lower part of the Upper *Didymograptus* Shale ('*Phyllograptus* shale'). The absence of Komstad Limestone is probably only apparent, however, in light of recent information gained from the fully cored Albjära-1 drill-hole. Without coring, a thin blackish limestone unit may be overlooked. Alternatively, the limestone may be absent because of a minor unrecognized fault.

Albjära-1 is a shallow drilling (T.D. 162 m) made in 1989, 5 km NE of Svalöv, western Scania (Fig. 7); the core has not yet been studied in detail. Komstad Limestone occurs in the interval 104.5–107.5 m and includes several bentonite layers.

Lindholm (1991) remarked briefly on the Tøyen Shale of the core.

The Krapperup drilling of 1946 (T.D. 155 m), positioned in the extreme NW Scania (Fig. 7), penetrated the lower part of the Upper *Didymograptus* Shale and encountered a very thick Tøyen Shale (cf. Lindholm 1981, 1991). Komstad Limestone is apparently not developed.

The fully cored Lovisefred drilling, spudded in 1977 and completed in 1979, penetrated to a depth of 530 m and encountered Lower Silurian to Lower Ordovician strata. Preliminary stratigraphical results were briefly mentioned by J. Bergström (1982b), and an account of the *D. hirundo* Zone was published by Nilsson (1984). Dr. R. Nilsson kindly provided me with unpublished data concerning bentonite levels and thicknesses of the drilled graptolite zones. The Tøyen Shale is very thick in the Lovisefred core, as in the nearby Krapperup drilling, and no Komstad Limestone is developed. Several bentonite levels are present in the *D. bifidus* and *D. hirundo* Zones (Fig. 38).

Other well-sections

Komstad Limestone, 3–4 m thick, has been encountered in a couple of deep wells in SE Scania (Skoglund 1977, p. 452; Larsson 1984), but no detailed information is available. The formation is 1.6 m thick in the German offshore drilling, G-14, located in the Baltic Sea north of Rügen (Piske & Neumann 1990). No limestone was penetrated by the Danish well Slagelse-1. The absence is believed real and not related to faulting.

Komstad Limestone was inferred present in the Danish offshore well Terne-1, situated in Kattegat, based on gamma-log interpretation (Michelsen & Nielsen 1991, 1992). The significant gamma-ray drop is, however, associated with a calliper-log response, and it is unlikely that a hard limestone is caved, whereas a caving may produce a low gamma-ray signal. Hence the presence of Komstad Limestone is questionable.

Slemmestad

The Slemmestad area south of Oslo, Norway, contains numerous outcrops of Ordovician rocks, which have been dealt with by many authors (e.g., Brøgger 1882; Öpik 1939; Spjeldnæs 1953, 1986; Størmer 1953; Berry 1964; Kohut 1972; Owen *et al.* 1990; Rasmussen 1991).

The present study, aimed at establishing a reference section in the area, focused on the exposures at Djuptrekkodden close to the Slemmestad harbour, 150 m north of Bjerkåsholmen. The Huk Formation is here repeated by thrusting and exposed both in the southern and northern points (Fig. 26), separated by a bay with discontinuous outcrops of Tøyen Shale. The strata are orientated at about 50°/45° NW;

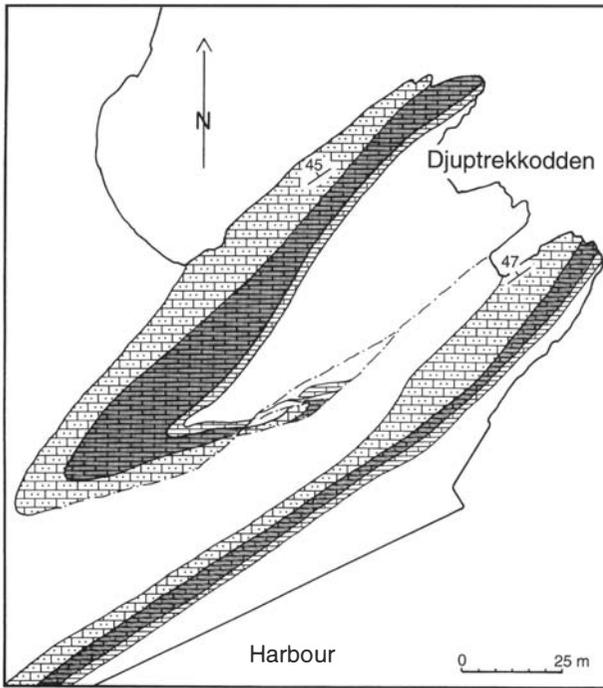


Fig. 26. Tectonic map of Djuptrekkodden, Slemmestad, showing the distribution of the Huk Formation (based on Morley 1986). The successions on each spit are similar for all practical purposes, and a composite log is presented in Fig. 28. Sampling has been undertaken in both outcrops.



Fig. 27. Tilted strata at the southern spit of Djuptrekkodden, Slemmestad. The picture shows recessive Tøyen Shale overlain by the massive Hukodden Limestone (ca. 1.5 m thick), in turn overlain by the nodulous Lysaker Member. Photograph: J.A. Rasmussen.

for a detailed account of the structural relations, see Morley (1986).

The Huk Formation, which is 8.6 m thick at Djuptrekkodden, consists of three members: Hukodden Limestone (1.6 m), Lysaker Member (4.4 m), and Svartodden Limestone (2.6 m) (Figs. 28, 30). The exact thicknesses are difficult

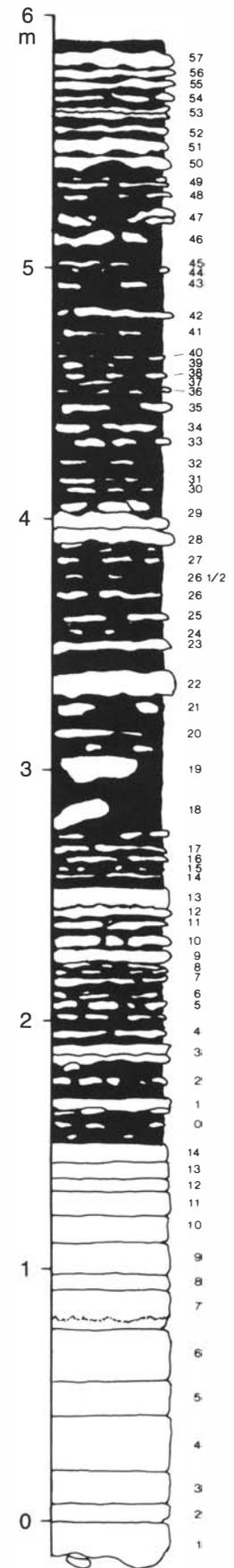


Fig. 28. Composite log of the lower members of the Huk Formation at Djuptrekkodden, Slemmestad (from Rasmussen 1989). The comparatively massive Hukodden Limestone is overlain by the Lysaker Member, comprising marly shales with numerous limestone nodule levels and limestone beds. Bed numbers from the Hukodden Limestone are referred to by adding the prefix M (= 'Megistaspis Limestone'), whereas bed numbers from the Lysaker Member are referred to by adding the prefix A (= 'Asaphus Shale'). The bed numbering of the Lysaker Member is from Rasmussen (1989); an extra limestone band between A-26 and A-27 is referred to as 26½. A conspicuous pyrite level within bed M-7 is indicated.

to obtain in the coastal sections, but can be measured in a vertical profile excavated on the harbour side of Djuptrækk-odden.

The Hukodden Limestone is a grey, quite compact, bedded limestone, rich in fossils. Several intervals are yellow-stained, indicating the presence of dolomite (Skaar 1972; see Bockelie 1982, p. 117), and pyrite is common. The content of clay increases near the top, and the beds are separated by thin shale seams. The beds were numbered M-1 to M-14 from below (Fig. 28). The unit is strongly condensed and represents the top of the *M. polyphemus*, the *M. simon* and the basal part of the *M. limbata* Zones.

The Lysaker Member consists of limestone nodules and beds intercalated in shale. The ratio limestone:shale varies vertically, with most limestone near the base, in the middle and near the top of the member, separated by shale-dominated intervals, about 1.3 and 1 m thick, respectively (Fig. 28). Rasmussen (1989, 1991) numbered the limestone levels A-0 to A-57 from below; this system is adopted here (Fig. 28). Phosphorite staining is seen in beds A-28–A-29. The Lysaker Member straddles the main upper part of the *M. limbata* Zone and most of or, very likely, the entire *A. expansus* Zone.

The Svartodden Limestone consists of thick-bedded, grey, very compact limestone, with several phosphorite-stained seams in the basal part of the unit. The lower 0.2 m is rich in brachiopods and corresponds to the so-called 'Porambonites bed' of Brøgger (1882). This bed presumably marks the boundary between the *A. expansus* and *A. 'raniceps'* Zones, and the main part of the Svartodden Limestone is believed to represent the *A. 'raniceps'* Zone. However, the unit has not been included in the present study (for details, see Rasmussen 1991). Judging from the conodont occurrences, an unconformity corresponding to the upper half of the *A. 'raniceps'* Zone is present between the Svartodden Limestone and the Elnes Formation.

Lithostratigraphy

Bornholm

The *Orthoceras* limestone of Bornholm was by C. Poulsen (1936) divided into a lower unit A, 0.30 m thick, referred to as *Umbonata* limestone, and an upper unit B, about 4.5 m thick, considered equivalent to the *Limbata* and Lower *Asaphus* limestones of Sweden (Fig. 29). The two units were distinguished primarily by their fossil content. The '*Umbonata*' limestone was formally separated as the Skelbro Limestone Formation by V. Poulsen (1965), motivated by its allegedly high content of phosphatic pebbles and glauconite, not found in the overlying unit, which in turn was included

Grönwall 1916	C. Poulsen 1936	V. Poulsen 1966	This paper
<i>Dicellograptus</i> -shales	Middle <i>Dicellograptus</i> Shale	<i>Dicellograptus</i> Shale	<i>Dicellograptus</i> Shale
	Lower <i>Dicellograptus</i> Shale		
<i>Orthoceras</i> Limestone	Orthocerate Limestone	(<i>L. Asaphus</i> & <i>Limbata</i> L.) Komstad Limestone Formation	Komstad Limestone Formation (Skelbro beds)
		<i>Umbonata</i> L. Skelbro Lmst. Fm.	
<i>Dictyograptus</i> Shale	<i>Dictyonema</i> Shale	<i>Dictyonema</i> Shale	Alum Shale Formation ' <i>Dictyonema</i> Shale member'

Fig. 29. Lithostratigraphic nomenclature of the Komstad Limestone and surrounding units, Bornholm.

in the Komstad Limestone Formation. The boundary between the two formations was defined at a phosphorite- and glauconite-impregnated discontinuity surface, described in some detail by Hadding (1958, pp. 181–182). It appears, however, that neither C. Poulsen (1936) nor V. Poulsen (1965) nor Hadding (1958) actually studied the '*Umbonata*' Skelbro Limestone *in situ* at Skelbro, as it was covered with scree (cf. C. Poulsen 1936, p. 47; V. Poulsen 1965, p. 53). Excavations in the Skelbro quarry demonstrated that

- 1 the phosphatic pebbles are mainly accumulated in the basal parts of beds nos. –21 and –20, and occur only very sparsely in the upper main part of each of these beds
- 2 the content of glauconite grains in the 'Skelbro Limestone' is negligible
- 3 the defined upper boundary of the Skelbro Limestone Formation is non-existent; the mineralized surface, described by Hadding (1958), is the base of bed –21 (with a cast of the basal conglomerate surface) turned upside down.

The conditions at Skelbro are identical to those at the nearby locality Limensgade, where the lower beds can be studied without excavations. It is concluded that the designation Skelbro Limestone Formation should be abandoned, since no lithological differences justify a distinction of two formations or members, nor is any distinct discontinuity surface present to serve as boundary marker. Beds nos. –21 and –20 are herein informally referred to as the Skelbro beds of the Komstad Limestone Formation.

The Komstad Limestone Formation of southern Bornholm varies in thickness from about 1.5–2 m in the Øleå area (drillings) to 4 m at Skelbro and 4.7 m at Vasegård (cored drill-hole). The limestone is slightly thicker at Hjulmagergård, according to Grönwall (1916), i.e. presumably about 5 m. The formation is separated by a major unconformity from the Alum Shale Formation below and by another major unconformity from the *Dicellograptus* Shale above.

Brögger 1882, 1887	Monsen 1937	Størmer 1953	Erdtmann 1965	Owen <i>et al.</i> 1990
4α	Upper <i>Didymograptus</i> -shale 4α	Upper <i>Didymograptus</i> Shale 4α		Elnes Fm. Helskjær Mb.
Fragment-limestone Orthoceratite-limestone 3cγ Porambonites-bed		Transition beds <i>Endoceras</i> Limestone 3cγ Porambonites bed		
<i>Expansus</i> -shale 3cβ		<i>Asaphus</i> Shale 3cβ		Huk Fm. Svartodden Limestone Mb. Lysaker Mb.
<i>Megalaspis</i> -limestone 3cα		<i>Megalaspis</i> Limestone 3cα	<i>Megistaspis</i> Limestone 3cα	
<i>Phyllograptus</i> -shale 3b	δ Lower <i>Didymograptus</i> -shale 3b γ β α ?	ε Lower <i>Didymograptus</i> Shale 3b δ γ β α	Slemmestad Mb. Tøyen Shale Galgebjerg Mb. Fm. Hagastrand Mb.	Tøyen Fm. Galgebjerg Mb. Hagastrand Mb.

Fig. 30. Lithostratigraphic nomenclature of the Huk Formation and surrounding units, Oslo Region.

Scania

The Orthoceratite/*Orthoceras* limestone of Scania was separated as the Komstad Limestone Formation by Jaanusson (1960, p. 300). The type locality is the old limestone quarries at Komstad, described by Funkquist (1919). These abandoned quarries are nowadays water-filled, with outcrop limited to the steep quarry faces, whereas the nearby Killeröd quarry is more readily approachable for study and sampling. The latter locality is therefore formally proposed herein as a paratype section for the Komstad Limestone Formation.

The thickness of the formation varies considerably within SE Scania from 9.5 m at Gislövshammar to more than 15 m in the type area (presumably totalling about 18 m). It is at least 12 m thick at Kivik (possibly about 15 m), and presumably amounts to about 12–14 m or even more at Tommarp (calculation based on informations from Funkquist 1919). In western Scania the formation is more than 4.5 m thick at Fågelsång, with an estimate arriving at about 6 m. It is uncertain whether or not Komstad Limestone is present at Röstånga, but in the nearby drill-hole Albjåra-1 the formation is 3 m thick. The Komstad Limestone wedges out to the northwest, and is absent in the Krapperup and Lovisefred drill-holes of NW Scania, where it is replaced by graptolitic shales (Tøyen Shale / Upper *Didymograptus* Shale).

The Scanian Komstad Limestone conformably overlies the Tøyen Shale, and in the western part of Scania and at Kivik it is in turn conformably overlaid by the 'Upper *Didymograptus* Shale'. A major unconformity separates the Komstad Limestone of SE Scania from the 'Upper *Didymograptus* Shale' (Killeröd) or the *Dicellograptus* Shale (Tommarp,

Gislövshammar), as on Bornholm. Locally, the basal part of the *Dicellograptus* Shale is referred to as the Killeröd Formation (J. Bergström 1982b; Månsson 1993).

Slemmestad

The history of the post-Tremadocian Lower Ordovician lithostratigraphy of the Oslo region is summarized in Fig. 30; see Erdtmann (1965) and Owen *et al.* (1990) for a more detailed review. Brögger (1882) subdivided 'Etagé 3', introduced by Kjerulf (1857, 1865), into 3a (*Ceratopyge* Limestone and Shale), 3b (*Phyllograptus* Shale) and 3c (*Orthoceras* limestone complex), the latter including subunits codified 3cα, 3cβ and 3cγ (Fig. 30). The lower part of 3cγ was referred to as the *Porambonites* bed, which may be up to 1 m thick.

Monsen's (1937) classification of the Lower *Didymograptus* Shale reflects biostratigraphy, despite the 'Broeggerian' usage of numbers and Greek letters. This also concerns 3be of Spjeldnæs (1953) and Størmer (1953).

The new lithostratigraphy for the Oslo area proposed by Owen *et al.* (1990) is used in the present work, which focuses on the Huk Formation. This unit is 8.6 m thick at the Slemmestad harbour (Bjerkåsholmen, Djuptrekkodden); the individual members measure 1.6 m (Hukodden Limestone), 4.4 m (Lysaker Member) and 2.6 m (Svartodden Limestone). The formation is conformably underlain by the Tøyen Shale Formation and succeeded by the Elnes Formation. Judging from conodont data (Rasmussen 1991) there is an unconformity between the Huk Formation and the Elnes Formation.

Moberg 1890		Bohlin 1949		Jaanusson 1952 Jaen. & Mutvei 1951, 1953			Tjernvik 1956	
Gigas limestone		Gigas Lmst.	<i>M. gigas</i>	Gigas B.	<i>M. gigas</i>	(Not treated)		
		<i>Centaurus</i> L.	<i>M. centaurus</i>		<i>M. obtusica</i>			
Asaphus l.	Upper	Asaphus Limestone	<i>Asaphus raniceps</i>	Vaginatum Lmst.	'Raniceps' Beds			Asaphus 'raniceps'
	Lower		<i>Asaphus expansus</i>		Expansus Beds			Asaphus expansus
Limbata limestone		Limbata Limestone	<i>Asaphus lepidurus</i>	Lepidurus Limestone	Asaphus lepidurus	Limbata Limestone	<i>M. limbata</i> var. <i>lata</i>	
			<i>Megalaspis limbata</i>	Limbata Limestone	(Not treated)			
Planilimbata limestone		Planilimbata Limestone	<i>Megalaspis planilimbata</i>	Planilimbata Limestone	(Not treated)	Planilimbata Limestone	Billingen group	<i>Plesiomegal. estonica</i>
								<i>Megalaspides dalecarlicus</i>
					Hunneberg group		<i>Plesiomegal. planilimbata</i>	
							<i>Plesiomegal. armata</i>	

Fig. 31. Stratigraphy of the lower part of the Swedish 'Orthoceras limestone' since Moberg (1890).

Chronostratigraphy

Previous work

The first crude division of the Swedish Ordovician was established by Angelin (1854). Towards the close of the nineteenth century, the Swedish 'Orthoceras limestone' was classified according to colour, i.e. Lower Red, Lower Grey, Upper Red, etc. (see, e.g., Nathorst 1881; Törnquist 1884). However, the 'colour index' proved inconsistent for correlation between regions, and Moberg (1890) introduced the long-standing Swedish division of the lower part of the 'Orthoceras Limestone' comprising *Planilimbata*, *Limbata* and *Asaphus* Limestones (Fig. 31). In the course of time, the *Asaphus* Limestone was substituted by the *Expansus* and *Raniceps* Limestones by some authors, while others preferred the eastern Baltic designation *Vaginatum* Limestone (including the *Gigas* Limestone *sensu* Moberg), and still others retained the original name. Tjernvik (1956) subdivided the *Planilimbata* Limestone into various units. Jaanusson (1951, 1957) inserted a *Lepidurus* Limestone (i.e. a *A. lepidurus* Zone) between the *Limbata* and the *Expansus* Limestones. The *Limbata* Limestone was cited as 'Limbata Limestone' by Jaanusson (1956 *et seq.*), based on the belief that *M. limbata*

(*s.str.*) is confined to the *Lepidurus* Limestone and that the traditional Swedish *M. limbata*, eponym of the *Limbata* Limestone, possibly ought to be assimilated within *M. elongata* (see taxonomical section on *M. limbata* for details). Further, it was uncertain whether or not the *Asaphus* Limestone *sensu* Moberg (1890) (of southern Öland) included the *Lepidurus* Limestone (of northern Öland). All of Moberg's designations largely went out of use after Jaanusson's revision of 1960 (Fig. 31), which incorporated large segments of the eastern Baltic chronostratigraphy (Fig. 32) into the Swedish classification of the Early and Middle Ordovician. The Hunderumian Substage was introduced for the *A. expansus* Zone, as no eastern Baltic name was available (Jaanusson 1960).

Tjernvik (1980) distinguished three trilobite zones within the Volkhov Stage, or the Lanna-Volkhov Stage, as he proposed to rename it, in order to distinguish between the eastern Baltic and the Swedish classification (Fig. 31). The Langevojan Substage was discarded, as the *A. lepidurus* Zone can be recognized only on northern Öland but not in mainland Sweden (see also Tjernvik 1972). Tjernvik also inserted the *M. aff. estonica* zone as a basal zone of the Billingen interval; these so-called 'Transition beds' were previously included in the Hunnebergian (Tjernvik 1956). Recently, Lindholm (1991) suggested adhering to Tjernvik's old defi-

Jaanusson 1956-1960			Tjernvik 1980		Jaanusson 1982			Present paper	
Kundán	Aluojan	<i>M. gigas</i> <i>M. obtusicauda</i>	?	(Not treated)	Kundán	Aluojan	<i>M. gigas</i> <i>M. obtusicauda</i>	Kunda	<i>M. gigas</i> <i>M. obtusicauda</i>
	Valasteán	<i>Asaphus</i> <i>'raniceps'</i>		<i>Asaphus</i> <i>'raniceps'</i>		Valasteán	<i>Asaphus</i> <i>'raniceps'</i>		<i>Asaphus</i> <i>'raniceps'</i>
	Hunde- rumian	<i>Asaphus</i> <i>expansus</i>		<i>Asaphus</i> <i>expansus</i>		Hunde- rumian	<i>Asaphus</i> <i>expansus</i>		<i>Asaphus</i> <i>expansus</i>
Volkhovian	Lange- vojan	<i>Asaphus</i> <i>lepidurus</i>	Lanna-	<i>Megistaspis</i> <i>limbata</i>	Volkhovian	<i>Megistaspis</i> <i>limbata</i>	Volkhov	<i>Megistaspis</i> <i>limbata</i>	
	?	?		<i>Megistaspis</i> <i>simon</i>		<i>Megistaspis</i> <i>simon</i>		<i>Megistaspis</i> <i>simon</i>	
			<i>Megistaspis</i> <i>lata</i>	Volkhov		<i>Megistaspis</i> <i>lata</i>		<i>Megistaspis</i> <i>lata</i>	<i>Megistaspis</i> <i>polyphemus</i>
Latorpian	Billin- genian	<i>Megistaspis</i> <i>estonica</i>	Latorp	<i>Megistaspis</i> <i>estonica</i>	Billingenian	<i>Megistaspis</i> <i>estonica</i>	Billingen	<i>Megistaspis</i> <i>estonica</i>	
		<i>Megalaspides</i> <i>dalecarlicus</i>		<i>Megalaspides</i> <i>dalecarlicus</i>		<i>Megalaspides</i> <i>dalecarlicus</i>		<i>Megalaspides</i> <i>dalecarlicus</i>	
	Hunne- bergian	<i>Megistaspis</i> <i>planilimbata</i>		Transition Beds <i>M. aff. estonica</i>					<i>M. aff. estonica</i>
				<i>Megistaspis</i> <i>planilimbata</i>	Hunnebergian	<i>Megistaspis</i> <i>planilimbata</i>	Hunneberg	<i>Megistaspis</i> <i>planilimbata</i>	
		<i>Megistaspis</i> <i>armata</i>		<i>Megistaspis</i> <i>armata</i>		<i>Megistaspis</i> <i>armata</i>		<i>Megistaspis</i> <i>armata</i>	

Fig. 31 (continued).

inition of the Hunnebergian and Billingenian, including the *M. aff. estonica* Zone and the equivalent *D. balticus* graptolite Zone in the Hunnebergian.

Discussion

The chronostratigraphical classification of Jaanusson (1960, 1982) has been strongly criticised by Tjernvik (1972, 1980), who emphasized that the eastern Baltic zonation cannot be directly implemented in Sweden because of faunal differences and the partial incompleteness of the eastern successions, causing ambiguity in correlation. Tjernvik disapproved of the replacement of traditional and well-established Swedish names by foreign ones, just for the sake of 'modernisation' and without an associated restudy of the strata in question. In particular, the insertion of a *Lepidurus* Limestone in the stratigraphical scheme (Jaanusson 1957, 1960) created a schism. Tjernvik (1972, 1980) vigorously rejected the presence of *Lepidurus* Limestone in Scandinavia outside northern Öland.

A simplified version of Jaanusson's latest classification is adopted in this paper (Fig. 31). I concur, nonetheless, with a significant proportion of the criticism raised by Tjernvik. It appears futile to replace well-established names by formally

more correct ones as long as the nature of the strata and their faunas are so poorly known. Inevitably, errors and misconceptions make their way into the chronostratigraphical classification – and experience shows that they are difficult to get rid off. For instance, the eastern Baltic BII α Zone *sensu* Lamansky (1905; see Fig. 32) includes levels corresponding to the *M. estonica* Zone of Sweden; only the upper part equals the *M. polyphemus* Zone. Hence the Volkhov Stage of Estonia, as defined by Orviku (1958), includes the top of the Billingen Stage in a Scandinavian sense (somewhat paradoxically, the Estonian classification of Billingen/Volkhov has been modified according to Swedish usage, see, e.g., Männil 1966 and Kaljo & Nestor 1990). Furthermore, the 'modern' names Latorp, Lanna and Holen Limestones (Jaanusson 1982) are just new terms for the older chronostratigraphical designations *Planilimbata*, *Limbata* and *Asaphus+Gigas* Limestones *sensu* Moberg (1890). These 'topostratigraphical' units (see Jaanusson 1982), as those introduced by Moberg, are characterized primarily by fossil content and only to a lesser extent by lithology, and they should not be confused with lithostratigraphical units, despite the 'correct' naming. The concept of topostratigraphy as formulated by Jaanusson (1976, 1982) has a long tradition in Swedish Ordovician stratigraphy, mixing bio- and lithostratigraphy with a clear chronostratigraphical aim. A consistent litho-

Schmidt 1858	Schmidt 1881	Lamansky 1905		Kaljo & Nestor 1990	Scandinavia
Vaginaten limestone (1)	Vaginaten or Orthoceras limestone B.3	BIII γ Zone of <i>A. eichwaldi</i>	Kunda Stage	BIII γ Aluoja Substage	<i>M. gigas</i> & <i>M. obtusicauda</i>
		BIII β Zone of <i>A. raniceps</i>		BIII β Valaste Substage	<i>A. 'raniceps'</i>
		BIII α Zone of <i>A. expansus</i>		BIII α Hunderum Substage	<i>A. expansus</i>
Chlorit limestone	Glauconite limestone B.2	BII γ Zone of <i>A. lepidurus</i>	Volkhov Stage	BII γ Langevoja Substage	<i>M. limbata</i> U L
		BII β Zone of <i>A. bröggeri</i>		BII β Vääna Substage	
		BII α Zone of <i>M. limbata</i> & <i>M. planilimbata</i>		BII α Saka Substage	<i>M. polyphemus</i>
Greensand	Glauconite sand B.1	BI β Zone of <i>T. angelini</i>	Latorp Stage	BI γ Billingen Substage	<i>M. estonica</i>
		BI α Zone of <i>O. siluricus</i>		BI β	<i>M. dalecarlicus</i>
				BI α Hunneberg Substage	<i>M. planilimbata</i>

Fig. 32. Classification of the lower part of the eastern Baltic 'Orthoceras limestone' since Schmidt (1858). The right column is an attempt to correlate the eastern Baltic stratigraphy with the Scandinavian zonation. For reviews of Estonian stratigraphy, see Jaanusson (1957, 1960) and Kaljo & Nestor (1990).

and biostratigraphy, as for example introduced for northern Öland by van Wamel (1974), appears preferable.

The tripartite zonal division of the Volkhov Stage outlined by Tjernvik (1980) is confirmed by the present study. Each zone is bounded by distinct palaeoenvironmental changes, which readily can be recognized in most sections, even if masked by faunal differences between regions. The environmental changes were caused by major sea-level events and are believed to be synchronous for all practical purposes throughout Baltoscandia. The late Volkhovian *A. lepidurus* Zone, the correlation of which has been the source of much controversy, is equivalent to only the upper part of the *M. limbata* Zone and roughly corresponds to one of two informal subzones of the *M. limbata* Zone distinguished in the present work. Hence the BII β Zone equals the *M. simon* Zone and the lower part of the *M. limbata* Zone (Fig. 32). On northern Öland, the lower part of the *M. limbata* Zone is very strongly condensed, and this is probably also the case in Estonia and the St. Petersburg Region.

The Kunda Stage was previously subdivided into three substages containing four trilobite zones (Jaanusson 1960, 1982; see Fig. 31). The substage/chronozone couplets cover identical time intervals, and the dual classification is of no practical use neither for the sequences nor for the academic

communication, and I suggest that the Scandinavian substage division of the Kunda Stage be abandoned. In this context it is also relevant to point out that the definition of the Hunderumian, typified by the Haget section of northern Öland (Bohlin 1949), is dubious. The rich trilobite fauna of beds 'd' and 'e' *sensu* Bohlin (1949, p. 537), overlying a conspicuous smooth discontinuity surface ('D' in Jaanusson 1957, Textfig. 27), definitely indicates the *A. expansus* Zone (unpublished data), which is also apparent from the illaenid species reported by Jaanusson (1957, Textfig. 27). It is not possible that the smooth discontinuity surfaces present in the Hagudden and Hälludden sections are synchronous, although this impression could arise from comparing Textfigs. 26 and 27 of Jaanusson (1957). The exact position of the boundary between the *A. expansus* and *A. 'raniceps'* Zones in the Haget section is currently unknown, but it is probably on top of, or just above Bohlin's unit e, i.e. about 1 m or more above the highlighted discontinuity surface. Whatever the circumstances, the Hunderumian concept remains ambiguous until the range of the *A. expansus* Zone at Haget is established. It is remarked that this zone appears to be strongly condensed at Hagudden and presumably is incomplete, and the locality should not be promoted as a type section.

Much further work is needed to characterize the zones of the Volkhov and Kunda Stages satisfactorily in terms of biostratigraphy. It is evident that the hitherto loosely defined zones, typically employing single forms as index species, are unsatisfactory and difficult to correlate between different facies. It further appears that several eponymous species are not confined to the zone that carries their name, which applies to *M. simon*, *M. limbata* and presumably (to a lesser extent) also *A. expansus*. The exact ranges of *A. raniceps* and *A. raniceps* (*s.str.*) also remain to be documented. The seemingly intricate correlation problems arising from these distributions are, though, easily overcome in practice by adopting a more dynamic approach to stratigraphy, since all the Lower Ordovician trilobite zonal boundaries of Scandinavia without exception reflect significant palaeo-environmental changes, which potentially are traceable all over the region.

Biostratigraphy

The Komstad Limestone of Scania–Bornholm and the two lower members of the Huk Formation at Slemmestad are divided into zones based on the distribution of species and subspecies of *Ampyx*, *Asaphus*, *Cyclopyge*, *Dysplanus*, *Illaeus*, *Lonchodomas*, *Megistaspis*, *Nileus*, *Niobe*, *Raymondaspis*, *Rhombampyx* and others. Five zones are recognized, representing the Volkhovian and early part of the Kundan Stages (late Arenig–earliest Llanvirn). It would have been desirable to include other trilobite taxa as well in the biostratigraphic analysis, notably *Symphysurus*, ptychopygids, and agnostids, but these large groups are in need of revision. Interregional correlation would also benefit greatly by a revision of the coeval Swedish and eastern Baltic trilobite faunas.

The Swedish chronozone names are used as labels for the biozones of the Komstad Limestone. Strictly speaking, this procedure is incorrect, as index fossils per definition must be present in biozones (Hedberg 1976), and, for instance, *Asaphus expansus* does not occur in the Komstad Limestone, *A. raniceps* is restricted to SE Scania, and *M. limbata* occurs only in the lower half of the zone carrying its name (and even ranges through the two preceding zones). On the other hand, there is little point in introducing new terms such as *Megistaspis geminus* n.sp. zone (for the upper subzone of the *M. limbata* Zone), *A. acuminatus* zone (for the *A. expansus* Zone) or *A. striatus* zone (for the *A. raniceps* Zone), if these units as far as can be established cover the same time intervals as the zones of central Sweden. The traditional zonal designations are therefore retained, except that *Megistaspis lata* is replaced by the senior synonym *M. polyphemus*. The zonal definitions thus correspond more or less to Opperl biozones *sensu* Hedberg (1976), which in practice is also the case for the Swedish zonation, notwithstanding the circumstance that those zones are intended as range zones (cf. Tjernvik 1980).

The zones are discussed in ascending order below, based on the trilobite range-charts of the investigated sections shown in Figs. 33–36. A synoptic chart of the Komstad Limestone biostratigraphy is presented in Fig. 37.

Volkhov Stage

MEGISTASPIS (MEGISTASPIS) POLYPHEMUS Zone

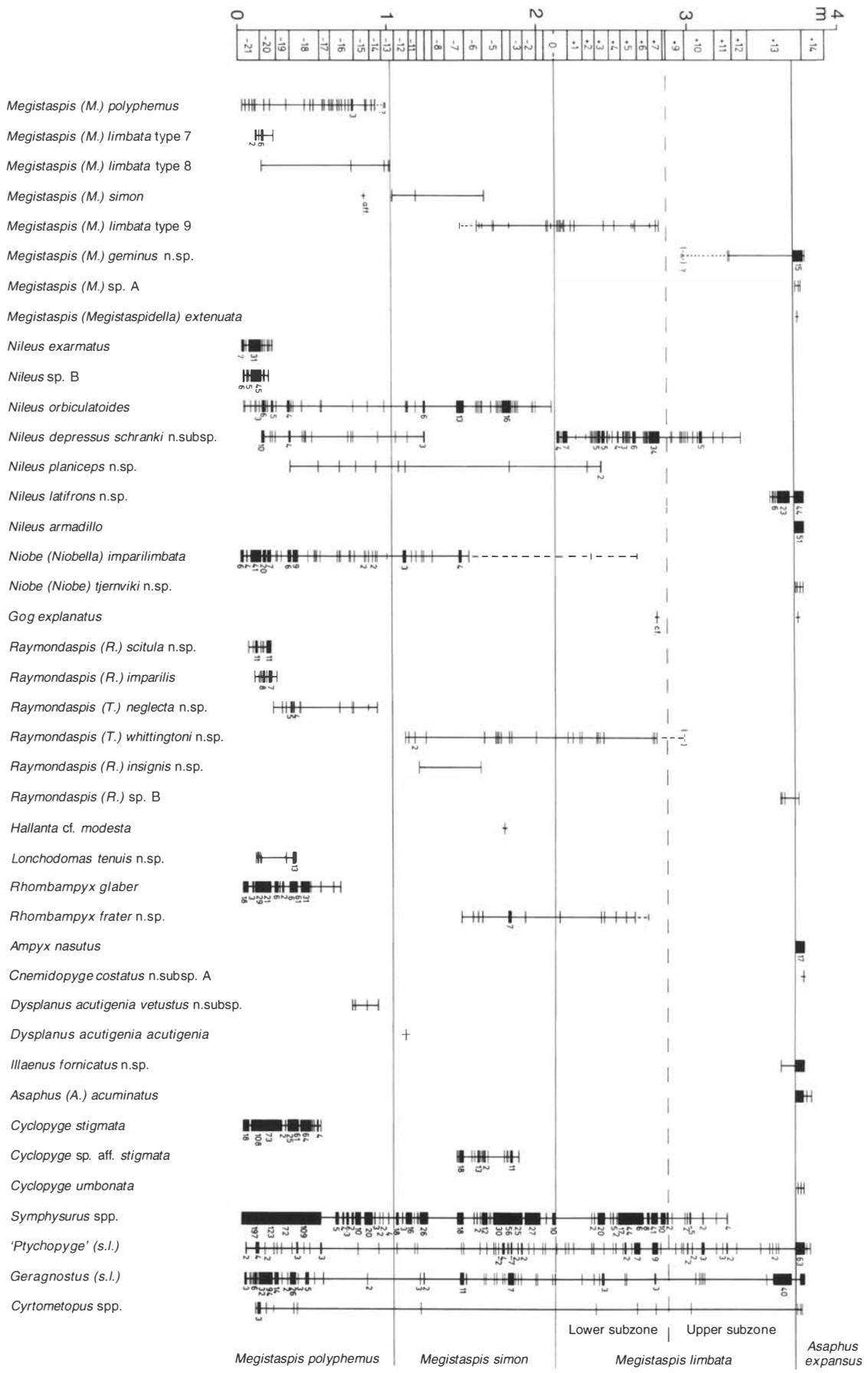
The *M. polyphemus* Zone is 1.02 m thick in the Skelbro section and about 0.12 m thick in the Slemmestad section, being represented by, respectively, bed –21 to 2.5 cm below top of bed –13 (Fig. 33), and bed M-1 (Fig. 36). The basal 0.40 m of the limestone at Gårdlösa-1a, bed interval A to E (Fig. 34), possibly belongs to the *M. polyphemus* Zone.

Skelbro. – The *M. polyphemus* Zone is characterized by *Megistaspis polyphemus*, *M. limbata* types 7–8, *Raymondaspis neglecta* n.sp. and *Dysplanus acutigenia vetustus* n.subsp. The basal conglomerate, 0.08–0.12 m thick, contains no trilobites, but the conodont fauna suggests a Volkhovian age (Stouge 1975), i.e. *M. polyphemus* Chronozone.

The highly fossiliferous lower half of the *M. polyphemus* Zone, bed interval –21 to –18, is recognized informally as the *C. stigmata* sub-biozone (compare V. Poulsen 1965). Besides *M. polyphemus* and *R. neglecta* n.sp., which range above the subzone, the *Cyclopyge stigmata* subzone is characterized by abundant occurrence of *C. stigmata*, *Rhombampyx glaber*, *Lonchodomas tenuis* n.sp., *Raymondaspis imparilis*, *R. scitula* n.sp., *Nileus exarmatus*, *Nileus* sp. B, and *Megistaspis limbata* type 7, in addition to several more rare taxa, many of which are not revised here (see V. Poulsen 1965). Thus *Remopleuridiella groenwalli*, *Ottenbyaspis* sp., *Megistaspis* cf. *knyrkoi*, *Celmus? longifrons*, *Selenoharpes nodorugosus*, *Trinucleoides praecursor*, *Pseudosphaerexochus inflatus*, *Aegerina* cf. *erratica* and several unnamed species are confined to the *C. stigmata* subzone (not shown on the range chart Fig. 33). The long-ranging *Nileus orbiculatoides*, *N. depressus schranki* n.subsp. and *Niobe (Niobella) imparilimbata* as well as unrevised representatives of *Symphysurus*, geragnostids (*s.l.*) and ptychopygids also occur abundantly in the subzone.

The boundary between the *M. polyphemus* and *M. simon* Zones is readily identified in the field, as the *M. polyphemus* Zone comprises a lower dark ‘massive’ interval, while light-coloured limestone with several shaly intercalations constitutes the succeeding *M. simon* Zone.

The trilobites found match the *M. polyphemus* Zone fauna of Sweden fairly well (cf. Tjernvik 1980, p. 191), but close comparison is impeded by the unrevised state of the Swedish fauna. The presence of *M. polyphemus* itself at Skelbro is certainly crucial for correlation, but *Megistaspis limbata* type 7 is also considered important, as it most likely is identical to *Megistaspis* sp. no. 1 Tjernvik, 1980, characteristic of the lower part of the *M. polyphemus* Zone. *Megistaspis limbata* type 8 may be identical to *M.* sp. 2 Tjernvik, characteristic of the upper half of the *M. polyphemus* Zone of Sweden, but this is less certain. The characteristic *Globampyx linnarssoni* has not been found at Skelbro. Tjernvik (1980) listed several ptychopygids characteristic of the *M. polyphemus* Zone. Even though the ptychopygids in the available material are not revised, *Metaptychopyge herambensis* and *M. minor* both



occur in the *Cyclopyge stigmata* subzone, whereas *Protychopyge prisca* has not been noted. The long-ranging *Nileus exarmatus*, *N. orbiculatoides*, *N. depressus*, and *Niobe imparilimbata* are constituents of the lower part of the *M. polyphemus* Zone in central Sweden as well as the Komstad Limestone.

The fauna of the *C. stigmata* subzone, which previously has been discussed at length by C. Poulsen (1936) and V. Poulsen (1965), resembles the fauna described from Herramb, Norway (Skjeseth 1952), but the exact distribution of the various species in the Herramb section is unknown. Common elements are *Megistaspis limbata* type 7, *Niobe imparilimbata*, *Nileus exarmatus*, *Metatychoyge herambensis*(?), and *Metatychoyge minor*(?). Besides, *Raymondaspis neglecta* n.sp., *Lonchodomas tenuis* n.sp. and *Rhombampyx glaber* of the Komstad Limestone resemble *Raymondaspis limbatus*' [= n.subsp. aff. *neglecta* n.sp.], *Lonchodomas volborthi*' [= n.subsp. aff. *tenuis* n.sp.] and *Ampyx pater* as determined by Skjeseth. The shaly lower part of the Herramb section is equivalent to the *M. estonica* Zone, but the upper part may range into the *M. polyphemus* Zone. The determination of *M. polyphemus* from Herramb (Skjeseth 1952) cannot be maintained; the fragments more likely represent *M. estonica* or *M. ringsakerensis*.

The *C. stigmata* subzone fauna is not restricted to the Skelbro beds, proper (i.e. beds -21 and -20), as previously thought (C. Poulsen 1936; V. Poulsen 1965), but characterizes the lower half metre of the Komstad Limestone, and no major hiatus separates the Skelbro beds from the remaining part of the Komstad Limestone (cf. V. Poulsen 1966).

Gårdlösa-1. – Only one species, *Megistaspis* sp. B, has been found in the lowermost 0.40 m of the Komstad Limestone at Gårdlösa-1, bed interval A–E. The species is presently known with certainty only from this locality, but it is closely related, if not identical, to *Megistaspis* sp. C, which in the Slemmestad section occurs associated with trilobites clearly indicative of the *M. polyphemus* Zone. This meagre evidence, combined with the absence of *Megistaspis simon* and *M. limbata* type 9 (characteristic of the *M. simon* Zone), makes it plausible that the basal part of the Komstad Limestone in the type area represents the *M. polyphemus* Zone.

The boundary between the *M. polyphemus*(?) and *M. simon* Zones is not accompanied by distinct lithological changes and is therefore difficult to recognize in the field. If accessible for sampling, bed F contains characteristic vertical burrows of *Diplocraterion*-type, often filled with a black substance enclosing large white gypsum crystals.

Slemmestad. – Bed M-1 has a planar upper surface, whereas the lower boundary is billowing, and the bed thickness varies

between 0.11 and 0.20 m. The bulk of the bed consists of fine-grained, dense limestone containing scattered small brachiopods. Trilobites are extremely rare, and none were found during the present investigation. A cranidium of *M. polyphemus* (Fig. 109A) was collected by Dr. T. Tjernvik at Bjerkåsholmen (south of the Slemmestad harbour), 3–4 cm above the base of the Hukodden Limestone. Another specimen of *M. polyphemus* was collected by Dr. D. Bruton, Oslo, in the 'Graptolite Valley' at Slemmestad, from a limestone nodule interval a few centimetres below the Hukodden Limestone (specimen PMO 94538). These two specimens are included in the diagram, Fig. 36. The holotype of *M. polyphemus* (Fig. 108A–B) without doubt also originates from the fine-grained lower part of bed M-1, 4–9 cm above the base, but the locality is unknown.

The upper 2–3 cm of bed M-1 are calcarenitic and rather fossiliferous. From this thin interval was collected a fauna containing *Megistaspis* sp. C, *Globampyx linnarssoni*, *Rhombampyx* cf. *glaber*, *Nileus exarmatus*, *N. depressus glazialis*, *Niobe* sp. aff. *lindstroemi*, and *Lonchodomas* cf. *tenuis*, plus some ptychopygids. This trilobite assemblage is clearly indicative of the *M. polyphemus* Zone; especially *G. linnarssoni*, *R. cf. glaber*, and *L. cf. tenuis* are significant (cf. Tjernvik 1980 and discussion of the Skelbro section above). Tjernvik (1980) listed *Niobe* cf. *lindstroemi* from the upper part of the *M. polyphemus* Zone, which may be analogous to the occurrence of *Niobe* aff. *lindstroemi* in bed M-1. This meagre evidence suggests that the bed belongs to the upper part of the *M. polyphemus* Zone, which is consistent with the graptolite dating of the subjacent shales (see Spjeldnæs 1953 and Erdtmann 1965, compared to Tjernvik 1956).

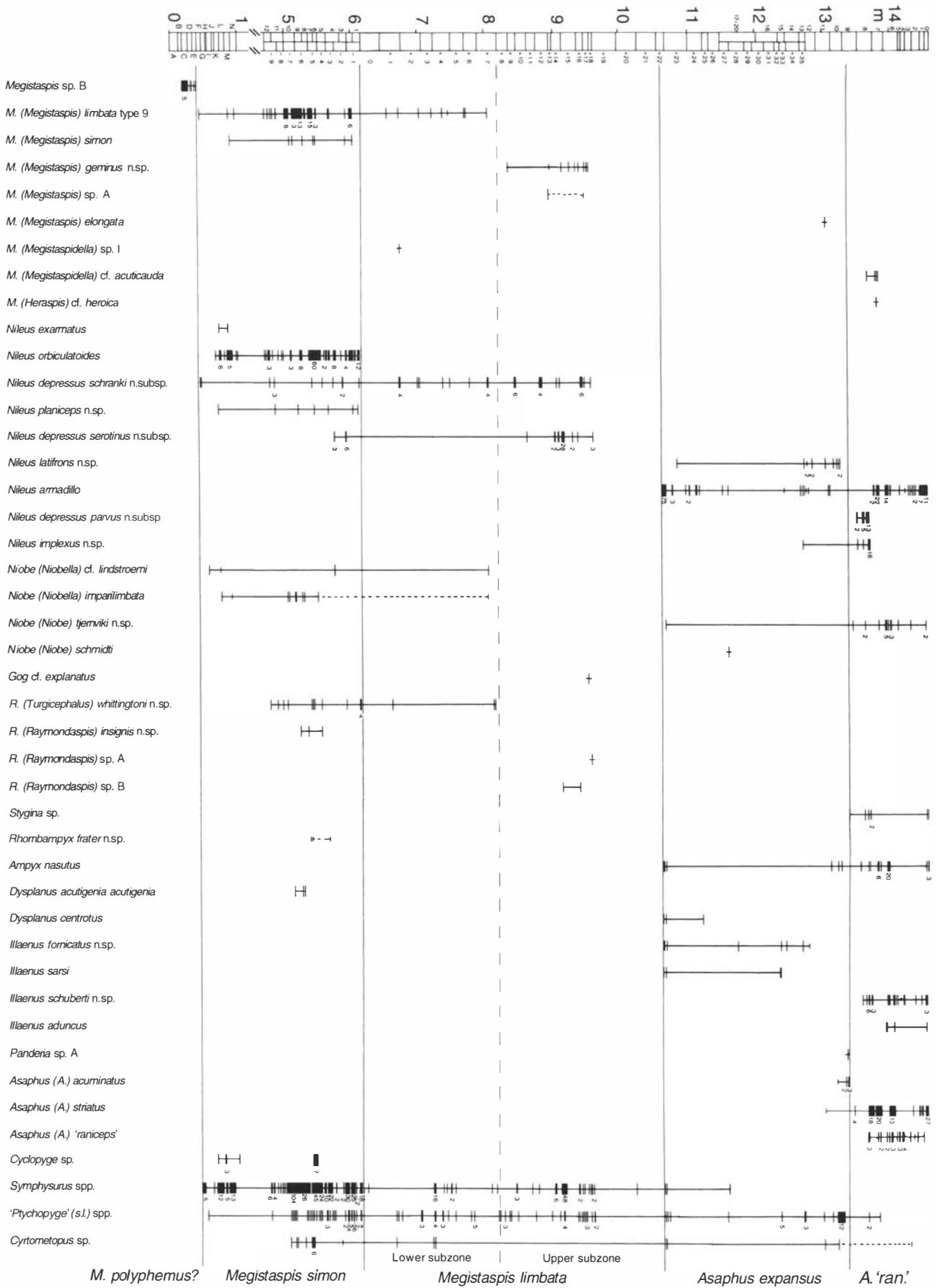
The boundary between the *M. polyphemus* and the *M. simon* Zones is indicated by a 'normal' distinct discontinuity surface.

MEGISTASPIS (MEGISTASPIS) SIMON Zone

The *M. simon* Zone is 1.10 m thick in the Skelbro section, about 5.8 m thick in the Killeröd area, and 0.76 m thick in the Slemmestad section. Within these sections, the zone is represented by, respectively, an interval from 2.5 cm below the top of bed -13 to 8.5 cm above the base of bed 0 (Fig. 33); bed interval E [at Gårdlösa-1] to -1 [at Killeröd, equal to bed 1 at Gårdlösa-4a] (Fig. 34); and bed interval M-2 to M-6 (Fig. 36).

Skelbro. – The lower boundary of the *M. simon* Zone is defined by the appearance of *M. simon* and by the coincident disappearance of *M. polyphemus* and *Megistaspis limbata* type 8. *M. simon*, which has been found only in the lower half of the zone, is very rare, and the more common *Raymondaspis whittingtoni* n.sp. is a better marker of the base of the zone. In SE Scania, *M. limbata* type 9 also ranges from the base of the *M. simon* Zone, but so far no specimens have been found below bed -7 at Skelbro. Beds -8 and -9 are for all practical purposes barren; a very large amount of rock has

Fig. 33. Range chart, Komstad Limestone, Skelbro. Legend as for Fig. 5. The Skelbro section is complete, or, at the most, 0.1 m of limestone may be missing on top.



been crushed, yielding only a single librigena of *N. imparilimbata* and an indeterminable nileid cranidium. *Nileus orbiculatooides* occurs abundantly in most beds of the *M. simon* Zone, and the disappearance of this species and the contemporaneous reappearance of *N. depressus schranki* n.subsp. define the upper limit of the *M. simon* Zone; *N. depressus schranki* n.subsp. is absent in the main upper part of the *M. simon* Zone at Skelbro. The upper boundary is also indicated by *Megistaspis limbata* type 9, which is comparatively narrow in the *M. simon* Zone, and becomes significantly broader in the *M. limbata* Zone (Fig. 52A).

The transition to the *M. limbata* Zone is indicated in the section by a change from light grey colours and 'shaly' structure to darker colours and a more compact appearance of the limestone.

The correlation of the *M. simon* Zone at Skelbro to Sweden (see Tjernvik 1980) is difficult without revision of the Swedish fauna, but *M. simon* itself and the common occurrence of *Nileus orbiculatooides* are similarities. Furthermore, *Raymondaspis insignis* n.sp. is of *R. 'limbata-type'* and may correspond to *R. limbata* subsp. *sensu* Tjernvik. It is unknown whether *Rhombampyx frater* n.sp. corresponds to *A. pater nasutus sensu* Tjernvik (1980, p. 192). *Niobe lindstroemi*, which is highly characteristic of the *M. simon* Zone in Sweden and southern Norway, and also occurs sporadically in SE Scania, has not been found at Skelbro.

By comparison to SE Scania, the *M. simon* Zone is strongly condensed. The upper part of the zone seems to be well-developed at Skelbro, judging, e.g., from the correlation of *Cyclopyge* sp. aff. *stigmata*, *Niobe imparilimbata*, and *Dysplanus acutigenia acutigenia*, whereas the lower part is inferred absent. The levels of condensation are possibly indicated by thin, inconspicuous 'gravel lags', consisting of more or less disintegrated trilobite material, near the top of bed -13 and at the base of bed -12.

Gårdlösa and Killeröd. – The *M. simon* Zone is characterized by the sparse occurrence of *M. simon*, common occurrence of *Megistaspis limbata* type 9 ('narrow' morph), very frequent *Nileus orbiculatooides*, and sparse *N. depressus schranki* n.subsp. *N. planiceps* n.sp. is, incidentally, confined to the *M. simon* Zone at Killeröd; this species ranges into the lower part of the *M. limbata* Zone at Skelbro. *Niobe imparilimbata* is moderately common in the lower main part of the zone, as at Skelbro, and *Cyclopyge* sp. aff. *stigmata* occurs in a narrow interval close to the top of the zone, also as at Skelbro. A few specimens of *Nileus exarmatus* were found near the base of

the zone. This species also occurs in the lower part of the *M. simon* Zone of central Sweden (Tjernvik 1980). Raphiophorids are very rare in the *M. simon* Zone of SE Scania; only a few poor specimens, presumably representing *Rhombampyx frater* n.sp., have been found near the top of the zone. *Raymondaspis insignis* n.sp. has so far been found only in a short interval close to the top of the zone; it is surmised to be an infrequent but diagnostic species of the *M. simon* Zone in SE Scania, judging from material housed at the University of Lund.

The sparse presence of *Niobe* cf. *lindstroemi* is important, as *N. lindstroemi* is a characteristic and frequent constituent of the *M. simon* Zone of Sweden (Tjernvik 1980) and Slemmestad (see below). A single specimen has, surprisingly, also been encountered in bed +7 at Killeröd, belonging to the lower part of the *M. limbata* Zone.

Dysplanus acutigenia acutigenia occurs in two beds close to the top of the *M. simon* Zone. This subspecies is by and large characteristic of the *M. limbata* Zone of Sweden (Jaanusson 1957; Tjernvik 1980) and Slemmestad (see below), but a few specimens have in fact been found in the uppermost part of the *M. simon* Zone also at Slemmestad.

The above remarks on the correlation of the *M. simon* Zone at Skelbro to Sweden are valid also for the Komstad Limestone of SE Scania. Additional points of similarity are, as already discussed, the presence of *N. exarmatus* and *Niobe* cf. *lindstroemi*.

The *M. simon* Zone of SE Scania is generally characterized by light-coloured, impure limestone. Intervals of very impure, shaly limestone occurs near base and near top of the zone, in particular the latter series of shale beds is readily recognized in the field (beds nos -8 to -1, Fig. 17; see, e.g., Fig. 15A). The transition to the *M. limbata* Zone is indicated by a change to darker colours and disappearance of the shaly appearance of the limestone.

Slemmestad. – The *M. simon* Zone at Slemmestad (beds M-2 to M-6) is characterized by the common occurrence of *M. simon* itself, by *M. limbata* types 1 (in the lower part) and 2 (upper part), quite frequent *Niobe lindstroemi*, sparse *N. exarmatus* in the lower part (a couple of poorly preserved specimens from bed M-4 may also represent the species), frequent *Nileus depressus glazialis*, especially in the lower part, replaced by *N. depressus* subsp. A in the uppermost part. Only one indeterminable raphiophorid was found at the base of the zone. A poorly preserved pygidium may represent *Raymondaspis insignis* n.sp. In addition to *Niobe lindstroemi* another niobinid of '*imparilimbata-type*' occurs sparsely, but most of the material is too poorly preserved to be identified. A few specimens from bed M-5 represent *N. cf. plana*, which ranges into the *M. limbata* Zone, and the earlier indeterminable specimens may belong to that species as well.

The occurrence of *M. simon*, *M. limbata* types 1 and 2, *Niobe lindstroemi* and *Nileus depressus glazialis* confirms the correlation between the *M. simon* Zones of Slemmestad and Sweden (cf. Tjernvik 1980). Likewise, the last representatives

Fig. 34. Composite range chart, Komstad Limestone type area, SE Scania. The chart is based on the sections investigated at Gårdlösa-1 (basal 1 m), Gårdlösa-4a (bed numbers left between 5 and 6 m), Killeröd (bed numbers right, -9 to +35), and Killeröd site b (bed numbers left in the upper part). The lower 1.6 m of limestone in the Killeröd section (Fig. 17) were inaccessible for sampling; note the omission of unsampled interval between 1 and 5 m. Between 2 and 4 m of Komstad Limestone is estimated to be missing on top of the combined sections. Legend as for Fig. 5.

of the long-ranging *Nileus exarmatus* occur in the lower *M. simon* Zone in Sweden as well as at Slemmestad. The only characteristic faunal element missing in the Slemmestad section is *N. orbiculatoides*.

The transition to the *M. limbata* Zone is not associated with macroscopic lithological changes. The zonal boundary is an ordinary discontinuity surface, situated a few centimetres below a comparatively conspicuous pyrite-rich marker level within bed M-7.

MEGISTASPIS (MEGISTASPIS) LIMBATA Zone

The *M. limbata* Zone is 1.57 m thick at Skelbro, 4.6 m at Killeröd, more than 2 m (probably about 4.5 m) at Fågelsång, and 3.2 m at Slemmestad. Within these sections the zone is represented by, respectively, the upper 6.5 cm of bed 0 to 6 cm below top of bed +13 (Fig. 33); bed 0 to 6 cm below top of bed +22 (Fig. 34); beds nos. 1–17, lower boundary unknown (Fig. 35); and bed interval M-7–A-28 (Fig. 36).

Two informal subzones of the *M. limbata* Zone, referred to as the lower and upper subzone, are recognized. *M. limbata* does not occur in the upper subzone of the Komstad Limestone. The lower–upper subzonal boundary presumably is not exactly synchronous between the Komstad Limestone and the Huk Formation (see discussion of ecostratigraphy).

Skelbro. – The *M. limbata* Zone is defined by the appearance of broad types of *M. limbata* type 9 (Fig 52A), associated with reappearance of *Nileus depressus schranki* n.subsp., and the disappearance of *N. orbiculatoides*.

The lower subzone (beds nos. 0 to +8 [+9?]) is characterized by *M. limbata* type 9 and frequent *N. d. schranki* n.subsp., as well as the top ranges of *Raymondaspis whittingtoni* n.sp., *Rhombampyx fraternus* n.sp. and *Nileus planiceps* n.sp. *Niobe imparilimbata* presumably occurs sparsely in this interval as well, but the few specimens found are too poorly preserved to be confidently identified, and could also represent *N. plana*.

The upper subzone (beds nos. +10 to +13) is defined by the appearance of *Megistaspis geminus* n.sp.; this species also enters the very base of the succeeding zone. The upper subzone is sparsely fossiliferous, and only *Nileus depressus schranki* n.subsp. is moderately common. The first representatives of *Nileus latifrons* n.sp., *Illaenus fornicatus* n.sp. and *Raymondaspis* sp. B (cf. *limbata*), all of which, generally speaking, are characteristic of the *A. expansus* Zone, appear close to the top of the *M. limbata* Zone.

A correlation with the Swedish mainland (Tjernvik 1980) is not possible at present. A few specimens of *M. cf. geminus* n.sp. have been found in the upper subzone of the *M. limbata* Zone at Slemmestad, where *Illaenus cf. fornicatus* n.sp. also appears close to the top of the zone.

The upper boundary of the *M. limbata* Zone is readily identified in the field, as the top of the *M. limbata* Zone comprises light grey limestone, whereas the *A. expansus* Zone interval is blackish.

Killeröd. – The lower limit of the *M. limbata* Zone is poorly defined at Killeröd because of the low yields of trilobites; the uncertainty regards 0.40 m. For the time being, the boundary is tentatively defined at the base of bed 0, but it may in reality be positioned slightly above.

The lower boundary is defined by the appearance of *Megistaspis limbata* type 9 ('broad morph'; see Fig. 52B), coinciding with the disappearance of *Nileus orbiculatoides* and *Megistaspis simon*. The lower subzone is characterized by *M. limbata* type 9, relatively abundant *Nileus depressus schranki* n.subsp., and top range of *Raymondaspis whittingtoni* n.sp. The upper subzone is defined by the appearance of *Megistaspis geminus* n.sp., but also *Nileus depressus serotinus* n.subsp. turns up again and is quite common. *Megistaspis* sp. A is also known from the upper subzone of Fågelsång and the base of the *A. expansus* Zone at Skelbro. The upper 1 m of the *M. limbata* Zone is virtually barren at Killeröd. Despite intensive search, only a single specimen of *Symphysurus* was found.

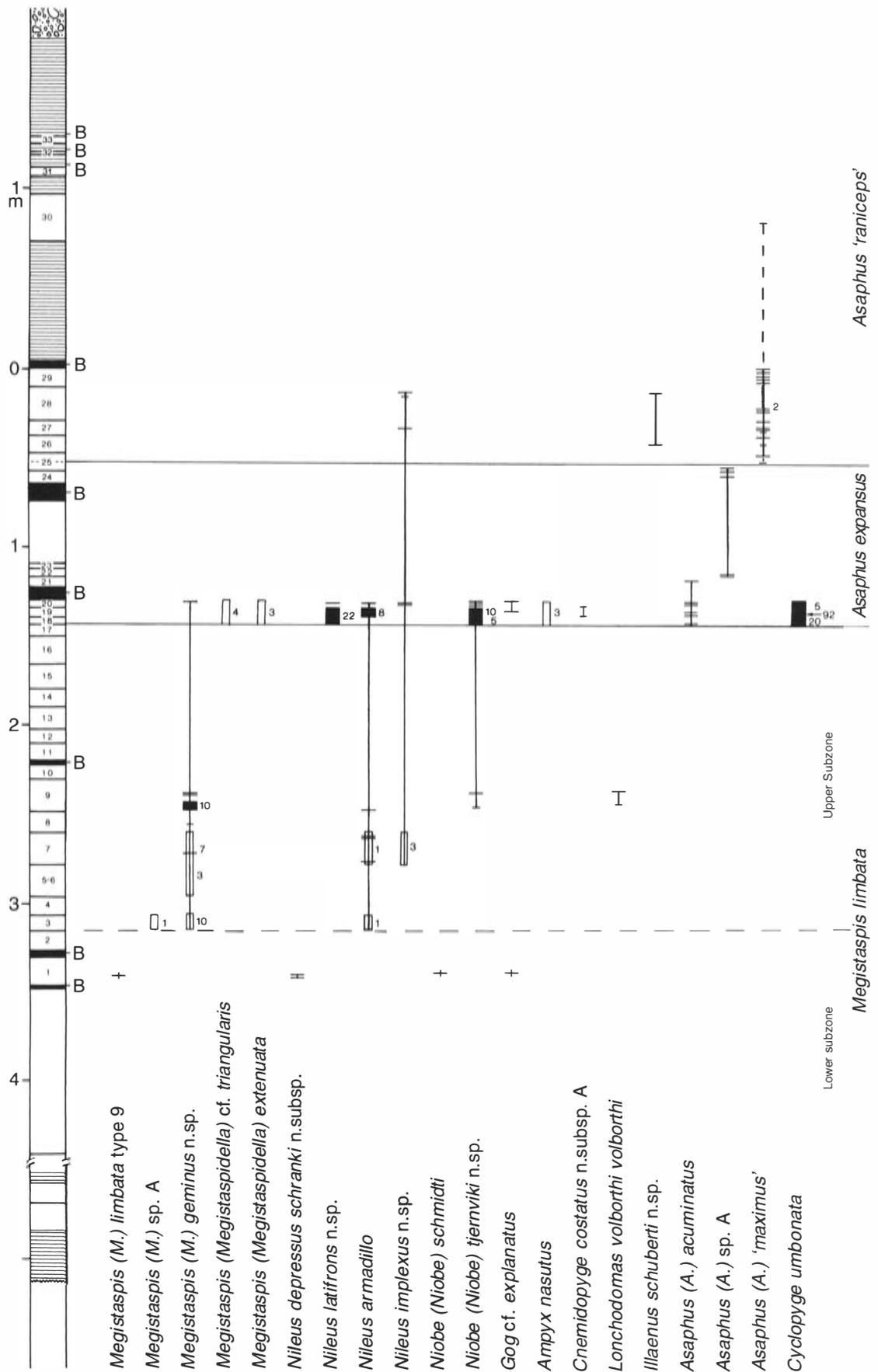
There is a striking coincidence of bed numbers between the Skelbro and Killeröd sections. The numbering of beds was made independently at the two localities, using at each place a distinct, thin shale intercalation as datum, but it is possible that bed interval –5 to about +7 actually can be correlated bed by bed between the two sections. Whatever the circumstances, the lithologies of the respective zones are similar, with light grey limestone including several shaly intercalations in the *M. simon* Zone and darker, more massive limestone in the lower part of the *M. limbata* Zone.

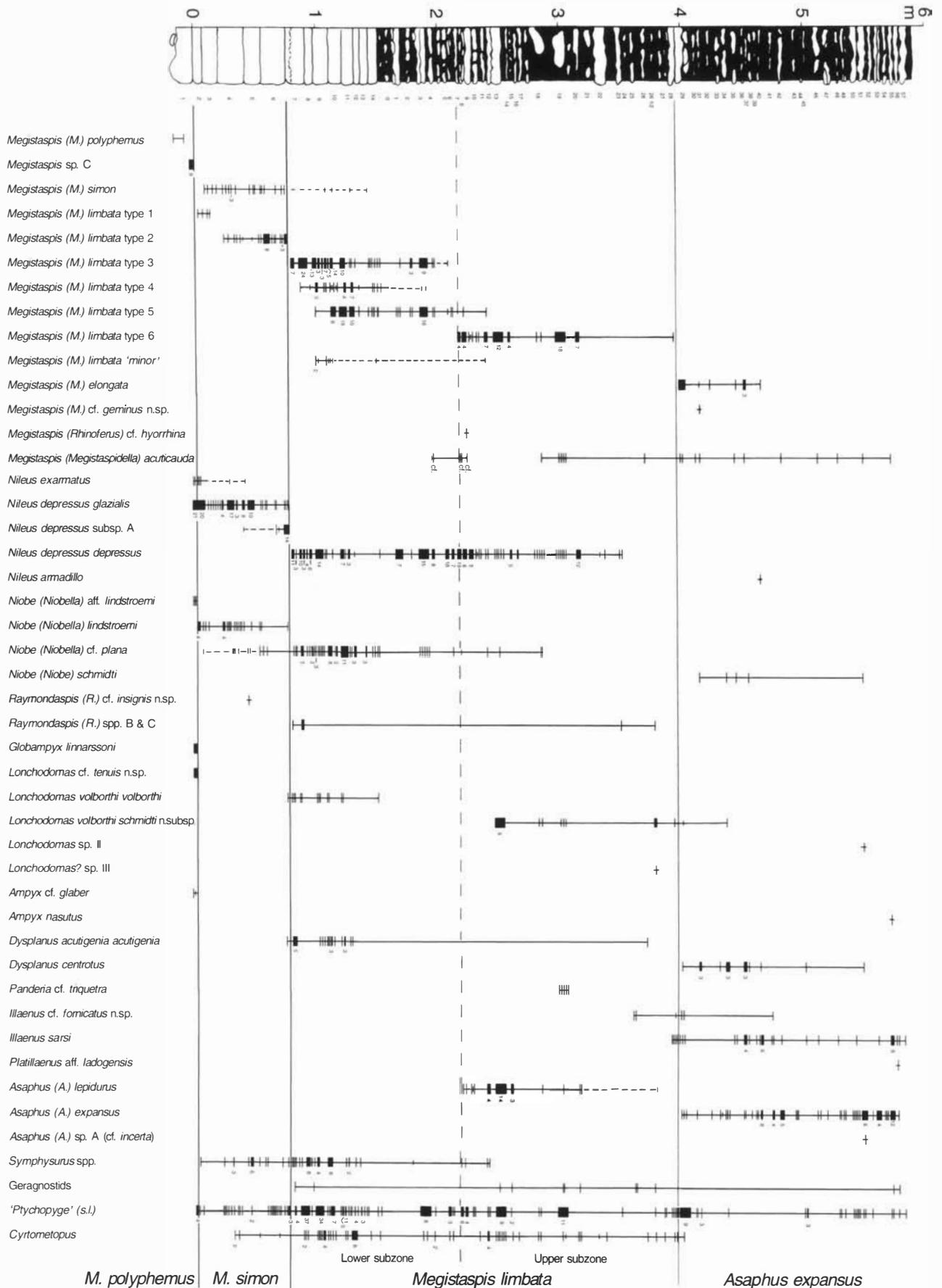
Except for *N. depressus serotinus* n.subsp., which is surmised to be closely related to *N. depressus depressus*, none of the faunal elements are in common with species known from the Swedish mainland (see Tjernvik 1980).

The boundary interval to the *A. expansus* Zone has a comparatively high clay content, and a series of 3–4 shaly beds catches the eye in weathered sections. When non-weathered, the boundary, positioned within the upper shaly bed, cannot be readily recognized.

Fågelsång. – The limestone intercalated in shale at loc. E22 yielded no determinable trilobites. The conodont fauna (Table 3) indicates an age corresponding to the *P. originalis* conodont Zone of Skelbro, i.e. the upper part of the *M. simon* Zone. Bed 1 of Loc. E21a is correlated with the lower *M. limbata* subzone, based on the occurrence of *Megistaspis limbata* type 9. The unknown succession between the strata at Loc. E22 and bed 1 of Loc. E21a thus appears largely equivalent to the lower subzone of the *M. limbata* Zone (but probably includes graptolitic Tøyen Shale).

Fig. 35. Composite range chart, Komstad Limestone, Fågelsång. The chart is based on the sections investigated at localities E21a and E21b. Beds nos. 11 to 17 yielded very limited raw material for sampling. Material kept in the collections at the University of Lund, referable to bed (or bed interval) only, are incorporated in the diagram; all LU material from the *M. limbata* Zone was collected by Ekström in 1917 (cf. Ekström 1937). Legend as for Fig. 5.





The presence of *Niobe schmidti* in bed 1 is surprising, as representatives of *Niobe* (*Niobe*) everywhere else in Baltoscandia is absent in the Volkhov Stage, while the associated species, *Nileus depressus schranki* n.subsp. and *Megistaspis limbata* type 9, are typical, albeit not diagnostic, of the lower *M. limbata* subzone. Bed 1 also yielded well-preserved ptychopygids.

Bed interval 3–17 (almost no material was available for sampling of beds nos. 11–17) is correlated with the upper *M. limbata* subzone, owing to the occurrence of *Megistaspis geminus* n.sp.. This species is associated with *Megistaspis* sp. A (also known from the upper subzone at Killeröd), *Lonchodomas volborthi volborthi* (known from the lower part of the *M. limbata* Zone at Slemmestad), *Nileus armadillo*, *Niobe tjernviki* n.sp. and *Nileus implexus* n.sp. The presence of the latter three species is puzzling, as they are typical representatives of the *A. expansus* Zone at Killeröd and Skelbro, and *N. implexus* n.sp. even extends into the *A. 'raniceps'* Zone at Killeröd site b (see, however, remarks in taxonomic section). Nevertheless, the presence of *M. geminus* n.sp. is diagnostic of the upper subzone of the *M. limbata* Zone, and a series of characteristic faunal elements occurring within the basal part of the above-lying *A. expansus* Zone can also be correlated unambiguously to the Skelbro and Killeröd sections. The presence of 'young' species in the upper subzone of the *M. limbata* Zone attests to an unusual palaeoenvironment at Fågelsång.

Except for *L. volborthi volborthi*, which has been found also in the lower part of the *M. limbata* Zone at Slemmestad and possibly occurs also in Sweden, none of the species found is shared with the *M. limbata* Zone of Sweden. *Megistaspis geminus* n.sp. seems to occur sporadically in the upper subzone of the *M. limbata* Zone at Slemmestad.

The transition to the *A. expansus* Zone is discussed below.

Slemmestad. – The base of the *M. limbata* Zone is defined by the appearance of very abundant broad *M. limbata* types 3–4, coinciding – or almost so – with the appearance of *Dysplanus acutigenia acutigenia*, abundant *Niobe* (*Niobella*) cf. *plana*, *Nileus depressus depressus*, *Raymondaspis* cf. *limbata*, *Lonchodomas volborthi volborthi*, and rather frequent *Symphysurus* spp. At the same time, *M. simon*, *M. limbata* type 2, *Niobe lindstroemi*, *Nileus depressus glazialis* and *N. depressus* subsp. A disappear. Single specimens of *Dysplanus acutigenia acutigenia* and *Lonchodomas volborthi volborthi* have, though, been found in the uppermost part of the *M. simon* Zone, and a few broad-axed pygidia of *M. simon* type were encountered in bed interval M-9–M-13. First occurrence of *Megistaspis limbata* type 5 (i.e. 's.str.') is in bed M-9.

Two informal subzones are recognized, but it is again emphasized that the boundary between them most likely is positioned stratigraphically slightly above the lower–upper

subzonal boundary defined for the Komstad Limestone (see section on ecostratigraphy).

The lower subzone includes bed interval M-7–A-6 and the upper subzone interval A-7–A-28. The lower subzone is characterized by *M. limbata* types 3–5 (a single specimen assigned to type 5 is from bed A-11), common *Nileus depressus depressus*, common *Niobe* cf. *plana* (lower part), *Lonchodomas volborthi volborthi*, *Dysplanus acutigenia acutigenia* (a single atypical specimen is from bed A-26), and common *Symphysurus* spp. The upper subzone is defined by the appearance of *Asaphus* (*Asaphus*) *lepidurus*, coinciding, or nearly so, with the appearance of *Megistaspis limbata* type 6 [the 'type-allocation' of the megistaspid pygidia from beds A-4–A-6 is dubious, because of poor preservation], *M. (Megistaspidella) acuticauda* (s.l.), *Lonchodomas volborthi schmidti* n.subsp., and *N. depressus depressus* with very steep librigenae. A single pygidium of *M. (Rhinoferus) cf. hyorrhina* was encountered in bed A-8. The first representatives of *Illaeus* cf. *forficatus* and later *I. sarsi* (bed A-28 only) appear close to the top of the *M. limbata* Zone.

The faunal pattern within the *M. limbata* Zone of Slemmestad closely matches the trilobite distribution sketched for Sweden by Tjernvik (1980). He reported broad *M. limbata* types from the base of the zone, *Dysplanus acutigenia*, *Asaphus lepidurus* (from the middle of the zone), *Megistaspis hyorrhina* (scarce), *M. aff. acuticauda*, *Raymondaspis limbata* with a short pygidial axis, *Symphysurus* n.sp., from the lower part of the zone, *Niobella* n.sp. (identical to the type that is common in the *Megistaspis* Limestone and *Asaphus* Shale of Norway, i.e. *Niobe* (*Niobella*) cf. *plana*), *Nileus glazialis glazialis* and *Nileus glazialis* subsp. 2. *N. glazialis sensu* Tjernvik is here transferred to *N. depressus*, and *N. 'glazialis glazialis'* is identified with *N. depressus* subsp. A, while subsp. 2 *sensu* Tjernvik is identified with *N. depressus depressus*. *N. d. depressus* is typical of the *M. limbata* Zone. The specimens from the lower subzone somewhat resemble *N. depressus glazialis* (= *glazialis* subsp. 1 Tjernvik, 1980), whereas those from the upper subzone have steeper librigenae and eventually may be separated in an ecophenotype of its own. T. Tjernvik (personal communication, 1983; see Fig. 145) also indicated that *N. 'glazialis* subsp. 2' shows up in the middle of the *M. limbata* Zone.

The material of *Ampyx* spp. from the *M. limbata* Zone of the Finngundet core, referred to by Tjernvik (1980), has been examined. Most of the specimens are too damaged to be assigned to species, but all preserved features support an assignment of the material to *Lonchodomas volborthi schmidti* n.subsp.

Kunda Stage

ASAPHUS (ASAPHUS) EXPANSUS Zone

The *A. expansus* Zone is 0.20 m thick at Skelbro, 2.7 m in the Killeröd area, 0.9 m at Fågelsång, and 1.9 m or more in the

Fig. 36. Range chart, lower members of the Huk Formation, Djuptrökkudden, Slemmestad. Legend as for Fig. 5.

Slemmestad section. Within these sections, the zone is represented by, respectively, the upper 6 cm of bed +13 plus bed +14 (Fig. 33); the upper 6 cm of bed +22 (at Killeröd) to the lower 8 cm of bed 9 (at Killeröd site b) (Fig. 34); bed 18 to the lower 4 cm of bed 25 (Fig. 35); and by bed interval A-28 to at least A-57 (upper boundary not defined by the present study) (Fig. 36).

Skelbro. – The *Asaphus expansus* Zone is defined by the appearance of *Asaphus acuminatus* in association with *Niobe tjernviki* n.sp., *Ampyx nasutus*, *Cnemidopyge costatus* n.subsp. A, *Megistaspis extenuata*, *Gog explanata*, *Nileus armadillo*, and common occurrence of *Illaeus fornicatus* n.sp. and *Nileus latifrons* n.sp. Moreover, the basal interval contains several undescribed species not present in the subjacent zones, and ptychopygids are very common. *Cyclopyge umbonata* also occurs sparsely at the base of the zone. Bed +14 is much less fossiliferous, but *A. acuminatus* and rare specimens of *N. armadillo* have been encountered.

Ampyx nasutus, *Megistaspis extenuata*, *Nileus armadillo* and illaenids also appear at the base of the *A. expansus* Zone in Sweden, and *Asaphus* and *Niobe* (*Niobe*) become common at the same horizon.

The limestone of the *A. expansus* Zone of Bornholm is readily recognized in the sections (and museum collections), being almost black. The lower part is highly fossiliferous and could be called coquinoid. The transition to the overlying conglomerate is not exposed at Skelbro, but by comparison to the Vasegård-1 drill-core it appears that only very little limestone (0–0.10 m), if any, is missing.

There is a considerable hiatus between the Komstad Limestone and the overlying *Dicellograptus* Shale, the lower part of which belongs to the *D. multidens* Zone (Bergström & Nilsson 1974), and it is conceivable that some limestone has been removed by erosion.

Killeröd. – The lower boundary of the *A. expansus* Zone (in the upper part of bed +22) is marked by a profuse occurrence of *Nileus armadillo*, but several other trilobites make their first appearance at the base of the zone as well, such as *Niobe tjernviki* n.sp., *Ampyx nasutus*, *Dysplanus centrotus*, *Illaeus fornicatus* n.sp., *I. sarsi*, and, immediately above the base, *Nileus latifrons* n.sp. This pattern is almost similar to the Skelbro section, except that *N. latifrons* n.sp. there is common from just below the *A. expansus* Zone.

Fossils are infrequent in the main part of the *A. expansus* Zone at Killeröd, but the interval is characterized by *Nileus armadillo* and *Ampyx nasutus*, both of which also continue into the next zone, as well as *N. latifrons* n.sp., *Illaeus fornicatus* n.sp., *I. sarsi*, *Dysplanus centrotus*, and, sporadically, *Asaphus acuminatus* and *Megistaspis elongata*. Many of these species are characteristic constituents of the *A. expansus* Zone in Scandinavia (Jaanusson 1957; Tjernvik 1972; Johansson 1980; present study).

Fågelsång. – The base of the *A. expansus* Zone is defined as at Skelbro by the appearance of *Asaphus acuminatus*, which

also at Fågelsång is associated with abundant *Nileus armadillo*, *N. latifrons* n.sp., *Niobe tjernviki* n.sp., and profuse abundance of *Cyclopyge umbonata* (rare at Skelbro). Less common are *Megistaspis* (*Megistaspidella*) *extenuata*, *M. (M.) cf. triangularis*, *M. (Megistaspis) geminus* n.sp., *Nileus implexus* n.sp., *Gog explanata*, and, questionably, *Cnemidopyge costatus* subsp. A.

There is no doubt that the local base of the *A. expansus* Zone corresponds to the lower boundary defined at Skelbro and Killeröd, despite the occurrence of surprisingly 'young' species in the underlying beds 1–9 (see above discussion of the *M. limbata* Zone). When all trilobite species are revised, the *A. expansus* boundary will appear much more conspicuous on the range chart, as beds 18–20 contain an unusually diverse trilobite fauna. The majority of the famous Fågelsång 'Orthoceras limestone' fauna (Angelin 1854, 1878) originates from this thin interval. The *Cyclopyge*-rich level constitutes the base of the *A. expansus* Zone, but not the base of the limestone, as assumed by some authors (C. Poulsen 1936; Regnéll 1960).

The lithology of the basal *A. expansus* Zone is nodulous with coquinoid coarse-grained limestone intercalated in a shaly matrix, i.e. it resembles the Lysaker Member of Oslo, and the boundary interval is easily identified in the field. Samples are also readily recognized in museum collections.

The middle part of the *A. expansus* Zone was not accessible for sampling, and the trilobite yield was generally very low above the base of the zone. *Asaphus acuminatus* ranges to bed 21 and is then replaced by *Asaphus* sp. A, which continues to the middle of bed 25; no other trilobites have been encountered in bed interval 21–25 so far. *Asaphus* sp. A is possibly identical to the '*Asaphus* n.sp.' of Johansson 1980, reported from the upper part of the *A. expansus* Zone of Sweden, but the material is too poorly preserved to confirm this conjecture. The assignment of this bed interval to the *A. expansus* Zone therefore remains tentative.

Slemmestad. – The *A. expansus* Zone at Slemmestad is defined by the appearance of *A. expansus* itself, coinciding with the appearance of *Megistaspis elongata* and *Dysplanus centrotus*, both of which are characteristic of the *A. expansus* Zone in Scandinavia (Tjernvik 1972; Jaanusson 1957). Several species, diagnostic of the *M. limbata* Zone, disappear just below the *A. expansus* Zone, viz. *M. limbata* type 6, *Dysplanus acutigenia acutigenia*, and *Asaphus lepidurus*. *Illaeus cf. fornicatus* n.sp. enters slightly below the base of the *A. expansus* Zone, in the same way as at Skelbro. *I. sarsi* turns up in bed A-28, immediately below the zone, but is otherwise a characteristic and frequent faunal element of the *A. expansus* Zone, as in Sweden (Jaanusson 1957; Tjernvik & Johansson 1980). *A. expansus* is most frequent in the upper half of the zone. In addition to the mentioned species *Megistaspis acuticauda*, *Niobe schmidtii* (scattered), and single specimens of *Platillaenus* sp. aff. *ladogensis*, *Lonchodomas volborthi schmidtii* n.subsp., *Nileus armadillo*, and *Asaphus cf. incertus* have been found. Several of these species are characteristic constituents

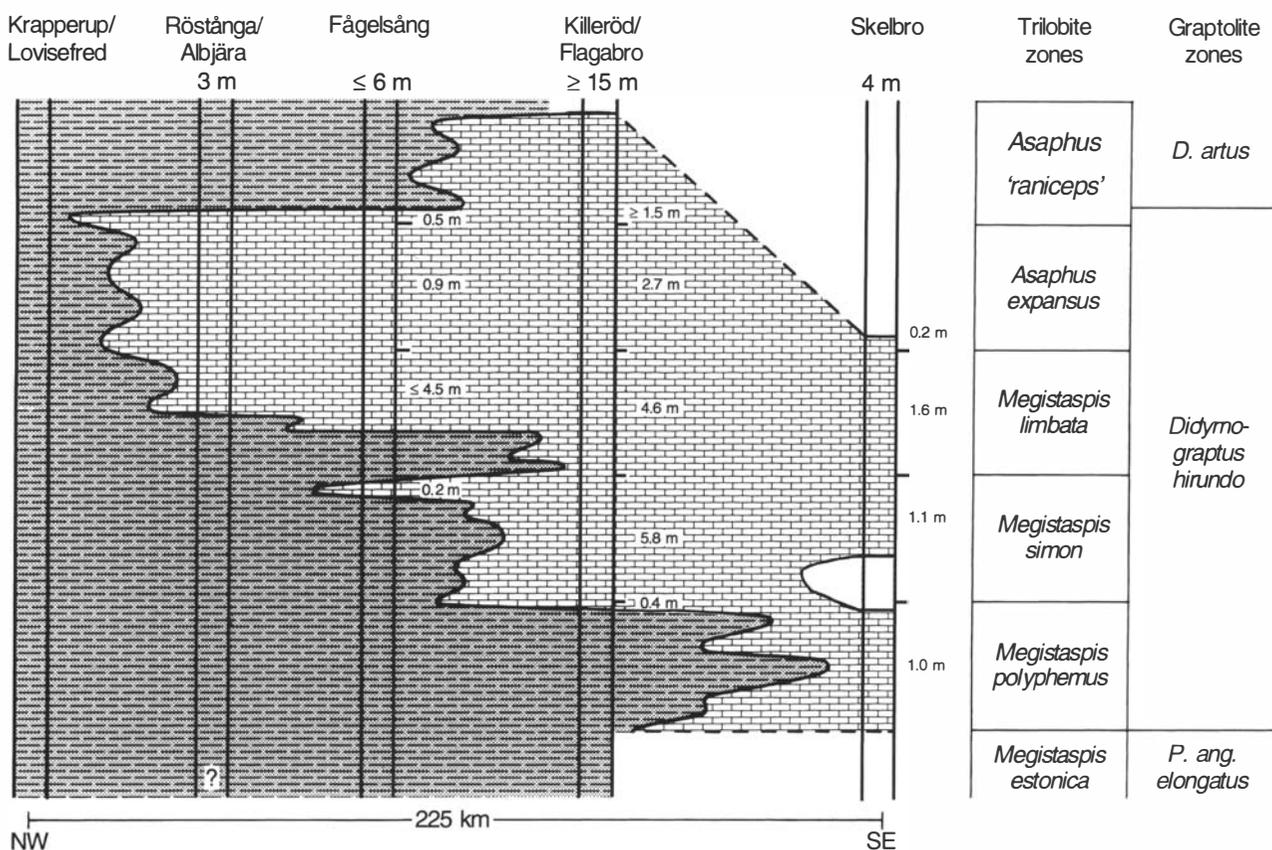


Fig. 37. Stratigraphy of the Komstad Limestone in a diagrammatic cross-section from Bornholm to NW Scania. The exact age of the top part of the Komstad Limestone at Killeröd/Komstad in SE Scania is currently unknown. Conodont dating of a single sample from 0.15 m below the top suggests a high level within the *A. 'raniceps'* Zone or an age corresponding to the *M. obtusicauda* Zone (Table 4).

of the *A. expansus* Zone of Sweden (Bohlin 1960; Jaanusson 1957; Tjernvik 1956). The fauna is comparatively diverse in the lower part of the zone, while the upper part is dominated by frequent *A. expansus*, *I. sarsi* and a ptychopygid, these three found mostly as complete specimens.

ASAPHUS (*ASAPHUS*) 'RANICEPS' Zone

The *A. 'raniceps'* Zone is more than 1.2 m thick at Killeröd site b, and 0.5 m at Fågelsång, where it is capped by graptolitic shales. Within these sections the zone is represented by, respectively, the upper 0.14 m of bed 9 to bed 0 (Fig. 34) and by bed interval 25 (main upper part) to 29 (Fig. 35).

The zone is undoubtedly much thicker in the Komstad region of SE Scania, but the upper part of the Komstad Limestone is poorly exposed in the area. Judging from conodont dating, the top of the Komstad Limestone, immediately below the Upper *Didymograptus* Shale at Killeröd site c, belongs to a high level within the *A. 'raniceps'* Zone but may even be within the *M. obtusicauda* Zone (see remarks below). This limestone, 0.65 m thick, plus the limestone exposed in the Killeröd Canal, representing 1.2 m of strata, should most likely be added to the *A. 'raniceps'* Zone, which thus totals

more than 3 m – and these discontinuous sections are separated by intervals of unknown thickness. It is estimated that the *A. 'raniceps'* Zone is about 4–5 m thick in the Killeröd area.

The *Asaphus 'raniceps'* Zone of Slemmestad has not been investigated, and the boundary towards the *A. expansus* Zone is not fixed. However, the boundary is marked by a sea-level lowstand event in all parts of Scandinavia, and the so-called 'Porambonites bed' in the Oslo region very likely signals this event. Provided that this assumption is correct, the base of the *A. 'raniceps'* Zone coincides with the base of the Svartodden Limestone, which entails that the entire *A. expansus* Zone is included in the present study. An examination of museum material from the Svartodden Limestone showed the presence of *Asaphus 'raniceps'*, *A. striatus*, *Illaeus aduncus*, and other elements typical of the *A. 'raniceps'* Zone.

Killeröd. – The *A. 'raniceps'* Zone is defined by the appearance of *Asaphus striatus* and *Illaeus schuberti* n.sp., but also *A. 'raniceps'*, *Illaeus aduncus* and *Stygina* sp. are confined to this zone. *Asaphus acuminatus* disappears at the top of the *A. expansus* Zone. The latest representatives of *A. acuminatus* occur associated with the first representative of *Stygina* sp. in

the middle of bed 9 at site b, and it is very likely that the entire bed 9 in fact belongs to the *A. 'raniceps'* Zone.

Niobe tjernviki n.sp. and *Ampyx nasutus* are rather frequent, whereas only a few specimens of *Megistaspis (Megistaspidella)* cf. *acuticauda* and *M. (Heraspis)* cf. *heroica* have been found. Several trilobite species of 'young affinity' remain to be revised. Agnostid trilobites are very abundant in some beds.

A. 'raniceps', *I. aduncus* and *M. (H.) heroica* are characteristic of the *A. 'raniceps'* Zone of Sweden (Jaanusson 1957; Bohlin 1960; Johansson 1980). *A. striatus*, as well as *I. aduncus*, also occur in the Svartodden Limestone of the Oslo region.

A study of the limestone above bed 0 is in progress. In the canal east of Killeröd, 1.2 m of limestone containing *Asaphus 'raniceps'* is exposed. The interval does not seem to overlap the limestone exposed at Killeröd site b, although this remains to be finally verified.

No trilobites have so far been found in the very top of the Komstad Limestone at Killeröd site c. The conodont content of an unaltered limestone sample (Table 4) suggests an age corresponding at least to the *Eoplacognathus variabilis* – *Microzarkodina ozarkodella* Subzone, i.e. probably a rather high level within the *A. 'raniceps'* Zone (see Löfgren 1985). The presence of *Protopanderodus robustus* with a well-developed anterior basal 'hook' (cf. Löfgren 1978) indicates that the level may even correspond to the *Eoplacognathus suecicus* Zone, but the index species itself has not been found. The *E. suecicus* Zone is traditionally correlated with the *M. obtusicauda* trilobite Zone (Jaanusson 1982).

Fågelsång. – The large *Asaphus 'maxima'* turns up in the middle of bed 25, replacing *Asaphus* sp. *A. Asaphus 'maxima'* is considered a close relative of *A. 'raniceps'* and is very likely an ecophenotype of that species. Accordingly, its presence is taken to indicate the *A. 'raniceps'* Zone.

A. 'maxima' is fairly common in bed interval 25–29; a juvenile specimen from bed 30 most likely also belongs to *A. 'maxima'*. The correlation of the interval with the *A. 'raniceps'* Zone is supported by the presence of *Iliaenus schuberti* n.sp. and *Nileus implexus* n.sp., both of which are typical of the *A. 'raniceps'* Zone in SE Scania.

Table 4. Conodont content of unweathered limestone sample ('nodule') from 0.15 m below top of the Komstad Limestone at Killeröd site c. Determinations by J.A. Rasmussen, Copenhagen.

<i>Baltoniodus medius</i>	6 specimens
<i>Dapsilodus mutatus</i>	1 specimen
<i>Drepanoistodus</i> sp.	2 specimens
<i>Microzarkodina ozarkodella</i>	9 specimens
<i>Periodon aculeatus</i> subsp.	2 specimens
<i>Polonodus</i> sp.	1 specimen
<i>Protopanderodus robustus</i>	23 specimens
Indet.	4 specimens
In total	48 specimens

The bewildering report of '*Megalaspis limbata*' from the limestone beds at the base of the Upper *Didymograptus* Shale (Ekström 1937) is probably based on misidentification of an *Asaphus 'maxima'* pygidium.

Notes on other localities in SE Scania

The Komstad Limestone is 9.5 m thick at Gislövshammar. A specimen of *M. simon* in the collections of the University of Lund is labelled 'Lower limestone bed at Gislövshammar', which is in accordance with the lithology of the sample. A poor pygidium that I collected from the basal limestone bed may represent *M. polyphemus*, but the identification remains tentative. The upper limestone bed at Gislövshammar, which has been sampled, is dominated by orthocone cephalopods and ptychopygids, but *Asaphus acuminatus* also occurs. The scanty information indicates that the limestone at Gislövshammar probably spans an interval from around the *M. simon* – *M. polyphemus* Zonal boundary to a level within the *A. expansus* Zone.

Samples collected by Funkquist 1915–1917 (see Funkquist 1919) from the uppermost part of the Komstad Limestone at Tommarp are calcarenitic and rich in orthocone cephalopods and ptychopygids, but also contain *Asaphus acuminatus*, *Megistaspis (Megistaspidella) extenuata*, *M. (M.)* cf. *spinulata* and *Nileus armadillo*. The uppermost limestone at Tommarp must therefore represent the *A. expansus* Zone.

Remarks on the previous biostratigraphical correlations of the Komstad Limestone and Huk Formations

Komstad Limestone. – The correlation of the Komstad Limestone has been commented upon by Tullberg (1883a, b), Holst (1892), Grönwall (1916), Funkquist (1919), C. Poulsen (1936, 1960), Ekström (1937), Regnéll (1960), Jaanusson (1960), Tjernvik (1960), V. Poulsen (1965, 1966), and Stouge (1975). A majority of these authors correlated the unit with the *Limbata* and Lower *Asaphus* limestones (of Moberg 1890), which, generally speaking, is confirmed by the present study. Tullberg (1883a, b) recognized that the limestone of SE Scania is older than the limestone at Fågelsång, but he probably did so for the wrong reasons, as *Megalaspis planilimbata* was listed from SE Scania. This misunderstanding (see also Funkquist 1919) was perhaps rooted in findings of *Megistaspis* sp. B. Ekström (1937) reported *M. limbata* from the upper part of the limestone at Fågelsång, which must be due either to a miscorrelation of strata or to confusion with *Asaphus 'maximus'*.

Many previous authors have attached importance to *Ptychopyge appplanata* as indicative of the 'Lower *Asaphus* limestone' (e.g., Holst 1892 [whose collections have been examined]; C. Poulsen 1936, 1960). Ptychopygids are, however, common even at lower levels and cannot at present be used

for correlation, as they are in need of a thorough revision. '*Ptychopyge applanata*' is a *nomen nudum* (Jaanusson 1956c).

The *Cyclopyge stigmata* Zone of V. Poulsen (1965) is here interpreted as a local sub-biozone of Bornholm, spanning the lower part of the *M. polyphemus* Chronozone, and there is no hiatus above it (cf. C. Poulsen 1936, and V. Poulsen 1966). The *C. umbonata* [*stigmata*] level of Bornholm was by C. Poulsen (1936) compared to the *Cyclopyge* level reported from Fågelsång by Moberg (1907). This correlation is incorrect (see also V. Poulsen 1965), and the *Cyclopyge* level of Fågelsång does not represent the basal Komstad Limestone at this locality (cf. C. Poulsen 1936; Regnéll 1960).

Stouge (1974, 1975) established a local conodont zonation for the Komstad Limestone of Bornholm. A lower interval (equivalent to beds -21 to -15) was correlated with the *Paroistodus originalis* Zone *sensu* Lindström (1971). The main upper part of the formation (equivalent to beds -14 to +10) could not be assigned to any Swedish zone, while the top (beds +11 to +13) was separated as the *Eoplacognathus variabilis* Zone, taken to represent the base of the Kunda Stage. The outlined conodont zonation is in conflict with the trilobite stratigraphy, especially regarding the lower part of the succession, but will not be discussed here, as revision is in progress by Stouge. The lower boundary of the *E. variabilis* conodont Zone consistently extends below the base of the *A. expansus* trilobite Zone in western sections, i.e. Skelbro, Killeröd and Slemmestad (compare Finngrundet core Löfgren 1985); conodont data from Stouge (1974, 1975), Hedvall (1982), Nyman (1982) and Rasmussen (1989, 1991).

Huk Formation. – The trilobite fauna of the Huk Formation was described by Brögger (1882); the biostratigraphical affinities have been discussed by Lamansky (1905), Størmer (1953), Jaanusson (1960), and Wandås (1984). Some of the trilobites mentioned from the Svartodden Limestone by Størmer (1953) were discussed by Bohlin (1955, 1960) and Jaanusson (1960). Other faunal groups are discussed by Öpik (1939), Spjeldnæs (1953), Berry (1964), Kohut (1972), and Rasmussen (1991).

Asaphus expansus was listed from the upper metre of the Lysaker Member and the lower metre of the succeeding Svartodden Limestone by Størmer (1953); Brögger (1882) also mentioned this species (or 'a closely related one') from the 'Porambonites bed'. *A. expansus* ranges from the middle of the Lysaker Member but is certainly most common in the upper part of the unit. The Svartodden Limestone has not been investigated, but the 'Porambonites bed', which is only 0.2 m thick at Slemmestad, most likely represents the very base of the *A. raniceps*' Zone (see discussion of zone above).

The trilobites listed by Jaanusson (1960, p. 345), including *Dysplanus acutigenia*, most likely came from the upper part of the Hukodden Limestone and cannot, as claimed, have been derived from the base of the unit.

A regional conodont zonation of the Huk Formation was established by Kohut (1972). A more detailed conodont

study has recently been published by Rasmussen (1991). The new conodont biostratigraphy is based on the sections at Djuptrekkodden, Slemmestad, and thus allows for a refined calibration of the conodont and trilobites zones (see Rasmussen 1991).

Correlation of the trilobite and graptolite zonations

The Komstad Limestone of Bornholm is bounded by major hiatus, and the conditions do not contribute to the correlation of the trilobite and graptolite zonations. The stratigraphy of the under- and overlying units is discussed by C. Poulsen (1922, 1936), V. Poulsen (1966), Jansson (1979) and Bergström & Nilsson (1974).

The Komstad Limestone of SE Scania succeeds the graptolitic Tøyen Shale without any obvious sedimentational break. The upper part of the SE Scania Tøyen Shale contains *Isograptus gibberulus* (Moberg 1892a; Moberg *in* Holst 1892; Törnquist 1901; Tjernvik 1960), which is characteristic of the lower part of the *D. hirundo* graptolite Zone (Nilsson 1984). The base of the Komstad Limestone is close to the *M. polyphemus* – *M. simon* trilobite zonal boundary. The onset of limestone deposition in SE Scania, at Hälleklis in Västergötland (Tjernvik 1956), and at Slemmestad thus appears contemporaneous, as far as can be established.

There is a considerable hiatus above the Komstad Limestone in SE Scania, although it is less extensive in the Komstad area than hitherto assumed and there is most likely no break at Kivik in NE Scania. The upper limestone bed at Tommarp and Gislövshammar is within the *A. expansus* trilobite Zone and is succeeded by the Killeröd Formation, probably representing the *Glyptograptus teretiusculus* graptolite Zone (S. Bergström 1973; Månsson 1993). The upper part of the Komstad Limestone at Killeröd is within the upper part of the *A. raniceps*' trilobite Zone, or even higher, and is overlain by 3 m of Upper *Didymograptus* Shale at Killeröd, of which the uppermost metre is correlated to the *Didymograptus murchisoni* graptolite Zone (S. Bergström 1973; see also Nilsson 1951). A sparse fauna from the lower part, excavated in connection with the present work, is poorly preserved but probably also represents the *D. murchisoni* Zone (J. Maletz, Berlin, personal communication, 1993). The break between the limestone and the overlying shale thus at the most spans the upper part of the *Didymograptus bifidus*' and the lower part of the *D. murchisoni* graptolite Zones.

The Komstad Limestone at Fågelsång is sandwiched between graptolite shales, but its lower boundary is not exposed and was faulted out in the Fågelsång drill-core (Hede 1951). The highest level preserved in the core belongs to the *D. hirundo* graptolite Zone (Lindholm 1991). The strata exposed at Loc. E22 represent a level in between the Tøyen Shale of the Fågelsång drill-core and the Komstad Limestone at Loc. E21a. The conodont fauna of the limestone at Loc.

E22 (Table 3) is comparable to the fauna present in the light grey impure limestones of Bornholm, i.e. the *M. simon* Zone. The graptolite fauna of the enclosing shales, comprising *Tetragraptus* (*T.*) *cf. serra*, *T. (T.) bigsbyi*, *Phyllograptus cor*, *Pseudoclimacograptus* sp., *Glyptograptus* sp., and extensive didymograptids (Cooper & Lindholm 1985, p. 284), represents either the upper *Didymograptus hirundo* or the lower part of the *D. 'bifidus'* Zone, according to these authors. However, the bentonite levels at 463–464 m in the Lovisefred core of NW Scania (Nilsson 1984) seem to match bentonite horizons in the lower part of the Komstad Limestone at Loc. E21a (Figs. 24, 38), which entails that the discussed strata represent a level below the upper third of the *D. hirundo* graptolite Zone. *T. bigsbyi* is common between 466 m and 475 m in the Lovisefred core (Nilsson 1984). *P. cor* is present between 462 m and 469 m (Nilsson 1984), but Cooper & Lindholm (1985) reassigned the specimen at 469.26 m to *Phyllograptus* sp. aff. *cor*, which leaves a range only between 462 m and 463.12 m. The first confidently identified diplograptid graptolite was found at 465.5 m in the Lovisefred core (K. Lindholm, personal communication, 1991), which should be compared to the presence of *Glyptograptus* sp. at loc. E22.

It appears that the succession at Loc. E22 in broad terms corresponds to the middle of the *D. hirundo* graptolite Zone and presumably ties to an interval somewhere between 466 m and 469 m in the Lovisefred core. The occurrence of diplograptids are indicative of Darriwilian-1, and the section may be assumed to be close to (and may straddle) the Yapeenian–Darriwilian boundary. It is plausible that the Ya–Da boundary approximates the *M. simon* – *M. limbata* trilobite zonal boundary, which coincides with a significant sea-level rise.

The Upper *Didymograptus* Shale overlying the Komstad Limestone at Fågelsång represents the *D. 'bifidus'* graptolite Zone (Ekström 1937; Hede 1951; Jaanusson 1960; Skevington 1967). Much speculation has been advanced on the key section at Fågelsång (Størmer 1953; Jaanusson 1960; Skevington 1967), partly as a consequence of the confusing (and erroneous) report of *M. limbata* in the limestone just below the shale (Ekström 1937). Correlation of bentonite levels between Fågelsång and the Lovisefred core of NW Scania (Nilsson 1984 and personal communication, 1985), demonstrates that the Arenig–Llanvirn boundary correlates to the uppermost part of the limestone and most likely coincides with the transition to the Upper *Didymograptus* Shale (Fig. 38). Graptolites are, however, absent in the Lovisefred core between 457.6 m and 454 m, and Nilsson (1984) defined the base of the *D. 'bifidus'* graptolite Zone by the first appearance of *D. obscurus*. In theory, the Arenig–Llanvirn boundary may therefore be anywhere between 457.6 m and 454 m in the Lovisefred core, although Cooper & Lindholm (1990, p. 523) emphasized that the first occurrence of *D. obscurus* usually is just below the series boundary. The base of the *A. expansus* trilobite Zone seems to correlate to a level just below the

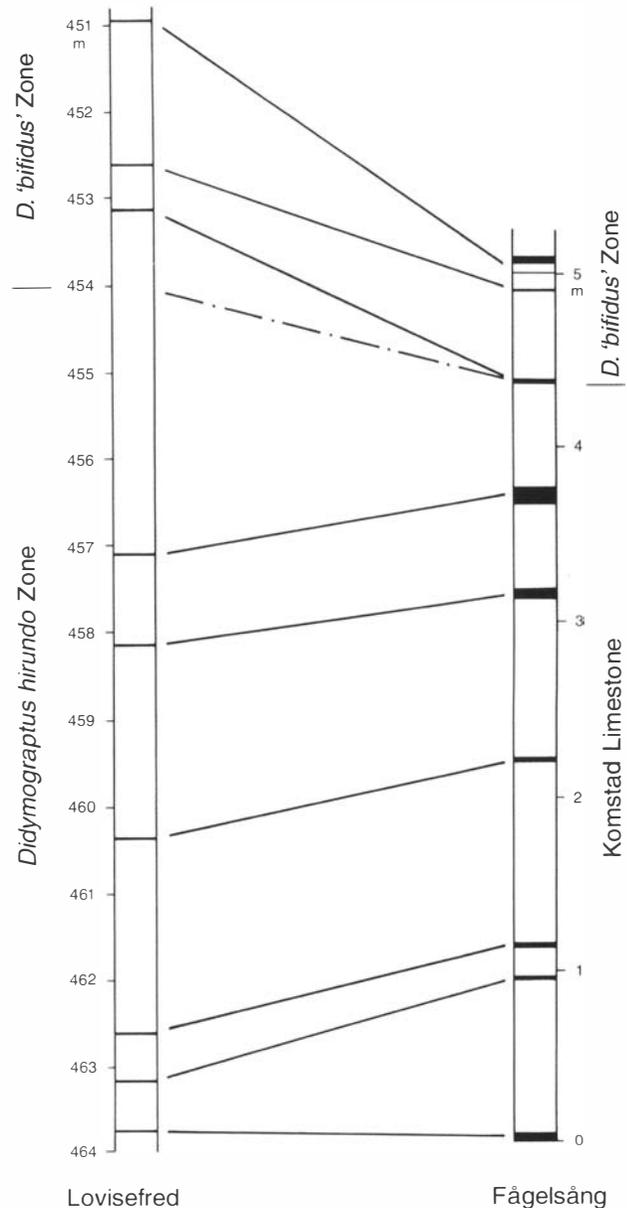


Fig. 38. Correlation of bentonite levels between Fågelsång and the Lovisefred core. Note the difference in vertical scale. The correlation suggests that the *D. hirundo*–*D. artus* graptolite zonal boundary correlates with the very top of the Komstad Limestone at Fågelsång or a level just below. Data from Lovisefred include unpublished information kindly placed at the authors disposal by Dr. R. Nilsson, as well as information from Nilsson (1984). The bentonite levels cannot be traced into the limestone of SE Scania or Bornholm.

bentonite at 458.1–458.2 m in the Lovisefred core (cf. Fig. 38), which makes the lack of graptolites between 457.6 m and 454 m striking, as the absence coincides with the inferred shallow-water conditions during the *A. expansus* and basal part of the *A. 'raniceps'* trilobite Zones (see discussion of palaeoecology below). This circumstantial evidence, combined with the remarks of Cooper & Lindholm (1990) re-

garding the range of *D. obscurus*, is taken as support of the correlation suggested by Nilsson (1984). It is believed that there is a common cause for the reappearance of graptolites in the Lovisefred core and the return to shale deposition in the Fågelsång area, namely a rapid rise of sea-level. The Arenig–Llanvirn boundary signals the sea-level rise (cf. Fortey *et al.* 1990).

The correlation of the Arenig–Llanvirn boundary with a level slightly above the *A. expansus* – *A. raniceps* trilobite zonal boundary is in accordance with the data from northern Öland, presented by Skevington (1967). Extending the interpretation from Fågelsång to northern Öland, the base of the *D. bifidus* graptolite Zone corresponds to the ‘safe’ base of the zone as recognized by Skevington, or, less likely, the ‘D-level’ 18 cm below (see Skevington 1967, Textfig. 73). The basal part of the *A. raniceps* trilobite Zone is either missing or strongly condensed in the Hälludden section. Again, it is logical to infer that the incoming of graptolites in the Hälludden section reflects a sea-level rise.

Depositional environment of the Komstad Limestone

Regional setting

The Ordovician of interior Baltoscandia is dominated by rhythmically bedded, monotonous, condensed limestones, collectively called ‘Orthoceratite limestone’. Graptolite mudstones were deposited along the peripheral parts of the platform to the west and south. The deposition took place in an extremely starved epicontinental sea, covering large parts of the Baltoscandian craton, and the Ordovician succession outside the Caledonides is normally less than 200 m thick. A virtually unfaulted, partly buried Ordovician platform cover is preserved in a continuous cover from the Isle of Öland in the Baltic Sea through the Eastern Baltic area and into the Moscow Basin (Fig. 39), whereas only isolated outliers of the

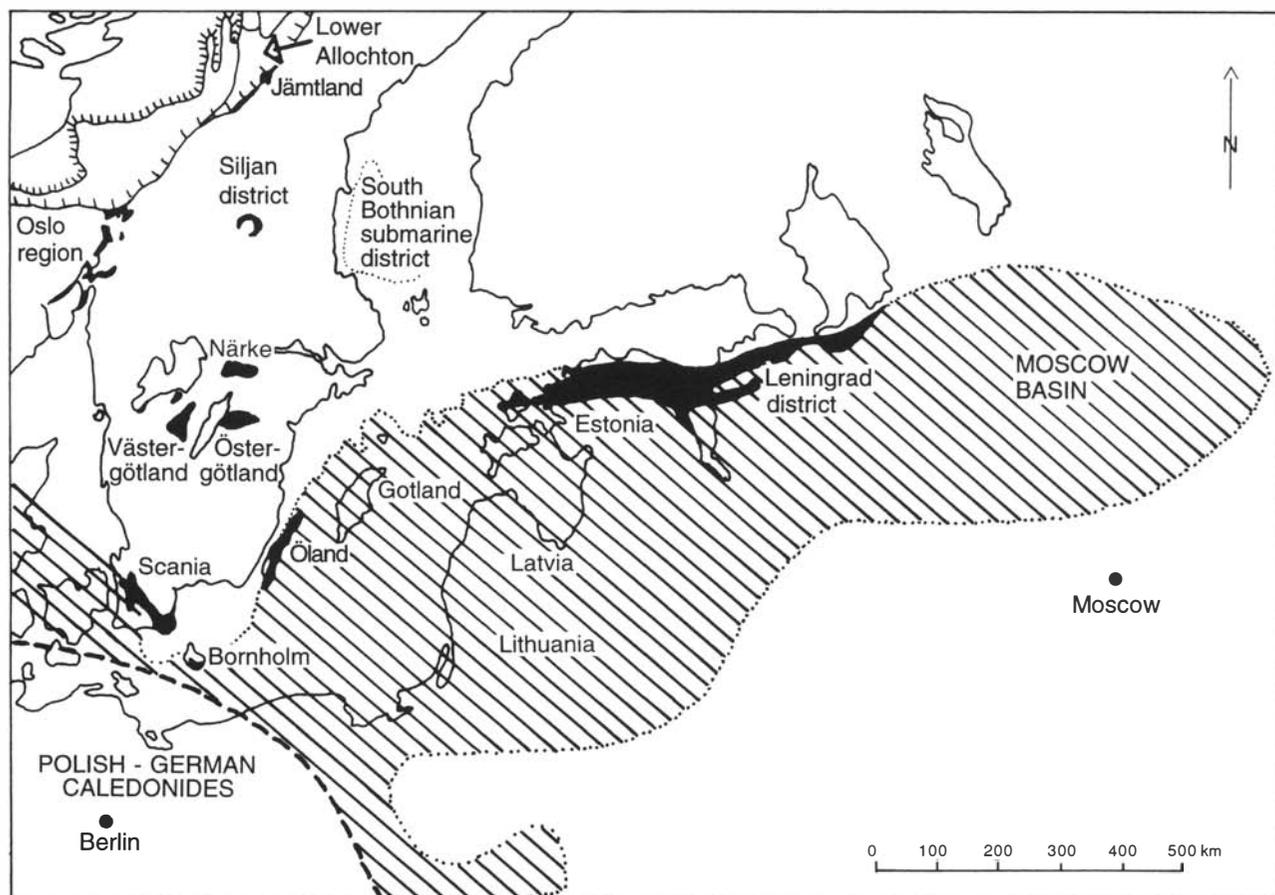


Fig. 39. Map showing the distribution of Ordovician deposits in Baltoscandia: outcrop areas (black), subsurface and submarine Ordovician (shaded). On mainland Sweden the entire outcrop areas of the Cambro–Silurian outliers are shown, of which Ordovician rocks occupy only a minor part. The pre-Permian of subsurface Denmark is dissected into numerous fault blocks, but no detailed maps on the distribution and thickness of the Lower Palaeozoic succession have been worked out as yet. The indicated distribution is therefore approximate only. (Modified after Jaanusson 1982.)

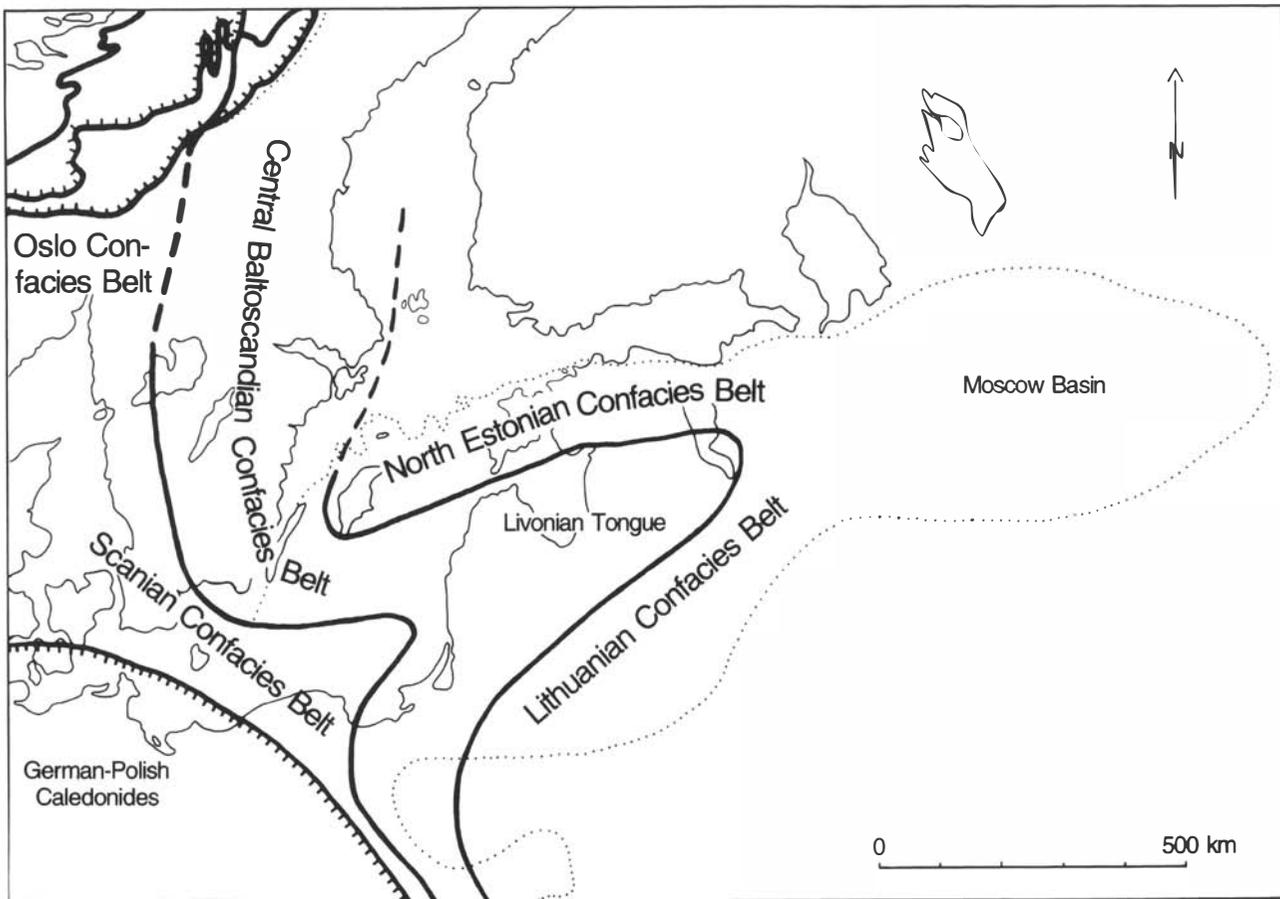


Fig. 40. Map showing approximate boundaries of the Ordovician confacies belts in the Baltoscandia region. (Modified after Jaanusson 1982; see also Männil 1966 and Jaanusson 1976.)

once continuous Lower Palaeozoic cover are preserved to the west in the mainland of Sweden, in the Bothnian Bay, in southern Norway, on the Island of Bornholm and in subsurface Denmark. Remnants of the platform cover are also preserved in a slightly tectonized brim along the Caledonian mountain chain to the west.

There is a consensus of opinion that the Lower and Middle Ordovician 'Orthoceratite limestones' of Baltoscandia represent temperate- to cool-water carbonates (Jaanusson 1973; Lindström 1984). The palaeolatitude is estimated to about 40–60° S during the early part of the Ordovician (Bergström & Noltimier 1982; Cocks & Fortey 1982; Torsvik *et al.* 1992), with a shift towards the palaeoequator during the Ordovician, leading to bahamitic carbonate deposition in the late part of the period (Jaanusson 1973; Webby 1984; Torsvik *et al.* 1992).

So-called confacies belts have been recognized within the Ordovician of Baltoscandia (Fig. 40). The array of facies belts in a crude way reflects the topography of the Ordovician basin, but the supply of terrigenous material from southern and western sources also influenced their character and position.

Lindström (1979, 1988; see also Lindström & Vortish 1983) regards the Ordovician topography as roughly identical to the present-day Precambrian topography. This conjecture may by and large be correct, but the geomorphological analyses of Lidmar-Bergström (1985, 1988) and Elvhage & Lidmar-Bergström (1987) suggest that the gentle doming of south-central Sweden (*vide* Lidmar-Bergström 1985, Fig. 1) was formed by Tertiary uplift. This interpretation is undermining the notion of a central Swedish Ordovician carbonate-production platform (Lindström 1979, Figs. 1, 5). Whatever the circumstances, there is little doubt that the Baltoscandian craton was exceptionally flat in Ordovician time and with strongly limited clastic supply.

There are two schools of opinion concerning palaeobathymetry of the 'Orthoceratite limestone' facies. Lindström (1963, 1971, 1979, 1984, 1988) has argued for a considerable depth of deposition, of the order of several hundred of metres, while others have put up a case for a shallow-water deposition, generally within the photic zone (see Jaanusson 1982). I consider a depth of deposition within less than about 100 m most likely.

The location of the boundary between the eastern 'Orthoceratite limestone' and the western graptolitic shale facies has been interpreted as resulting from 'competitive sedimentation' (Jaanusson 1982). The transition from shale to limestone deposition was, according to this hypothesis, determined by the influx of winnowed carbonate mud from the carbonate-production areas to the east in 'competition' with the influx of terrigenous mud from island chains in the Caledonian mobile belt to the west. Thus, the limestone belt transgressed westwards at times of high carbonate production and eastwards at times of high clastic influx.

The notion of 'competitive sedimentation' is not supported by the present study. It appears that the distribution of limestones was governed mainly by the sea-level, with a downslope (westwards) migration of the limestone facies during lowstand periods, and vice versa during highstands. The clastic influx actually increased during periods with low sea-level, as the result of a lowered base level in the source areas, and maximum clastic influx was concomitant with the most widespread limestone deposition, i.e. contrary to the basic idea of 'competitive sedimentation'. It is, however,

probably correct that a major proportion of the lime-mud in the western facies belts was not produced *in situ*, but derived from more easterly situated carbonate areas, as envisaged by Jaanusson (1982), Lindström (e.g., 1979) and Lindström & Vortish (1983). If the rock-forming lime-mud was partly or largely allochthonous, the effect of a sea-level lowering could have been increased winnowing of lime-mud in the eastern facies belts, and thereby an increased supply to the western facies, but it is reasonable to assume that the carbonate production area also migrated westwards during lowstands.

Local setting

The Ordovician succession is about 30–40 m thick on Bornholm but gradually expands across Scania to reach more than 200 m in the extreme NW Scania (Fig. 41). It appears that this variation is a continuation of the condensation seen along the edge of the East European Platform in Poland (Modliński 1976, 1977, 1982), and the trend probably continues westwards along the Caledonian Front across south-

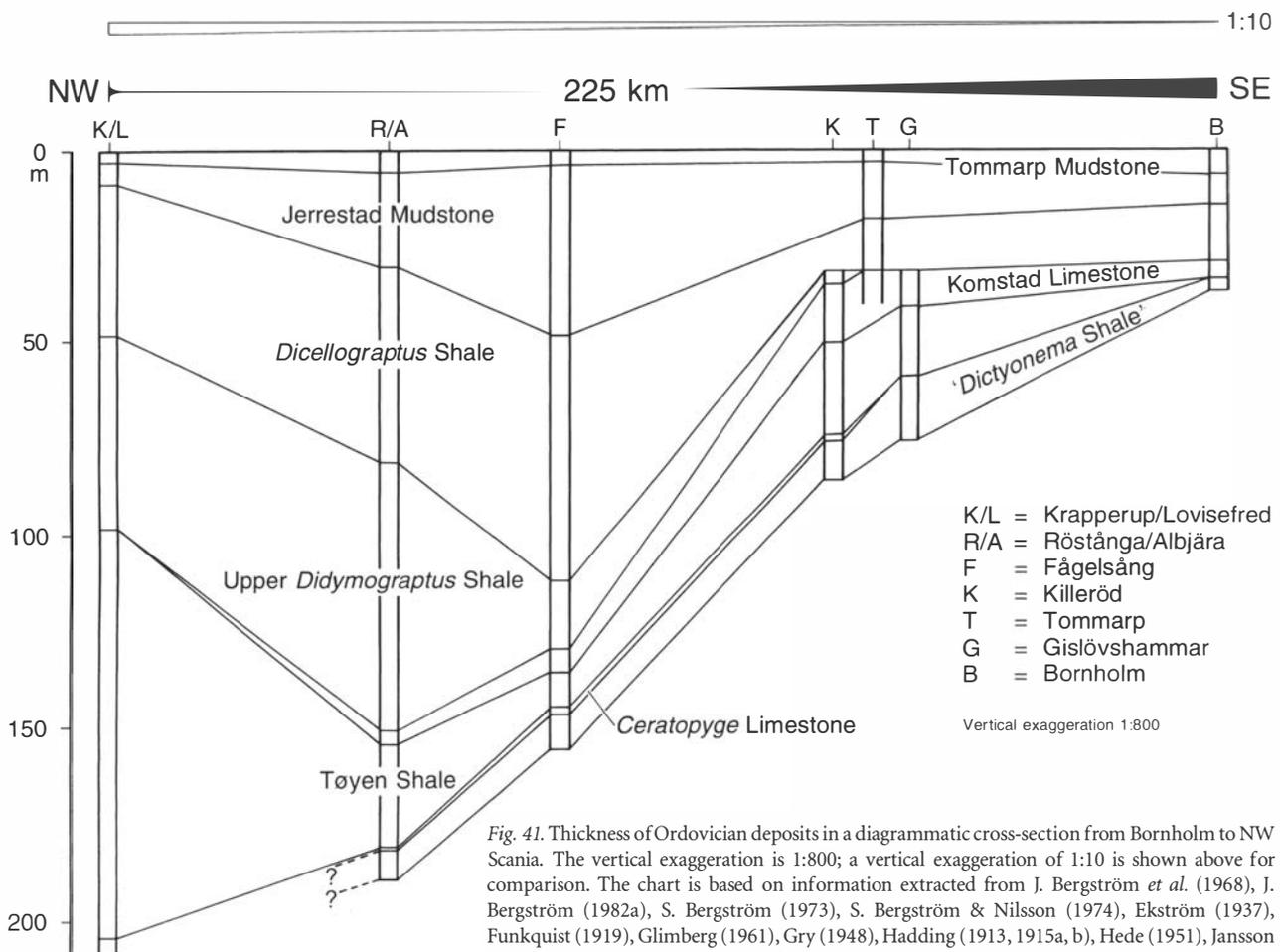


Fig. 41. Thickness of Ordovician deposits in a diagrammatic cross-section from Bornholm to NW Scania. The vertical exaggeration is 1:800; a vertical exaggeration of 1:10 is shown above for comparison. The chart is based on information extracted from J. Bergström *et al.* (1968), J. Bergström (1982a), S. Bergström (1973), S. Bergström & Nilsson (1974), Ekström (1937), Funkquist (1919), Glimberg (1961), Gry (1948), Hadding (1913, 1915a, b), Hede (1951), Jansson (1979), Lindholm (1981, 1991), Nilsson (1951, 1977, 1979, 1984, unpublished), Olin (1906), Pedersen (1989), V. Poulsen (1978), Tjernvik (1958, 1960), Troedsson (1918, 1920), Westergård (1944), and unpublished results from the drill cores Albjära-1 and Gislövshammar-2.

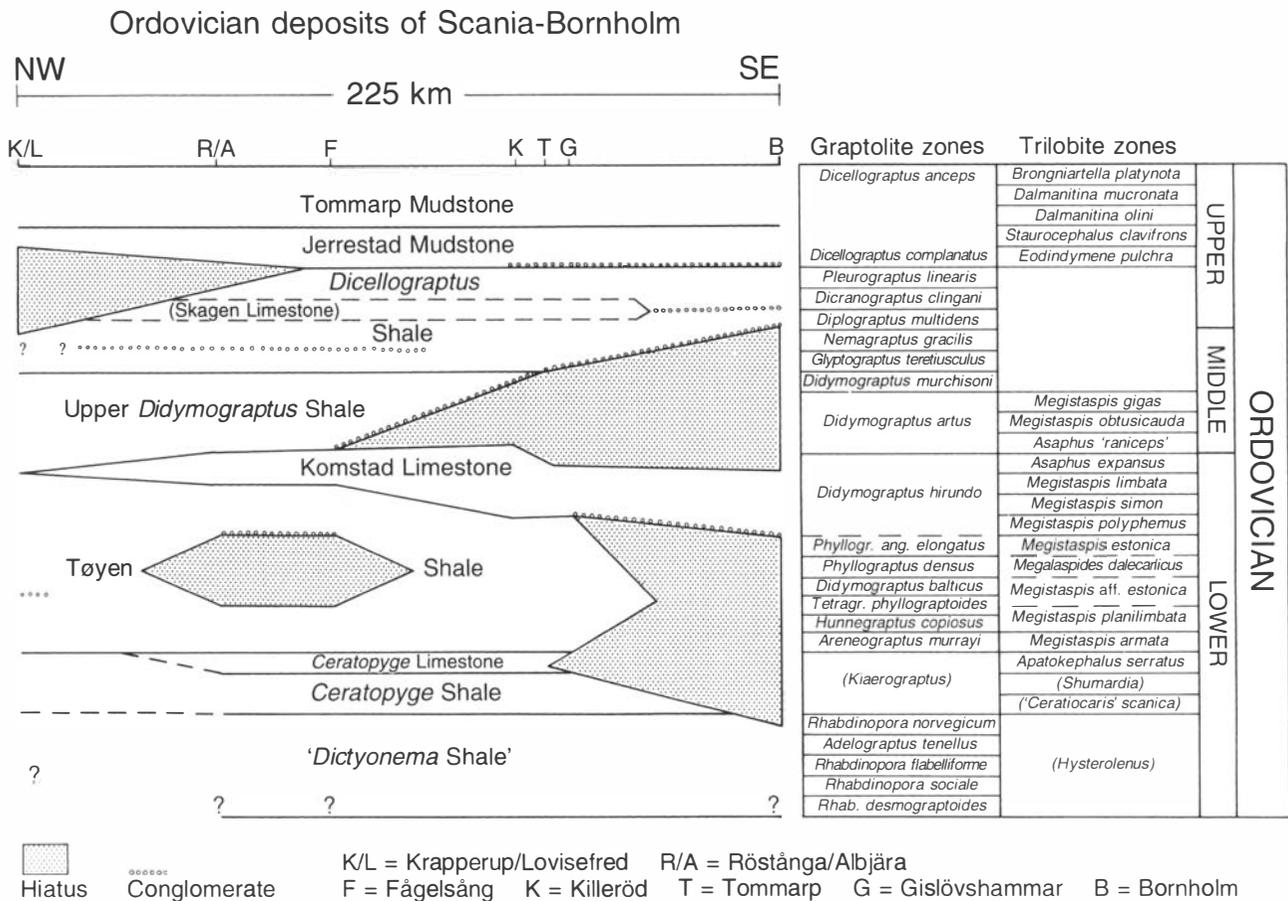


Fig. 42. Diagram of the Ordovician stratigraphy in Bornholm – NW Scania. The cross-section is based on information extracted from the same sources as for Fig. 41.

ern Denmark, judging from the condensed Ordovician successions encountered in the G-14 and Slagelse-1 wells (the Ordovician is represented in the Slagelse-1 well by the Tremadocian 'Dictyonema Shale' and about 3 m of Caradocian mudstone (C. Kock Clausen, Copenhagen, personal communication, 1988); G-14 reviewed by Piske & Neumann 1990).

The plate margin apparently exhibited a higher degree of isostatic mobility than the platform interior, and the thinning of the Ordovician succession along the southern plate edge is interpreted as reflecting diminished (or lack of) subsidence of the margin, combined with isostatic uplift during two periods. A first uplift occurred in the latest Tremadocian – early Arenigian and was associated with erosion of the Tremadocian in Poland (Modliński 1971), but the uplift seems to have affected the entire area southwest of the so-called 'Colonus trough' across central Scania, where strata of Billingen age are absent (Bornholm, Fågelsång-1, Albjära-1, G-14, Slagelse-1). A second and more prolonged uplift is inferred to have taken place during the late Llanvirnian, Llandeilian and early Caradocian; it caused a major

gap in the succession on Bornholm. This hiatus extends into SE Scania, gradually decreasing in extent towards the north (Fig. 42). The timing of the uplifts suggests a connection to the Finnmarkian and Taconian orogenic phases (Sandomirian and Lysogorska phases in Polish terminology, see Pozaryski 1977; Pozaryski *et al.* 1982).

Palaeoenvironment of the Komstad Limestone

The grey to blackish Komstad Limestone represents the only major limestone intercalation in the shale-dominated Scanian Confacies Belt (Fig. 40). The bulk of the unit is fine-grained (clay- or silt-fraction), but some intervals are calcarenitic (especially the *A. expansus* and *A. 'raniceps'* Zones). The clay content is typically 10–20% but reaches 40% in some intervals, and thin shale seams occasionally separate the limestone beds. Although accentuated by diagenetic processes, the shale intercalations were primary, as shown by the clay infilling of subjacent burrows. Likewise, the bedding

appears to be primary, as demonstrated by burrows, incipient mineralisation of some bedding planes, lags, etc., but it was also reinforced by diagenesis (cf. Bathurst 1987).

The substrate represented by the Komstad Limestone was a level-bottom environment, basically consisting of mud with a very small content of coarse material, composed by disintegrated skeletal parts (see thin-sections in Nørregaard 1907). Only the upper part of the Komstad Limestone at Skelbro and Killeröd and the basal part of the *A. expansus* Zone at Fågelsång, contain a fair proportion of skeletal grains (compare thin-sections shown by Hadding 1958, pp. 177–183). (The substrate, represented by the Hukodden Limestone at Slemmestad, contained a comparatively higher proportion of skeletal grains, and, paradoxically, this also appears to be the case for many of the limestone levels in the succeeding clay-rich Lysaker Member).

The Komstad Limestone is mostly highly bioturbated, although individual burrows commonly are difficult to discern, except if indicated by another colour of infilling or by pyritization; the intense bioturbation often produces a subtle mottled appearance of the limestone. The burrows do not cross preserved bedding planes, even incipient ones, but it is impossible to determine whether or not any bedding planes were destroyed by bioturbation at an early stage. Borings have been recognized only in the top of bed –21 at Skelbro; they are of the same type and age as the well-known amphora-shaped borings distinctive of the boundary interval between the Billingen and Volkhov Stages throughout Baltoscandia and eastern Russia (e.g., the ‘Flowery Sheet’ of Öland, see Lindström 1979). Sharply delimited boring-like bioturbation is seen at a few higher levels, notably within the *M. limbata* Zone, but these structures appear to bypass shells and are presumably firm-ground burrows.

The limestone of Bornholm and SE Scania exhibits vertical changes in degree of darkness, to a certain extent linked to grain size. The limestone at Fågelsång is almost black throughout. The colour variation of SE Scania and Bornholm appears connected to the oxygen content at the time of deposition, and in combination with the variable grain sizes it appears to reflect a variable energy level, in turn most likely connected with sea-level.

Palaeoecology

Sampling bias and taphonomy

The available trilobite material has been collected by bulk sampling from hard rock *sensu* Jaanusson (1979). It is not possible to estimate, even tentatively, how many specimens avoided detection and how many were destroyed during sampling. Most of the tiny fossils were discovered in the laboratory, including the bulk of the ostracodes. Intervals

containing many trilobites therefore automatically yielded many ostracodes as well. To avoid this bias, the ostracode density of Fig. 44 is indicated as average number of specimens per sample.

It is well-known that trilobites with a fragile or otherwise ill-suited skeleton in terms of preservation and sampling are greatly under-represented in the fossil record. This bias is definitely very important in the available material, as demonstrated by the fact that virtually all trilobites are represented predominantly by either cranidia or pygidia. There are, however, no means to correct or even quantify the error when it comes to trilobites whose skeletal parts have low preservational potential or easily break during sampling (e.g., because of strong convexity).

A crucial point in palaeoecology is whether the fossil material is *in situ* with regard to life environment. Several criteria influenced by transportation have been enumerated in the literature, notably degree of skeletal breakage, sorting, presence of articulated specimens or specimens in assumed life position, etc. (e.g., Fortey 1975b). In the actual case, the bulk of the Komstad Limestone consists of lithified fine-grained mud, and it is unlikely that large fossil grains could be transported without at the same time winnowing the sediment. Accumulations of fossils are present at a few levels, and it is possible that some of those have been transported (alternatively they may represent a ‘winnowed’ situation). However, it is a plausible conjecture that the ecological zones were very broad because of the low palaeoslope, and transportation for moderate distances thus would not disturb the overall picture. The low palaeoslope at the same time restrained the transportation mechanisms, and it seems unlikely that material was transported very far. In general, the degree of skeletal breakage is small, and there are no signs of sorting by size, hence there are no obvious reasons to believe that the fossils should not be in place.

Trilobite biofacies of the Komstad Limestone

Trilobite ecology is here treated at the genus level. This approach has its hazards, however, as different species of the same genus may have had quite dissimilar environmental preferences, which is illustrated by the discussion of *Nileus*. However, focusing on individual species requires a much larger database and a thorough taxonomic revision of all groups, and for the moment it is difficult to proceed beyond speculation regarding particular functions of single species. Because of the various taphonomic processes mentioned above, it is not possible to reconstruct the original trilobite communities accurately. An additional obstacle is the insufficient knowledge on trilobite ecdysis. It is therefore emphasized that the recurrent trilobite associations recognized are fossil assemblages, which are distorted relative to the original biome, and the term community is best avoided.

The palaeoecological interpretation is based on relative frequencies, as the sampling method employed obstructs strictly quantitative techniques (see also discussion by Jaanusson 1976, 1979). The approach has the advantage of being largely independent of the uneven sample sizes, but a few inherent pitfalls are mostly omitted from palaeoecological discussions. Thus it seems necessary to have at least some idea of the environmental significance of the taxa included, as the interaction between forms with different ecological requirements may create incidental and strongly misleading relative frequencies (e.g., pelagic versus benthic taxa). Likewise, a patchy or scattered occurrence affects relative frequencies in an unfortunate way, so that the vertical distribution of individual taxa cannot be compared in a consistent manner. In order to minimize these complex problems, the present approach is based on the four most common (and long-ranging) trilobite genera from the Komstad Limestone, namely *Nileus*, *Symphysurus*, *Megistaspis* (*Megistaspis*) and *Geragnostus* (*s.l.*), which account for approximately 60% of the total trilobite material. The frequencies are calculated by counting all identifiable skeletal parts from each analysed interval, no attempt was made to correct for over-representation caused by growth or the adding up of different skeletal parts from the same individuals. The rare complete specimens rate as two counts.

Palaeoecology is in most cases addressed either by an empirical recognition of recurrent patterns (e.g., Fortey 1975b), or by a statistical treatment of the data (e.g., Ludvigsen 1978). The latter approach normally makes use of some kind of cluster or ordination analysis (see Shi 1993 for a review). The major advantage of statistical multivariate techniques is their capability of summarizing variation patterns of large, multi-dimensional data sets – their major drawback is the unavoidable alienation between the actual fossils and the statistical results resulting from a more or less impenetrable calculation process.

The available material comprises a few dominant long-ranging trilobite groups and several subordinate taxa occurring only in parts of the studied sections. Taxa limited to parts of the interval, and in particular those occurring in great abundance, such as *Cyclopyge*, will automatically influence the statistical analysis, and beds containing such species or genera become statistical ‘outliers’. For palaeoecological purposes it is therefore preferable to analyse groups with an extended range. In the present context it is essential to maintain as fine a resolution as possible, hence pooling of faunas from adjacent beds (in order to get a bigger database) is generally avoided. However, the material from some beds is actually too limited to be included in a mathematical treatment. For these reasons the present approach to palaeoecology is based on an empirical recognition of recurrent assemblages, whose boundaries are defined arbitrarily. This interpretation has subsequently been tested by running a detrended correspondence analysis on the data set (see Hill & Gauch 1980).

Definition of biofacies

The diagrams of relative abundance (Figs. 44–46) of the four most common trilobite genera in the Komstad Limestone reveal that these genera are unevenly distributed. A number of other trilobite groups actually follow the same pattern of occurrence in a fairly consistent way (see remarks on autecology below). Based on the diagrams, four trilobite assemblages are empirically recognized, characterized by, respectively, a relatively high abundance of smooth *Nileus*, *Geragnostus* (*s.l.*), *Symphysurus* and *Megistaspis* (*Megistaspis*). Intervals containing these benthic assemblages are referred to as *Nileus* biofacies, *Geragnostus* biofacies etc. A fifth trilobite biofacies is defined by the patchy, but abundant occurrence of *Cyclopyge* (which is the fifth most common trilobite group of the Komstad Limestone). The *Cyclopyge* assemblage occurs superimposed upon the other assemblages and was most likely pelagic (cf. Fortey 1985).

The NILEUS biofacies. – Defined by dominance of *Nileus* (40–100%) and less than 15% *Geragnostus* (*s.l.*). *Nileus depressus* is uncommon (0–5% of the nileid species). *Symphysurus* may be very frequent (up to 50%) or absent; this apparently depended on substrate conditions. *Megistaspis* (*Megistaspis*) makes up a smaller part of the four genera, less than 15%, typically 2–5%. The total faunal density and diversity are very high for trilobites, brachiopods and ostracodes.

The GERAGNOSTUS biofacies. – Defined by more than 15% *Geragnostus* (*s.l.*) and common occurrence of *Nileus*. *Geragnostus* represents 15–85% and *Nileus* 20–60% of the assemblage; *Nileus depressus* is uncommon (0–20% of *Nileus*). *Symphysurus* may be very frequent (up to 40–50%) or absent; as for the *Nileus* biofacies this appears to relate to substrate conditions. *Megistaspis* (*Megistaspis*) accounts for less than 15%, and typically 0–10% of the four genera. The total faunal density and diversity are fairly high but lower than in the *Nileus* biofacies.

The SYMPHYSURUS biofacies. – Defined by dominance of *Symphysurus* (45–80%) and less than 15% *Megistaspis* (*Megistaspis*). ‘Smooth’ *Nileus* (i.e. exclusive of *N. depressus*) usually accounts for 0–15%. *Geragnostus* (*s.l.*) comprises around 10% or less of the four genera. The total faunal density and diversity are rather low; brachiopods and ostracodes occur only scattered.

The biofacies may be divided into two subtypes:

- 1 The *Symphysurus* biofacies *s.str.* with 65–80% *Symphysurus* and less than 25% *Nileus*, dominated by *N. depressus*.
- 2 The *Symphysurus*–*Nileus depressus* sub-biofacies with 45–55% *Symphysurus* and 35–45% *Nileus*, strongly dominated by *N. depressus schranki* n.subsp. (95–100% of *Nileus*).

It appears that the distribution of *Symphysurus* was greatly influenced by substrate conditions, with a maximum abundance in *muddy* shallow-water environments and total absence in more coarse-grained shallow-water environments. The pronounced link to muddy substrate of *Symphysurus* is the main reason for the strong variability of the relative frequencies in the individual biofacies, as the lower part of the *M. polyphemus* Zone at Skelbro, even if representing shallow-water *Nileus* and *Geragnostus* biofacies, contains an unusually low proportion of grains, and *Symphysurus* is very common.

The MEGISTASPIS (MEGISTASPIS) biofacies. – Defined by more than 15% *Megistaspis* (*Megistaspis*); typical *Megistaspis* assemblages contain 20–35% *Megistaspis*. *Symphysurus* may be relatively frequent (30–50%) but is rare in some intervals (0–15%). *Nileus* accounts for 15–50% and is by far dominated by *N. depressus schranki* n.subsp.; *Geragnostus* (*s.l.*) is rare (0–5%). The total faunal density and diversity are low, brachiopods are few, and nearly no ostracodes occur.

The CYCLOPYGE biofacies. – Characterized by frequent or extremely frequent occurrence of *Cyclopyge* (15–35% of the entire trilobite fauna). The total faunal density and diversity varies, but are typically high.

Correspondence analysis

The recognized biofacies do not represent discrete trilobite communities but reflect overlapping tolerance ranges of genera along an environmental gradient. Since the palaeoslope of the Baltoscandian carbonate platform was extremely low, the assemblage transitions are, as should be expected, gradual, and the definition of individual biofacies must therefore be tentative. In order to test the arbitrarily defined biofacies, a detrended correspondence analysis was performed, using the MVSP program (Kovach 1993). This statistical approach is preferential to a cluster analysis, as it presumes continuity in the data and does not force the faunules into discrete groups. The data points are rearranged in a multidimensional space, where the first axis represents the direction of principal variation, the second axis shows the second-most significant variation etc. The data matrix consists of all fossiliferous beds from the Skelbro and Killeröd sections (including site b and Gårdlösa) containing 10 specimens or more of the analysed taxa. Beds containing less than 10 specimens were pooled with adjacent beds or omitted. Two runs were executed, one with all beds included (Fig. 43A) and one excluding all beds above bed +22 of SE Scania (Fig. 43B). The latter experiment was performed since the limestone of the *A. expansus* and *A. raniceps*' Zones is coarse-grained and dominated by *Nileus* and *Geragnostus* (*s.l.*) (Fig. 46) and therefore deviate from the remaining beds. As it appears from both resulting diagrams (Figs. 43A–B), the

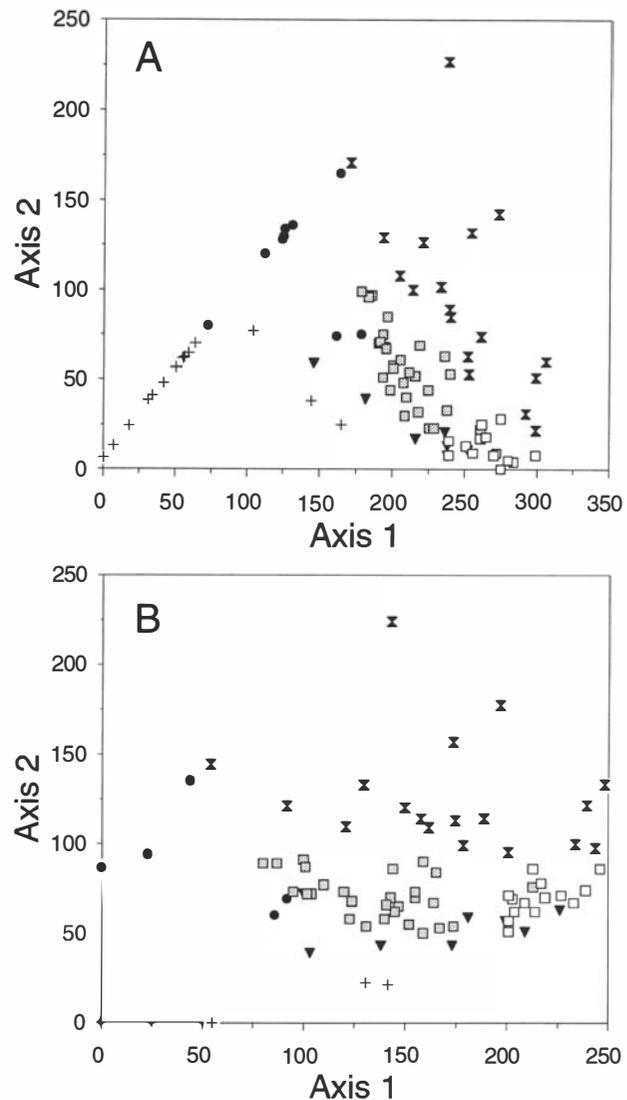


Fig. 43. Detrended correspondence analysis, Komstad Limestone samples, testing empirically recognized trilobite biofacies. The calculation is based on the genera *Megistaspis*, *Symphysurus*, *Nileus* (of which *N. d. schranki* n.subsp. is treated separately) and *Geragnostus* (*s.l.*). Legend: + *Geragnostus* biofacies, ● *Nileus* biofacies, ■ *Symphysurus* biofacies, □ *Symphysurus* – *N. d. schranki* n.subsp. biofacies, ✕ *Megistaspis* biofacies, and ▼ transitional *Geragnostus*/*Symphysurus* biofacies. The indicated biofacies are those empirically recognized. □A. Fossil material of the analyzed genera from all fossiliferous beds of the Skelbro and combined Killeröd sections, totalling 96 entries (beds or smaller intervals) containing 3993 specimens. Several beds from the upper part of the section at Killeröd contain only *Geragnostus* and 'smooth' *Nileus*, and the resulting markers lie on a straight line in the plot. The diagram shows position of beds on Axis 1 (accounting for 42.7% of total variation) versus Axis 2 (accounting for 14.1% of total variation). □B. Same approach, but excluding all beds above +22 of the Killeröd section (see text for discussion). The analysis includes 78 entries (beds or smaller intervals) containing 3508 specimens. Axis 1 accounts for 45.7% of the total variation, axis 2 for 16.4%.

The test shows that the empirically recognized biofacies can also be defined from a statistical analysis, but because of their intergrading nature the boundaries remain arbitrary.

empirically recognized assemblages plot reasonably consistently together, with some boundary problems between the *Geragnostus* and *Symphysurus* biofacies. The *Symphysurus*–*N. depressus* sub-biofacies clearly clusters away from the main *Symphysurus* group, and inferred deeper-water *Megistaspis* biofacies plot towards the upper right corner. All irregularities in the *Symphysurus*–*N. depressus* sub-biofacies cluster are represented by beds from the lower part of the upper subzone of the *M. limbata* Zone in the Killeröd section containing *Geragnostus* and *N. depressus serotinus* n. subsp.

It is likely that a statistically based definition of biofacies can be designed in the future; currently more material is sampled from all beds of SE Scania to enhance the resolution and increase the database. It is also surmised that *Ptychopyge* and raphiophorids can be included in due time, but at least the former appears to contain species with different ecological preferences, and it is thought premature to include the group in the analysis. However, a statistical treatment of the data is no panacea to remedy for the intergradational nature of the trilobite assemblages, and the definition of biofacies remains arbitrary.

Distribution and interpretation of the biofacies

Bed interval –21 to –17 at Skelbro, representing the lower half of the *M. polyphemus* Zone, is a convenient starting point for the interpretation of the trilobite biofacies (cf. Fig. 44). The conglomerate at the base of the Komstad Limestone and the lower 1 cm of the limestone on top of the conglom-

erate contain small-scale stromatolites; the conglomerate is quite glauconitic, whereas beds –21 and –20 have only a small content of glauconite grains. Bed –21 is a light grey, highly fossiliferous limestone; in the successive beds the fossil content decreases markedly to reach almost zero in bed –17, accompanied by an increasingly darker colour of the rock, and bed –17 is a blackish, pyritic calcilitite. These sedimentological changes are associated with the *Nileus*→*Geragnostus*→*Symphysurus*→*Megistaspis* biofacies series, which is inferred to signal a depth gradient.

Judging from the lithology, the associated fossil fauna, and the distribution of various species of *Nileus* (see discussion of autecology below) it appears that the *Symphysurus* biofacies *s.str.* represents shallower water than the *Symphysurus*–*Nileus depressus* sub-biofacies, as defined above. It is possible that a third *Symphysurus* sub-biofacies is characterized by the common presence of *Rhombampyx*, characterizing yet shallower water than the *Symphysurus* biofacies *s.str.*

It is acknowledged that water depth by itself exerts limited physical influence on organisms, but several essential biological parameters are more or less directly linked to depth, such as amount of food, dissolved oxygen, temperature, and, to a certain degree, substrate conditions. In combination, these factors distil into a depth gradient. The use of the unifying term *water depth* is therefore practical, especially since it is difficult or impossible to assess the influence of individual parameters.

Bornholm

Above bed interval –21 to –17 at Skelbro (Fig. 44), the relative abundance of *Symphysurus* again increases in beds –15 and

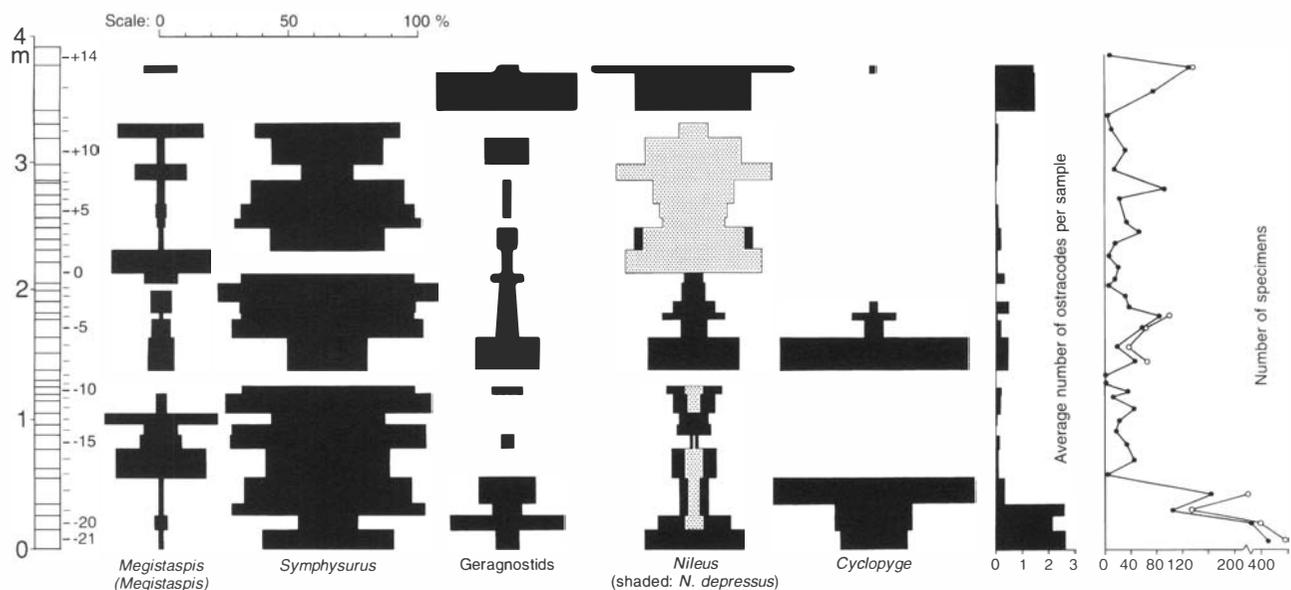


Fig. 44. Chart showing the relative abundance distributions of the genera *Megistaspis*, *Symphysurus*, *Nileus* and *Geragnostus* (*s.l.*) through the Komstad Limestone at Skelbro. The mentioned four genera make up 100%. The abundance of *Cyclopyge* is expressed as percentage relative to the total amount of these genera. Bed numbers are shown to the right of the column. Curve fragments with open symbols in curve to the right denote total number, including *Cyclopyge*.

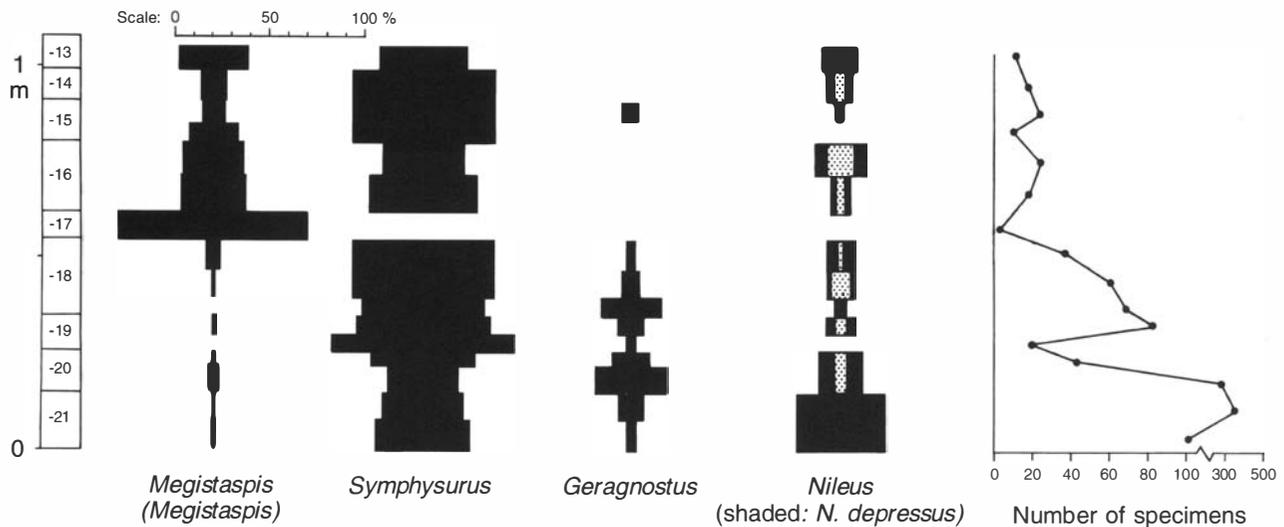


Fig. 45. Chart showing the relative abundance distributions of the genera *Megistaspis*, *Symphysurus*, *Nileus* and *Geragnostus* (s.l.) through the *M. polyphemus* Zone at Skelbro. The mentioned four genera make up 100%. The chart is based on the same data as Fig. 44, but the sampling intervals are made as short as possible, enhancing the resolution.

–14, but a *Megistaspis* biofacies reappears in bed –13, which seems to signal a moderate-shallowing–abrupt-deepening cycle. It is, though, of concern that the *M. polyphemus* Zone of Bornholm is strongly condensed as compared to the mainland of Sweden and the Finngrundet core, and unknown parts of the zone may not be represented in the Skelbro section. The recognition of abrupt ‘events’ may therefore be artificial, as intermediate environmental oscillations may have escaped preservation. There is almost certainly a hiatus between the *M. polyphemus* and *M. simon* Zones of Bornholm. Because of the condensation, a reprocessing of the data was attempted, analysing smaller intervals defined by the discontinuity surfaces. Because of the intense bioturbation, there is no point in examining narrower intervals, as they are thoroughly mixed. The more detailed chart (Fig. 45) still outlines a succession from *Nileus* via *Geragnostus* to *Symphysurus* biofacies in bed interval –21 to –19, but with more gradual transitions. The *Symphysurus* biofacies of bed –19 is succeeded by a *Geragnostus* biofacies in the lower part of bed –18, in turn replaced by a *Symphysurus* biofacies in the upper main part of bed –18, seemingly reflecting a gentle shallowing–deepening couplet. The latter *Symphysurus* biofacies is abruptly replaced by a *Megistaspis* biofacies in bed –17, suggesting a significant and, possibly, fast drowning. The sequence of environmental changes in the upper part of the *M. polyphemus* Zone is the same as revealed by Fig. 44.

The reappearance of a *Symphysurus* biofacies (Fig. 44) in the lower part of the *M. simon* Zone (beds –12 to –10), followed by a *Geragnostus* biofacies (beds –6, –7), coincides with a distinctly lighter colour of the rock and the presence of numerous shale intercalations. This may easily be interpreted as a period of shallowing, but a series of trilobite

biofacies is almost certainly missing between the top of *M. polyphemus* Zone and the base of the *M. simon* Zone, as a fairly extensive hiatus, comprising most of the lower part of the *M. simon* Zone and possibly the top part of the *M. polyphemus* Zone as well, is believed present at this level. The ‘smooth’ shallowing sequence across the biozonal boundary is, accordingly, probably incidental.

The *Geragnostus* biofacies of beds –6 and –7 is succeeded by a *Symphysurus* biofacies in the upper part of the *M. simon* Zone (beds –5 to –1), which in turn is abruptly replaced by a *Megistaspis* biofacies within bed 0, i.e. at the base of the *M. limbata* Zone. Simultaneously, the limestone becomes dark and the ‘shaly’ character disappears; a drowning event is inferred. *Symphysurus* is absent in this *Megistaspis* biofacies, whereas *Nileus depressus schranki* n. subsp. is relatively abundant, which is taken to signal deep water. Upwards, the *Megistaspis* biofacies is replaced by a *Symphysurus* biofacies in bed +2; the content of *N. depressus* decreases to bed +4, then increases, and a *Megistaspis* biofacies is again developed in bed +9, suggesting an increased depth of deposition. The overlying bed +10 contains a *Symphysurus* biofacies with a high content of *Geragnostus* (bed +10 is the base of the upper subzone of the *M. limbata* Zone). The faunal shift is accompanied by a sudden change to light grey colours, and the limestone is also comparatively coarse-grained. Above, the limestone becomes dark grey again, and there seems to be a return to a *Megistaspis* biofacies, but the assignment to biofacies is tentative, as the number of sampled specimens is low. In bed +13 the limestone again turns light grey, and the rock is distinctly coarse-grained (packstone?); fragments of *Girvanella* have been identified in thin sections. *Geragnostus* is very frequent in the lower main part of this bed. This biofacies is in turn followed by a *Nileus* biofacies in the

uppermost part of the bed, associated with an increasing abundance of fossils. This is the base of the *A. expansus* Zone. The top of the limestone at Skelbro is quite glauconitic (bed +14), which, though, is concealed by the black colour of the rock.

Ostracodes are common in bed interval -21 to -19, and in bed +13, with a smaller peak in abundance in beds -7 to -3 (Fig. 44). These intervals coincide exactly with inferred shallow-water biofacies. Small brachiopods are also most frequent in these intervals (not shown).

Cyclopyge occurs in the bed intervals -21 to -18, -7 to -4 and in the top of bed +13. The association with initial sea-level rises is remarkably consistent, although not all deepening periods were associated with influx of cyclopygids. The mechanism responsible for these cyclopygid 'invasions' remains enigmatic – see discussion of autecology below.

The trilobite diversity is conspicuously higher in the two intervals assigned to the *Nileus* biofacies than in the remaining part of the section, but because of the unfinished state of taxonomic revision, exact calculations of diversity cannot be presented.

SE Scania

The basal part of the limestone at Gårdlösa-1, possibly representing the top of the *M. polyphemus* Zone, is characterized solely by megistaspids (Fig. 46). The fossil density in the section is low, but it appears that the *Megistaspis* biofacies is succeeded by a *Symphysurus*–*N. depressus schranki* n.subsp. biofacies, in turn followed by a *Symphysurus* biofacies *s.str.* with a high content of 'smooth' *Nileus*. This pattern clearly indicates a shallowing. The section at Gårdlösa-1 is rather weathered, and the faunal changes are not accompanied by any reliable lithological changes. The *Symphysurus* biofacies is upwards replaced by a *Megistaspis* biofacies in bed C, which, however, has a rather high content of 'smooth' nileids. The inferred deepening is associated with an influx of cyclopygids (bed interval L–N; see Fig. 34).

Above the Gårdlösa-1 section follows approximately 4 m of limestone, which has not been accessible for sampling. The base of the next interval investigated is still within the *M. simon* Zone. The lower beds represent a *Symphysurus* biofacies, in bed -5 with abundant *Nileus orbiculatoides*, but few geragnostids [bed -5 of Killeröd = beds 6 and 7 at Gårdlösa-4a]. Bed -5 most likely represents maximum lowstand in the upper part of the *M. simon* Zone, analogous to beds -6 and -7 at Skelbro. A few cyclopygids have been found in bed -5 at Killeröd (and the corresponding beds 6 and 7 at Gårdlösa-4a, Fig. 34).

The *Symphysurus* biofacies interval is abruptly replaced by a *Megistaspis* biofacies in bed 0, i.e. at the base of the *M. limbata* Zone, associated with a change of lithology from light-coloured, impure limestone to dark-coloured, more compact limestone. The content of *Symphysurus* is very low

in the *Megistaspis* biofacies in the basal part of the *M. limbata* Zone, whereas *N. depressus schranki* n.subsp. is relatively common (note that biofacies of beds 0, +1, +5, +6 and +7 are defined on the basis of very sparse material). Beds +2 to +4 at Killeröd contain a *Symphysurus* biofacies; geragnostids are uncommon. A *Megistaspis* biofacies again takes over in beds +6/+7. These changes indicate a fairly high sea-level in the lower subzone of the *M. limbata* Zone, with a transient moderate shallowing in its lower middle part. The abundance of megistaspids decreases rather suddenly in beds +8/+9 at Killeröd, coinciding with reappearance of geragnostids; this is about the base of the upper subzone of the *M. limbata* Zone, and the faunal change indicates a seemingly abrupt shallowing. The fauna of beds +8/+9 may be classified as a transitional *Symphysurus*/*Geragnostus* biofacies, developing into a proper *Geragnostus* biofacies in beds +11/+12. The content of *Nileus depressus* is unusually high for a shallow-water biofacies but covers two subspecies, *N. d. schranki* n.subsp. and *N. d. serotinus* n.subsp., adapted to different substrates (Fig. 56; see also section below on autecology). The *Geragnostus* biofacies is in turn replaced by a *Symphysurus* biofacies in bed +13 and later a *Megistaspis* biofacies in beds +17/+18, signalling a deepening. The top of the *M. limbata* Zone is virtually barren in the Killeröd section, and biofacies type cannot be assessed.

The base of *A. expansus* Zone contains a *Nileus* biofacies, and the entire *A. expansus* Zone is characterized by shallow-water facies; minor fluctuations are indicated by varying proportions of *Nileus* versus *Geragnostus*, but the biofacies are defined on the basis of rather few specimens, and some of the changes may be fortuitous. To overcome this problem, material from adjacent beds were pooled to get a better statistical basis, but experience shows this to be a hazardous procedure, and it lowers the resolution. The *Nileus* biofacies is replaced by a *Geragnostus* biofacies in bed +27, but the content of *Nileus* increases again towards the top of *A. expansus* Zone, with an abrupt drop in the boundary interval towards the *A. 'raniceps'* Zone (beds 9–10 of Killeröd site b). Beds 9 and 10 are calcarenites and contain common gastropods as well as numerous cephalopods, and all evidence except the relative drop in *Nileus* points to a lowstand at the *A. expansus* – *A. 'raniceps'* boundary. The difference is most likely caused by the arenitic substrate (see discussion of autecology below). *Asaphus* and other incoming genera are comparatively common above this level (Fig. 34), and an analysis based only on *Megistaspis* (*Megistaspis*), *Symphysurus* (both of which are not present), *Geragnostus* and *Nileus* is insufficient. Judging from the lithology and the trilobite fauna in general, it is likely that the lower part of the interval was deposited at slightly greater depth than the upper part.

The succession exposed in the Killeröd Canal, which almost certainly succeeds the section at Killeröd site b, appears to represent somewhat deeper water, but the interval has not been studied systematically.

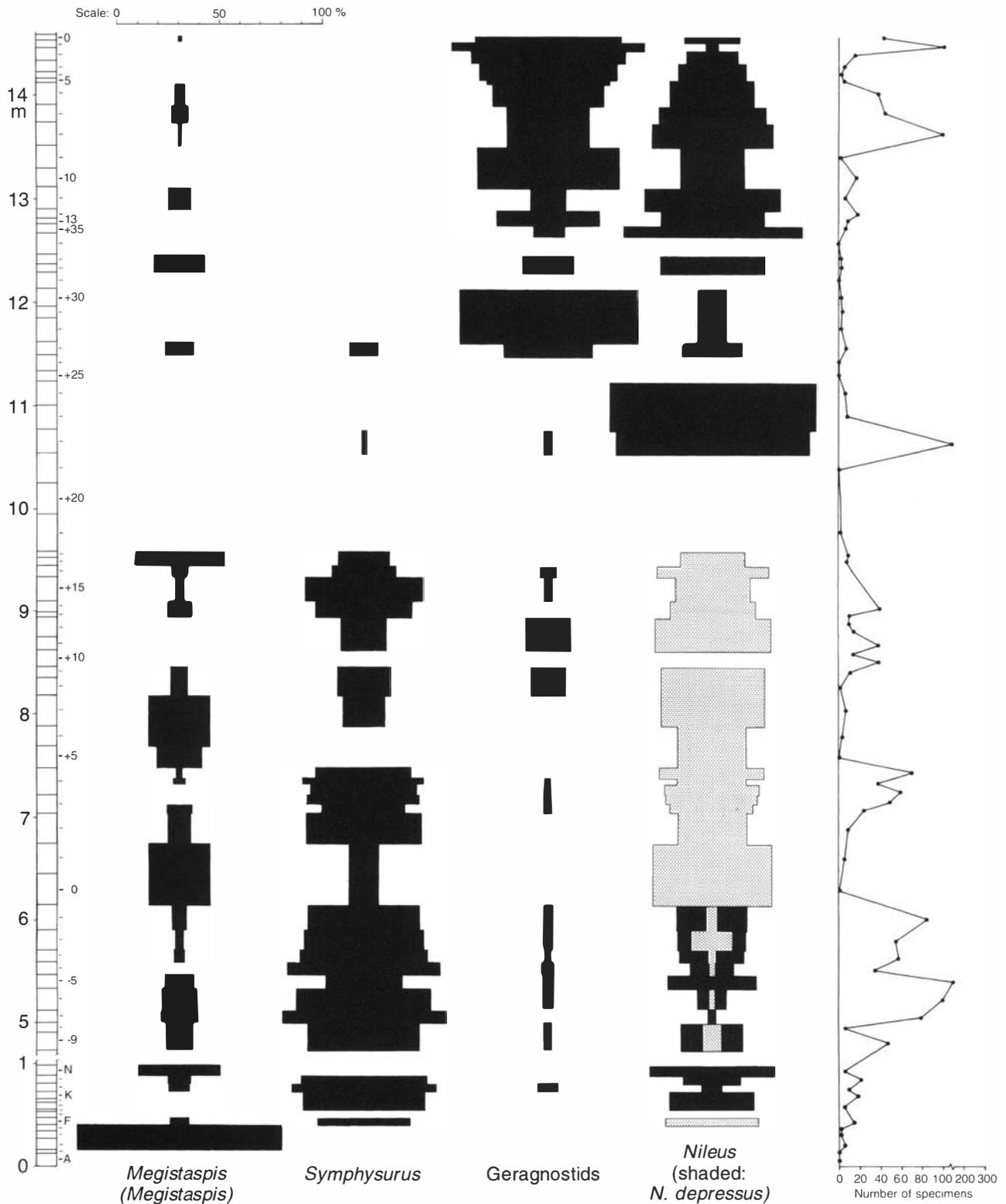


Fig. 46. Chart showing the relative abundance distributions of the genera *Megistaspis*, *Symphysurus*, *Nileus* and *Geragnostus* through the Komstad Limestone at Killeröd. The mentioned four genera make up 100%. For occurrence of *Cyclopyge*, consult Figs. 34 and 47. *Megistaspis* in beds 0–8 (top of section) covers *M. (Megistaspidella)* and *M. (Heraspis)*. The data base from beds +3 and +4 comprises a newly sampled large material, included neither in the taxonomical nor in the stratigraphical analyses. Observe the omission of non-sampled strata between the 1 and 5 m ticks. Each fifth bed number is indicated on the right side of the log.

Fågelsång

The section at Fågelsång yielded too few fossils to be analysed in detail. The lowermost part of the accessible section, which is close to the boundary between the lower and upper sub-zone of the *M. limbata* Zone, may belong to a *Symphysurus* biofacies. Upwards, the limestone contains many megistaspids and at face value belongs to a *Megistaspis* biofacies. However, this interpretation does not tally with the presence of *Niobe* (*Niobe*) and *Nileus armadillo*, pointing to a shallow-water environment. The base of the *A. expansus* Zone is highly fossiliferous and may be classified as transitional between a *Geragnostus* and a *Nileus* biofacies; cyclopygids are very common. Calcareous algae have been reported from the corresponding interval at Röstånga (Hadding 1958, pp. 180–181). The upper part of the succession cannot be assigned to any of the defined biofacies types.

Towards an ecostratigraphy

No exact definition of 'ecostratigraphy' has been agreed upon (see for instance Waterhouse 1976; Hoffman 1980, 1981; Martinsson 1980; Erdtmann 1976, 1984, 1986; Nielsen 1992a, b), and the concept needs clarification. Ecostratigraphy, as understood here, is a correlation of assumed coeval palaeoenvironmental changes between sections, as revealed by changes in the fossil faunal (or floral) composition. This definition of ecostratigraphy resembles the 'faunal dynamics' concept of Jaanusson (1976). The correlation of faunal changes obviously must be constrained by a biostratigraphic framework, and it is preferable to correlate series of shifts of variable magnitude instead of individual events. For different approaches to ecostratigraphy, see, e.g., Cisne & Rabe (1978), Rabe & Cisne (1980), Retallack (1978), and Boucot (1982). Provided that the palaeoecological information is detailed, regional or even global recognition of palaeoenvironmental shifts produces a more refined correlation than established via conventional biostratigraphy.

The present version of ecostratigraphy is not based on statistics (compare Cisne & Rabe 1978 and Rabe & Cisne 1980), because it is considered necessary to collect additional material from almost all of the studied sections, before implementing such techniques. However, even in its preliminary, somewhat primitive state, ecostratigraphy is a valuable adjunct to biostratigraphy with an enormous potential for calibrating and refining correlation. At the same time, some of the classical biostratigraphical pitfalls may be avoided, since the ecostratigraphical insight to a large extent discloses the basic faunal dynamics responsible for the observed faunal ranges ('causal biostratigraphy'). It is well-known that although biostratigraphy ideally correlates the appearance and extinction of taxa, it very often instead mirrors faunal migrations relating to palaeoenvironmental changes, or, as Retallack (1978, p. 82) phrased it: 'Once one has grasped the ecological bull by the horns, it is very difficult

to discern biostratigraphic zones anywhere...'. Even in its strict sense, however, biostratigraphy will mostly reflect palaeoenvironmental alterations, as there is a causal relation between extinctions/evolution and changing living conditions. Most major palaeoenvironmental changes will therefore, one way or the other, be reflected by the biostratigraphy, and an ecostratigraphical approach entails a different biostratigraphical philosophy.

The potential for detailed Early to Middle Ordovician ecostratigraphical correlation within the Baltoscandian area, reflecting sea-level oscillations, appears even more promising than elsewhere, because of the combination of palaeotectonic stability, the extremely flat ancient topography of the area, the low depositional rate and the absence of reef build-ups. The error introduced from diachronism of sea-level changes is far below any stratigraphical resolution, hence the changes are for all practical purposes synchronous throughout the region. The inferred isostatic adjustments of the southern plate edge are of a much different time-scale and skew the local sea-level on a first-order level. (The terminology *first-, second- and third-order sea-level changes* is adopted from sequence stratigraphy; see, e.g., Wagoner *et al.* 1988 for a review).

To unravel the eustatic component of ancient sea-level changes, it is necessary first to make local detailed studies in various regions, then to correlate between the regions, and finally to compare the obtained sea-level curves from the various continents in order to filter out local 'noise' (see also Fortey 1984). Following this strategy, the preliminary discussion of ecostratigraphy is divided into three successive parts, treating local, regional, and global conditions.

Local ecostratigraphy (Komstad Limestone)

The discussion of local ecostratigraphy is rendered difficult by the facts that the *M. polyphemus* Zone is developed in limestone facies only on Bornholm, that the major part of the *M. simon* Zone has not been accessible for sampling in SE Scania, and that the *A. expansus* Zone is largely cut out on Bornholm.

At a second-order level, the trilobite biofacies of the *M. polyphemus* Zone at Skelbro indicates a low sea-level within the lower part of the zone, and a high sea-level within the upper part. This pattern is also signalled by the graptolite fauna in the Tøyen Shale of SE Scania, where Tjernvik (1960) defined two Volkhovian zones, a lower *Didymograptus distinctus* – *D. 'patulus'* Zone and an upper *D. distinctus* – *Isograptus gibberulus* Zone. The presence of *Isograptus* points to deep-water conditions (Cooper *et al.* 1991). An abrupt influx of isograptids is also seen in the *D. hirundo* Zone of NW Scania (472–474 m interval of the Lovisefred core; Nilsson 1984).

The sequential order of trilobite biofacies in the upper part of the *M. simon* Zone and through the *M. limbata* Zone in SE Scania and Bornholm is strikingly similar (summarized in Fig. 47). The trilobite biofacies indicate a sea-level lowstand

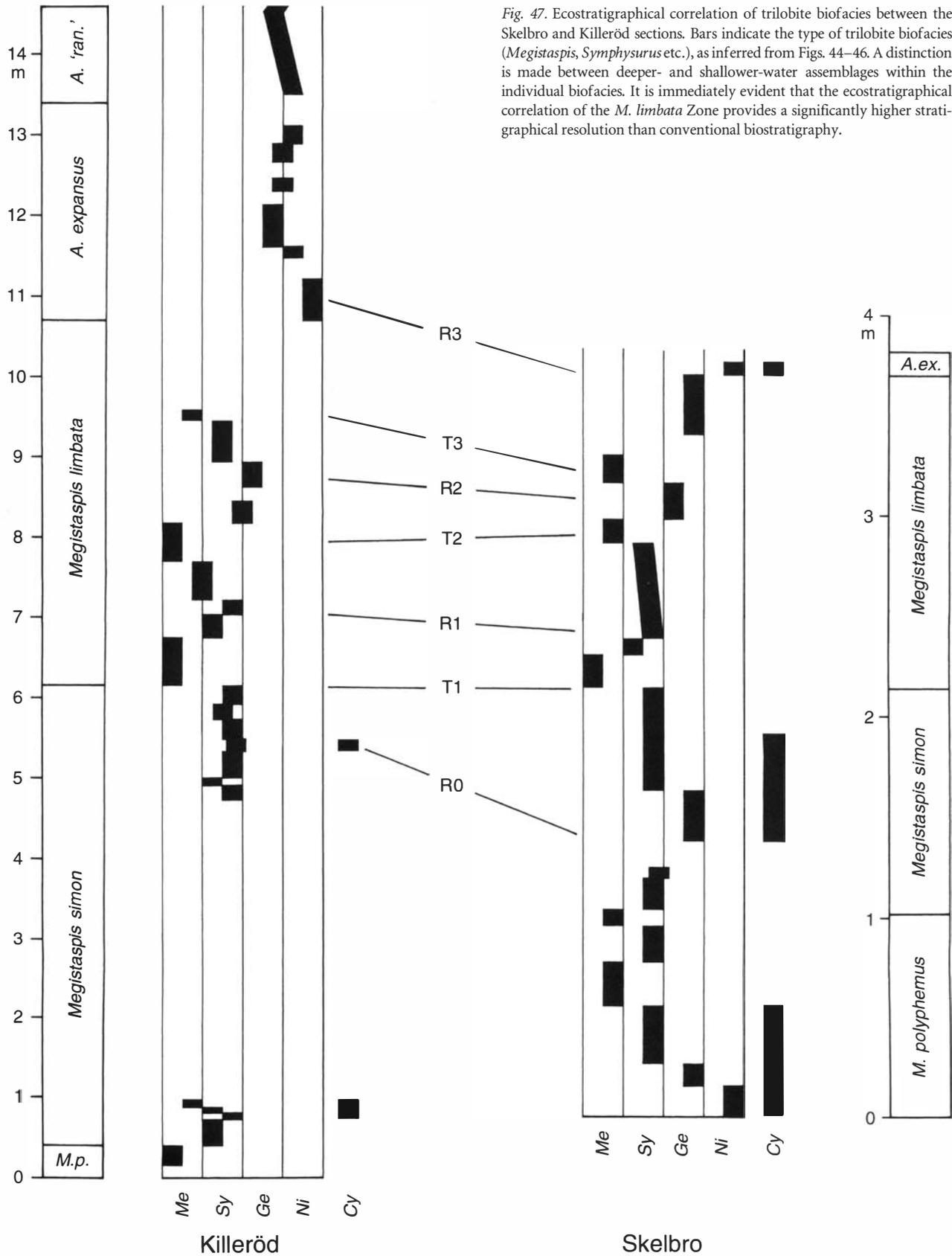


Fig. 47. Ecostratigraphical correlation of trilobite biofacies between the Skelbro and Killeröd sections. Bars indicate the type of trilobite biofacies (*Megistaspis*, *Symphysurus* etc.), as inferred from Figs. 44-46. A distinction is made between deeper- and shallower-water assemblages within the individual biofacies. It is immediately evident that the ecostratigraphical correlation of the *M. limbata* Zone provides a significantly higher stratigraphical resolution than conventional biostratigraphy.

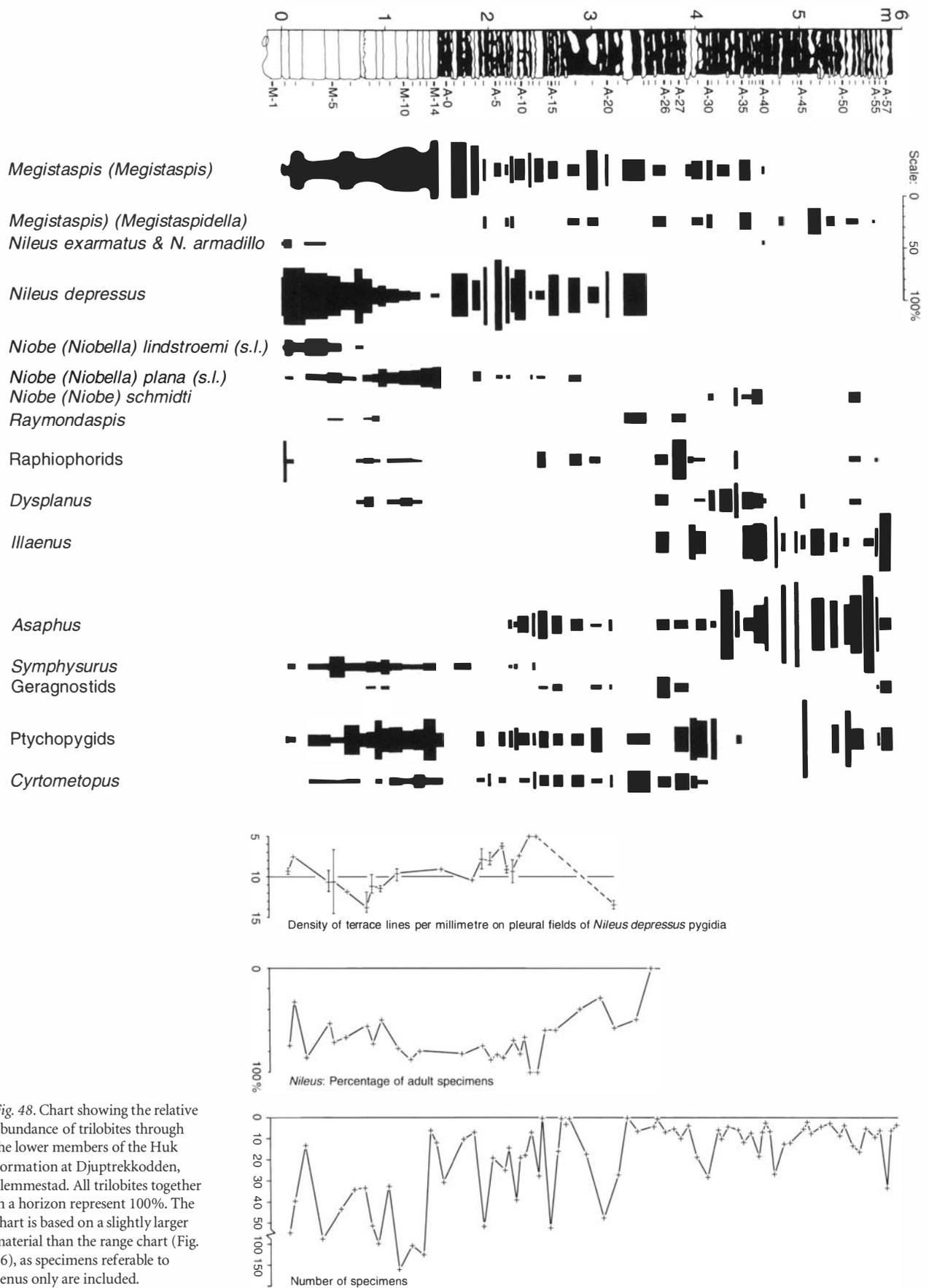


Fig. 48. Chart showing the relative abundance of trilobites through the lower members of the Huk Formation at Djuptrakkodden, Slemmestad. All trilobites together in a horizon represent 100%. The chart is based on a slightly larger material than the range chart (Fig. 36), as specimens referable to genus only are included.

pidella) in the *M. limbata* Zone also points to shallower water (see section on autecology below).

The *M. polyphemus* Zone is very thin in the Slemmestad section. Only rare megistaspids are known from the base of bed M-1 (Fig. 36), whereas the upper part contains a more diverse fauna, with raphiophorids and *N. depressus glazialis* as the dominant groups. This faunal pattern, as well as the change from shale to limestone deposition by itself, is in accordance with a shallowing event. The development appears to be in agreement with the environmental changes observed around the *M. polyphemus* – *M. simon* Zonal boundary in SE Scania.

The *M. simon* Zone is condensed at Slemmestad; the lower part cannot be compared to the Komstad Limestone as the corresponding interval in the Killeröd area remains to be sampled. The Nileid fauna changes towards the top of the *M. simon* Zone (*N. depressus* subsp. A replaces *N. depressus glazialis*), and *Niobe* (*Niobella*) becomes rare. This faunal signal is compatible with a shallowing, and the upper part of bed M-6 most likely represents peak lowstand, and is inferred coeval to bed –5 of Killeröd and beds –6/–7 at Skelbro. The gently deepening interval at the very top of the *M. simon* Zone is either missing or represented by the uppermost part of bed M-6, in which single specimens of *Dysplanus acutigenia*, *Niobe lindstroemi*, *Lonchodomas volborthi volborthi*, and a fair amount of *Megistaspis limbata* type 2 have been found (Fig. 36).

The base of the *M. limbata* Zone is very distinct on the range chart. Broad *M. limbata* ecophenotypes appear, *N. depressus depressus* replaces *N. depressus* subsp. A, *Raymondaspis* sp. C occurs, *Dysplanus acutigenia acutigenia* is common, *Lonchodomas volborthi volborthi* is fairly common, and so is *Symphysurus*. It is plausible to infer a deepening, because *Megistaspis* is very common (and broad), *Symphysurus* is fairly common, and the abundance of *Nileus depressus depressus* types (typical of moderately coarse-grained beds) goes down.

The pattern of drowning–moderate–shallowing–deepening observed in the lower subzone of the *M. limbata* Zone of the Komstad Limestone is not recognizable at Slemmestad. It is interpreted that the base of bed M-7 corresponds to the first shallowing interval, slightly above the base of the *M. limbata* Zone in the Komstad Limestone, and the initial deep-water interval of the *M. limbata* Zone is believed missing (condensed drowning surface). The content of *Megistaspis* above bed M-7 increases to reach a maximum in bed M-14; at the same time the content of *Nileus* decreases to almost nil, *Niobe* cf. *plana* increases slightly, whereas the (relative) content of *Symphysurus* is fairly constant. These trends are consistent with a rising sea-level, and the interval is taken to reflect the second deepening period of the *M. limbata* Zone in the Komstad Limestone.

The content of *Megistaspis* diminishes from the base of the Lysaker Member and upwards, while *N. depressus* becomes increasingly abundant and *Niobe* cf. *plana*, *Lonchodomas*

volborthi volborthi, *Dysplanus acutigenia acutigenia* and *Symphysurus* disappear or become infrequent. The first representatives of *Megistaspis* (*Megistaspidella*) cf. *acuticauda* appear in bed A-4, and *Asaphus lepidurus* turns up in bed A-7, followed by *Megistaspis* (*Rhinoferus*) cf. *hyorrhina* in bed A-8. This faunal assemblage very strongly points to shallow-water conditions. *Asaphus* is a typical East Baltic genus, which makes its main appearance in the Scandinavian area at the base of the Kunda Stage. The incoming megistaspids are of East Baltic affinity, and *M.* (*Megistaspidella*) is also well-known from the Kunda Stage of the Scandinavian area. This shallowing event is suggested to match the second shallowing interval in Komstad Limestone terminology (R2 of Fig. 47), marking the start of the upper subzone of the *M. limbata* Zone. The lowstand appears to have been triple-peaked, culminating in beds A-1, A-6–A-7 and A-12–A-13, with a maximum in the latter. The faunal evidence for this is meagre and will not be further discussed; a similar situation is possibly indicated in SE Scania (cf. Fig. 56). By itself, the lithological shift from the Hukodden Limestone to the Lysaker Member is suggested to reflect the abrupt drop of sea-level in the middle of the *M. limbata* Zone, causing an increased influx of terrigenous material from the source areas to the west. The event is likely to correlate with +10 of Skelbro and beds +8/+9 of Killeröd, i.e. the base of the upper subzone of the *M. limbata* Zone. If so, the sub-biozonal boundary is defined at a lower level in the Komstad Limestone than in the Huk Formation.

The total content of fossils is rather low following the lowstand interval. Upwards, the low content of *Megistaspis* (*Megistaspis*) remains fairly stable (with a rise in beds A-19 and A-20), the content of *N. depressus* rises, and the abundance of *Asaphus* decreases. These trends are taken to indicate the third deepening interval in Komstad Limestone terminology (T3 of Fig. 47).

Nileus depressus disappears above bed A-23, *Megistaspis* (*Megistaspis*) comprises only a smaller part of the fauna in beds A-25 to A-28, *Illiaenus* turns up in bed A-25 and then continues upwards, and *Asaphus* ‘reappears’ (Fig. 48). Geragnostids are uncommon in the Slemmestad section, except for beds A-25 to A-27, although this statement is based on very limited material. Nevertheless, the faunal evidence points to a shallowing, suggested to correspond to the third and major lowering of sea-level towards the close of the *M. limbata* Zone.

In the Komstad Limestone, the beginning of the *A. expansus* Zone coincides with a peak lowstand (R3 of Fig. 47), suggesting correlation with beds A-28–A-29 at Slemmestad. *A. expansus* itself turns up in bed A-29, and *Illiaenus sarsi*, as well as ptychopygids, are common in the boundary beds.

The faunal data from the *A. expansus* Zone of the Komstad Limestone are scarce but broadly indicate a slight initial deepening, followed by a shallowing in the upper half of the zone, culminating in a pronounced lowstand peak at the beginning of the *A. ‘raniceps’* Zone (cf. Fig. 46). The lower

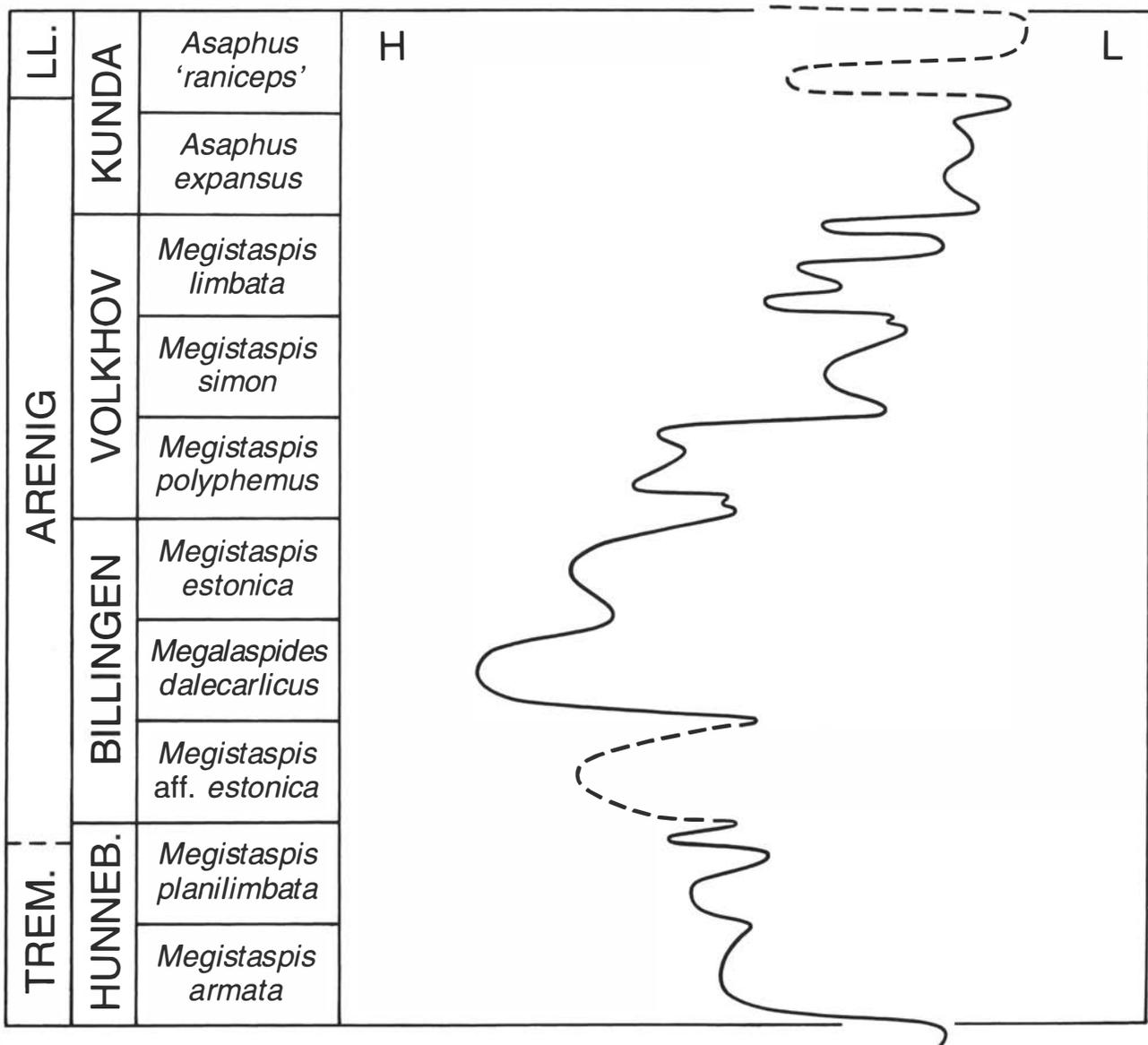


Fig. 50. Relative sea-level curve for the Arenigian of Scandinavia, as inferred from faunal and lithological data (see text for discussion). The degree of detail is higher for the Volkhov and lower Kunda Stages, which are based on interpretation of data from Tjernvik (1956, 1960, 1980), Löfgren (1978, 1985), Lindholm (1981, 1991), and others. For a yet more refined curve including Australian data, see Nielsen (1992a, b).

part of the *A. expansus* Zone at Slemmestad is characterized by *Megistaspis* (*M.*) *elongata*, *Dysplanus centrotus* and rare *Niobe* (*Niobe*) *schmidtii*, while *A. expansus* itself is comparatively infrequent, as are ptychopygids and *Iliaenus sarsi* (Fig. 48). This pattern is fully consistent with slightly deeper-water conditions during the lower part of the *A. expansus* Zone, as indicated in the Killeröd section. A faunal change takes place towards bed A-40, where *Megistaspis elongata* disappears, *Dysplanus centrotus* becomes infrequent, and only a single specimen of *Niobe schmidtii* has been found above this level. Simultaneously, *A. expansus* and *I. sarsi* become frequent. This faunal change is certainly compatible with a reduced depth of deposition. The fauna in the upper half of the *A. expansus* Zone is still in agreement with

a shallow-water habitat, being dominated by *I. sarsi*, *A. expansus* and ptychopygids, often occurring as complete specimens.

The transition to the *A. 'raniceps'* Zone in the Slemmestad section is not included in the present study, but the lower part of the Svartodden Limestone is known to contain *A. expansus* (see Størmer 1953) and abundant brachiopods (Brögger 1882). The lowermost part of this member, called the '*Porambonites* bed' by Brögger (1882), has hitherto been regarded as the upper part of the *A. expansus* Zone, but I am more inclined to correlate it with the base of the *A. 'raniceps'* Zone. In any case, the abundant brachiopods point to shallow-water conditions, and it is hardly controversial to infer a lowstand peak.

Fig. 49 shows the environmental preferences of the trilobite genera based on the interpretation outlined above.

Global ecostratigraphy

Fortey (1984) reviewed the indications for regressions caused by eustasy at several levels within the Ordovician, and he suggested that a major late Arenigian drop of sea-level is marking the boundary towards the Llanvirnian. Similar ideas have been advanced by Lindström & Vortisch (1983), Fortey & Cocks (1986) and Erdtmann (1986). This event has generally been referred to as the Whiterock regression, but the intercontinental correlation of the Whiterock Series is in dispute, and it seems under all circumstances to span numerous sea-level lowstand periods (see, e.g., Ross & Ross 1992). Hence the term 'Whiterock regression' should either be avoided or more precisely defined. An Arenigian sea-level curve for the Canadian craton was compiled by Barnes (1984); on a second order level the pulses are similar to the major trends in the Scandinavian curve (compare Fig. 50 with Barnes 1984, Fig. 4).

When trying to unravel Arenigian or, for that matter, Ordovician sea-level changes, it is a fundamental problem that basically all published information is too crude to resolve the multiple events. The present discussion is therefore restricted to dealing with the Arenig of Spitsbergen, from where comparatively extensive data are available. Very detailed data are currently being processed from Central Australia (Nielsen, unpublished; cf. Nielsen 1992a, b).

Ecostratigraphical correlation of the Valhallfonna Formation, Spitsbergen

The Arenig of Spitsbergen has been dealt with by Fortey (1974b, 1975a, b, 1976, 1980a, b, and others), Fortey & Bruton (1973), Archer & Fortey (1974), Fortey & Barnes (1977), and Cooper & Fortey (1982). For correlation purposes it is a drawback that conodont data are sparse. The Early Ordovician is represented on northern Spitsbergen by the Kirtonryggen and Valhallfonna Formations (Fortey & Bruton 1973). The upper part of the Kirtonryggen and the lower main part of the Valhallfonna Formation appear to be of Arenigian age (Fortey 1980b; Cooper & Fortey 1982).

The trilobite biofacies of the Valhallfonna Formation (Fortey 1975b) reveal a series of relative major sea-level changes entirely identical to the general Scandinavian pattern (compare Fig. 50). Thus, the drowning caused by the profound 'evae transgression' (S. Bergström 1988) at the base of the *M. dalecarlicus* Zone of Scandinavia is reflected by the shift from the bathyurid-dominated Kirtonryggen Formation to the olenid-bearing Valhallfonna Formation of Spitsbergen. This interpretation challenges the idea of a local subsidence, put forward by Fortey (1980b, p. 35). The marked sea-level drop towards the top of the Billingen Stage, culminating at the entrance to the Volkhov Stage, intro-

duced a nileid biofacies in the middle of the Olenidsletta Member (zone V2). Hence zone V2 is inferred to correlate with the lower part of the *M. polyphemus* Zone. The following sea-level rise replaced the nileid facies by a new olenid-bearing facies, suggested to match the upper part of the *M. polyphemus* Zone. The latter, in turn, was brought to an end by a marked drop of sea-level, assumably the significant event towards the close of the *M. polyphemus* Zone, culminating at the base of the *M. simon* Zone. A new nileid biofacies was introduced, and the lithology changed to grey limestones, the Profilbekken Member, the lower part of which is considered equivalent to the *M. simon* Zone of Scandinavia. Twenty-eight metres above the base of the Profilbekken Member, the lithology changes to brown and black limestone, and a 3 m thick blackish limestone 28–31 m above base is characterized by *Peraspis* and *Shumardia* (Fortey & Bruton 1973). This interval is followed by a 1.5 m thick greenish marker bed characterized by glauconite, oolites, oncholites and orthocone cephalopods (Fortey & Bruton 1973; Fortey 1980a). This 'Green marker bed' is interpreted to signal the sea-level lowstand near the top of the *M. simon* Zone, and the blackish interval below is believed to represent an as yet poorly constrained sea-level rise a little above the middle of the *M. simon* Zone. If this interpretation is correct, the sea-level rise at the entrance to the *M. limbata* Zone is comparatively poorly expressed by the faunal composition (Fortey 1975b, Fig. 2), but this may relate to the fairly large sampling intervals (2 m). The range chart indicates a short-lived event of some kind (cf. Fortey 1980a, Fig. 1), as a few species have a very short range just above the 'Green bed', and several new forms appear in the interval 35–40 m above base of Profilbekken Member. Hence the base of zone V4b is considered equivalent to the base of the *M. limbata* Zone.

It is not possible to resolve the sea-level changes in the lower part of the *M. limbata* Zone in a convincing way; the fauna and lithology point to intermediate water depth, which on a second order scale is identical to the pattern seen in Scandinavia. The thick conglomerate at about 70 m above the base of the Profilbekken member (Fortey & Bruton 1973, p. 2234) is interpreted as signalling the abrupt sea-level drop in the middle of the *M. limbata* Zone; faunally, this event introduced a change to shallow-water illaenid biofacies (Fortey 1975b). The upwards lithological change, showing an increase in massive algal-containing limestone (Fortey & Bruton 1973) and characterized by a shallow-water illaenid fauna (Fortey 1975b), is interpreted as reflecting the lowering of sea-level towards the *A. expansus* Zone. From then on, shallow-water reefal limestones dominated during the lowstand of the *A. expansus* – basal *A. raniceps* Zones. No detailed faunal data are available, so an ecostratigraphical approach is not possible. The sea-level rise at the base of the Llanvirnian is considered equivalent to the greenish graptolite-bearing shale on top of the Profilbekken Member (see Fortey & Bruton 1973).

The interpretation of the Spitsbergen section is slightly modified compared to that presented by Nielsen (1992b).

Closing remarks on ecostratigraphy

Ecostratigraphy is still in its initial phase, and the techniques involved have not attracted as much attention as the theoretical discussion of ecostratigraphical concepts (Martinsson 1973, 1976, 1978, 1979, 1980; Waterhouse 1976; Hoffman 1980, 1981; Boucot 1982, 1984, 1986, and others). The overall problem of the method is the overwhelming amount of material necessary, requiring much sampling effort. Secondly, the sensitivity of the method depends on palaeodepth. If an investigated section represents a shallow-water environment, minor sea-level oscillations may cause comparatively significant faunal changes, which cannot be recognized in sites representing deeper water. This 'hyper-sensitivity' obviously calls for caution in the interpretations. Furthermore, shallow-water sites are more prone to have an incomplete sedimentary record. At the other extreme, very deep-water sites may show no faunal changes at all, but this condition rarely applies to shelfal settings.

Leaving these theoretical problems aside, the ecostratigraphical correlation of the *M. limbata* biozone between Killeröd and Skelbro serves to make the point that the discipline potentially has a far higher degree of resolution than conventional biostratigraphy and within the Komstad Limestone almost provides a bed-by-bed correlation. On a regional scale, the same palaeoenvironmental changes are recognizable within the Slemmestad section, despite the fact that the trilobite fauna is rather different from that of the Komstad Limestone, and the ecostratigraphical approach allows for a detailed correlation. The much debated *A. lepidurus* Zone (e.g., Tjernvik 1972) is also readily explained as a shallow-water biofacies.

On a yet larger scale, there is a striking coincidence between the major relative changes of Arenigian sea-level as seen in Scandinavia and on Spitsbergen. Accordingly, the inferred sea-level changes are believed to be of eustatic nature. At the present stage, a correlation with a resolution comparable to that of Scandinavian trilobite zones, or even subzones, seems possible, even though the two areas belong to different biogeographical provinces. An even higher precision is probably achievable if more detailed data became available.

Notes on the autecology of selected trilobite genera

The general environmental preferences of the most common trilobite genera from the Komstad Limestone and Huk Formations are reviewed. The deductions on mode of life are based on the occurrence in comparison to biofacies, lithology, skeletal morphology, etc. An obstacle to more detailed

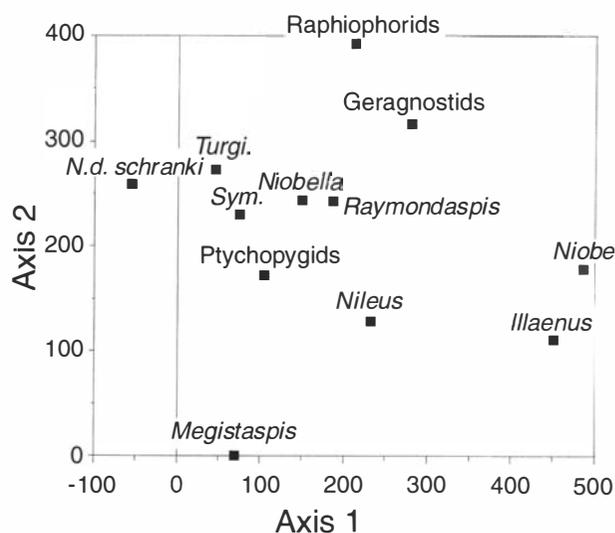


Fig. 51. Detrended correspondence analysis, Komstad Limestone samples. The analysis is based on 96 entries (beds or smaller intervals) containing a total of 5043 specimens, representing the genera or trilobite groups (shown abbreviated on the diagram) *Symphysurus*, *N.* (*Niobella*), *R.* (*Raymondaspis*), *R.* (*Turgicephalus*), *Nileus depressus schranki* n.subsp., 'smooth' *Nileus* [marked as '*Nileus*'], *M.* (*Megistaspis*), *Ptychopyge* (s.l.), raphiophorids, geragnostids, *Illaeus* and *N.* (*Niobe*). Axis 1 represents 28.8% of the total variation and axis 2 represents 11.3%; these are comparatively low values. Like Fig. 49, the present diagram seems, in broad terms, to outline an increased preference for shallow-water habitats towards the right.

inferences about trilobite biology is the lack of quantitative sedimentological data.

SYMPHYSURUS

Approximately one quarter of the assembled trilobite material belongs to *Symphysurus*, which is the most common trilobite group in the Komstad Limestone. Although no quantitative work has been undertaken on the sedimentology, or on *Symphysurus*, it is obvious that the genus is strongly associated with muddy substrates. *Symphysurus* thus disappears in the upper part of the *M. limbata* Zone at Skelbro, Killeröd and Fågelsång, coinciding with an increasing content of grains in the sediment; only rare specimens have been found above this level. *Symphysurus* is also far less common in remaining Baltoscandia, compared to the Komstad Limestone, and the genus is virtually absent in the eastern Baltic area (cf. Schmidt 1907; Balashova 1976).

With regard to autecology, the term *SYMPHYSURUS* biofacies, based on relative abundance, is somewhat misleading. In terms of absolute frequencies, *Symphysurus* is most common in *Nileus* biofacies, when developed on muddy substrate, and it then gradually decreases in abundance through the *Geragnostus*–*Symphysurus* biofacies, to become rare in intervals with typical *Megistaspis* biofacies (Figs. 44–46). The *Symphysurus* biofacies, with relatively high frequency of the genus, typifies intervals between habitats with numerically abun-

dant *Geragnostus* (*s.l.*) and *Megistaspis* (*Megistaspis*). However, because of its link to muddy substrate, *Symphysurus* is outside the Komstad Limestone domain typical of intermediate to deeper-water settings (for references, see Fortey 1986; cf. also Fig. 48). The mode of life of *Symphysurus* was discussed by Fortey (1986).

It is evident even from a superficial examination of the material available (ca. 2000 specimens) that there are pronounced average size differences between *Symphysurus* 'populations' from different palaeodepths. Thus, juveniles are very abundant in muddy shallow-water environments, and much more infrequent in deeper-water settings. This appears to be a general phenomenon for most trilobites present in the Komstad Limestone and Huk Formation, see, e.g., *Nileus* (Figs. 48, 55, 56). It is uncertain whether this size distribution reflects biology or preservational bias.

Megistaspis

Megistaspis is a common and characteristic faunal element of the post-Tremadocian Lower Ordovician of Baltoscandia. The various subgenera of *Megistaspis* undoubtedly had dissimilar environmental preferences, as shown by their uneven distribution, and the *Megistaspis* biofacies of the Komstad Limestone comprises only members of *M.* (*Megistaspis*). The older *M.* (*Paramegistaspis*) group probably had similar environmental preferences, whereas *Megistaspis* (*Megistaspidella*) and *M.* (*Rhinoferus*) are more frequent in the East Baltic area, as well as in the Kunda Stage of the Scandinavian region, and it is not contentious to claim that the latter two megistaspid groups are characteristic of shallower-water settings.

The representatives of *M.* (*Megistaspis*) show a wide variation of relative width of exoskeleton, although the adult

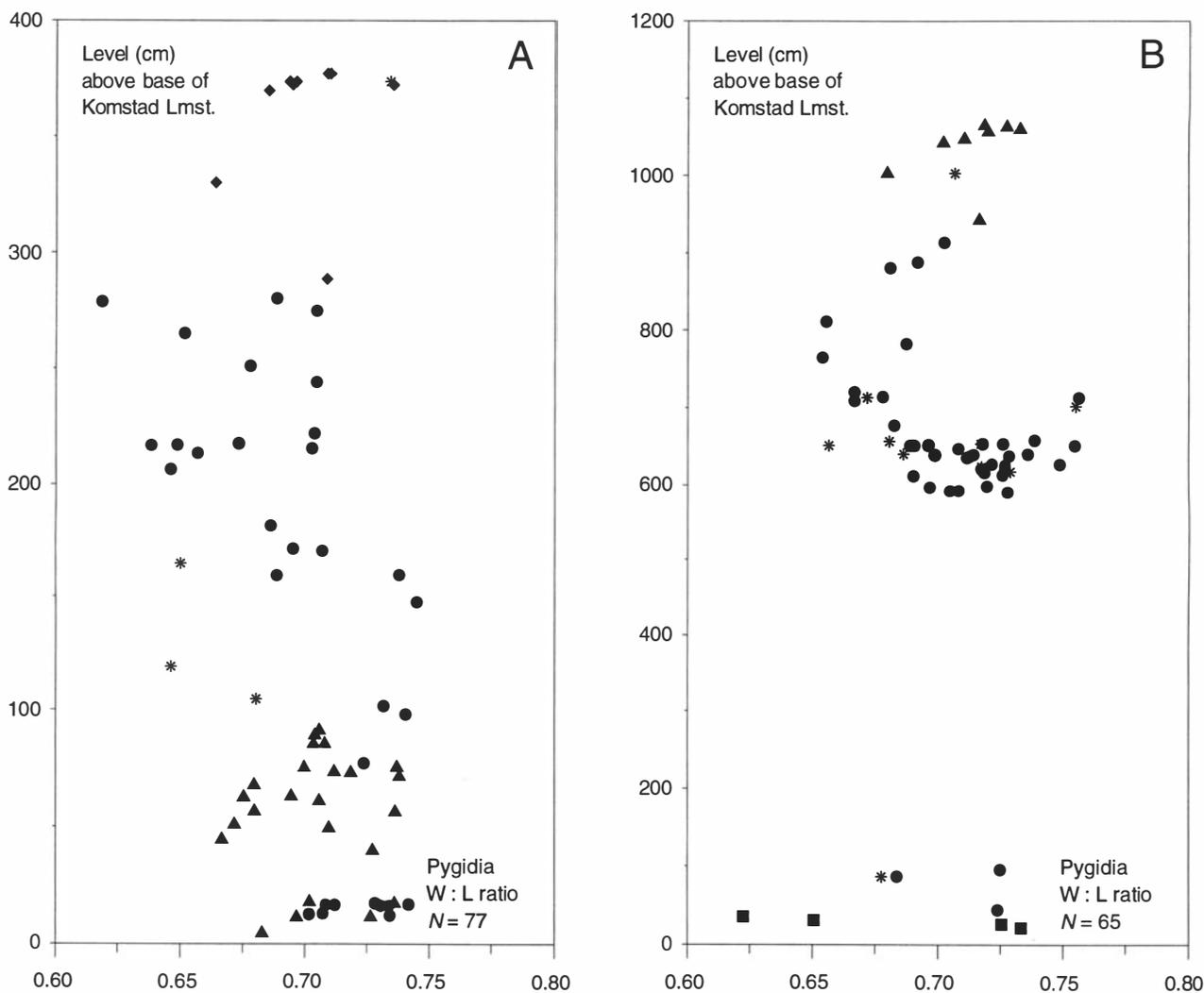


Fig. 52. Relative width of adult *Megistaspis* pygidia plotted against stratigraphic occurrence. ● *M. limbata*, * *M. simon* (*s.l.*), ▲ *M. polyphemus*, ◆ *M. geminus* n.sp., ■ *M. sp. B/C*, ▼ *M. elongata*. □ A. Skelbro section ($N = 75$). The scale of the X-axis refers to Fig. 5. □ B. Killeröd section ($N = 65$). The scale of the X-axis refers to Fig. 34.

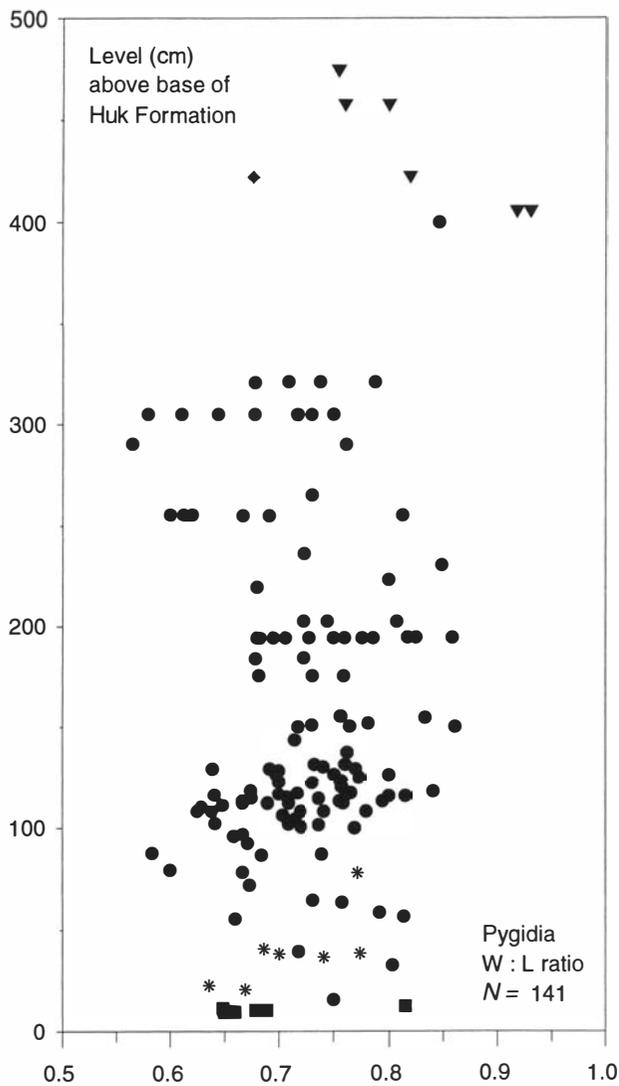


Fig. 53. Relative width of adult *Megistaspis* pygidia plotted against stratigraphic occurrence, Djupprekkodden, Slemmestad ($N = 141$). Legend as in Fig. 52. The scale of the X-axis refers to Fig. 28.

length:width ratio in single horizons usually varies only within a range of about 15%. Specimens from deep-water settings, as inferred from the trilobite biofacies array, are consistently broader than shallow-water morphs. Broadly speaking, the inferred sea-level oscillations are therefore mirrored by the width of the megistaspid exoskeleton (Figs. 52–53), but the trends are blurred by the biological variation of *Megistaspis* as well as by the repeatedly changing environment, and much material is required to outline the variation. The variable width is assumed to be a 'snow-shoe effect', connected to the mud content of the substrate.

As the width of exoskeleton was affected by the environment, it follows that caution should be taken in attaching taxonomical importance to this feature (cf. Jaanusson 1956a; Tjernvik 1980). Another important megistaspid character,

highlighted in taxonomy but here believed to be governed by the environment, is the development of a cephalic posterior border furrow. This feature is generally faint or absent in the Scandinavian representatives of *M.* (*Megistaspis*), but becomes better developed towards the close of the *M. limbata* Zone (see *M. geminus* n.sp. and *M. limbata* type 6), and a distinct border furrow is present in *M. elongata* from the *A. expansus* Zone. *M.* (*Megistaspis*) representatives in the eastern Baltic area show a well-defined furrow as early as the *M. polyphemus* Zone (Balashova 1976). The biological significance of the feature is unknown, but it seems to be a reflection of the doublure, which in turn possibly had a function in contact with the substrate. A number of megistaspid features, listed in Table 5, appear to vary according to environment.

The different species of *M.* (*Megistaspis*) seem to have had slightly dissimilar environmental preferences. *Megistaspis limbata* types 7 and 8 of the *M. polyphemus* Zone are more common in shallower-water facies than the large, broad *M. polyphemus*, which dominated at greater depth. *M. simon* (s.l.) is characteristic of shallower-water settings, and *M. elongata* and *M. geminus* n.sp. both occur in shallower-water facies than *M. limbata* (s.l.). It is possible that the poorly known megistaspids of spp. B and C types, including *M. ringsakerensis*, were inhabitants of very deep water; all three species seem to occur in the deepest-water environments containing trilobites.

A few specimens of *Megistaspis* (*Megistaspis*) with a down-flexed posterior part of body, like the lectotype of *M. limbata* (see Jaanusson 1956a), strongly suggest that this was at least one of the life positions of the animal. The elevation of the eyes makes it plausible that the margin of the cephalon was also slightly buried at times. Whether the same burrowing habit was exercised by the various other groups of *Megistaspis* is questionable; an outstretched attitude with slightly lowered thorax appears to be more typical for *M.* (*Megistaspidella*). Again, the elevated eyes indicate that these animals were shallow burrowers. The anterior and posterior mesial spines, repeatedly developed in a number of megistaspid groups, are surmised to have had a connection with

Table 5. General trends of characters within *M.* (*Megistaspis*) representatives from shallow- versus deep-water environments.

Feature	Shallow environment	Deep environment
Width of exoskeleton	Narrow	Broad
Mesial depression, frontal area	Absent/faint	Distinct
Glabellar lateral furrows	Distinct	Indistinct
Bacculae	Distinct	Indistinct
Posterior cephalic border furrow	Distinct	Effaced/faint
Glabellar convexity (tr.)	Strong	Low
Pygidial segmentation	Distinct	Fairly indistinct
Postaxial pygidial border	Effaced/faint	Present
Number of pleural ribs on pygidium	8 pairs	7 pairs

burrowing and may have been instrumental in maintaining a water flow below the animal in the half-buried state. The cephalic 'snout' is typically turned gently upwards (Fig. 118C).

NILEUS

Nileus is next to *Symphysurus* the most common trilobite group in the Komstad Limestone. A treatment of *Nileus* at the genus level in palaeoecology introduces a loss of information, as the different species and subspecies quite clearly were adapted to different environments. A strong facies-dependency is also evident from the distribution of *Nileus* species in the Valhallfonna Formation of Spitsbergen (see Fortey 1975a, 1980b).

Species distribution. – The inferred distribution of nileid species along a depth gradient in the *M. simon* – *M. limbata* Zones of the Komstad Limestone is shown in Fig. 54. Three nileid biofacies, characteristic of muddy substrate, can be distinguished, ranging from the shallow-water *N. orbiculatooides* [and *armadillo*] biofacies, to the slightly deeper-water *N. orbiculatooides* and *N. planiceps* n.sp. biofacies to the *N. depressus schranki* n.subsp. biofacies at greatest depth.

Nileus orbiculatooides and *N. armadillo* were confined to shallow and intermediate water depths and are absent in deeper-water environments. In shallow-water intervals of the Komstad Limestone, these species are dominant and may be the only *Nileus* representatives present (see Figs. 55–56 versus 44). It is, however, obvious that substrate conditions played an important role too, as the two nileids are absent in coarse-grained limestones (see also remarks by Jaanusson 1984). This may be why *N. armadillo* is not found in the very shallow-water facies represented by the pronouncedly coarse-grained beds 9 and 10 at Killeröd site b. Substrate conditions are probably also responsible for the total lack of *N. orbiculatooides* in the *M. simon* Zone at Slemmestad. *N. armadillo*, and perhaps also *N. orbiculatooides*, also seem to be

absent in the East Baltic area (see taxonomic section). It remains puzzling, however, that *N. armadillo* is virtually absent in the Lysaker Member at Slemmestad, as the upper part of this unit certainly appears to have been a shallow-water muddy environment.

N. planiceps n.sp. is a less common nileid, which was characteristic of intermediate water depths, where it was typically associated with *N. orbiculatooides*. *N. planiceps* n.sp. never accounts for more than 25% of the fossil *Nileus* fauna in any one bed, usually about 5–15% (Figs. 55–56).

N. depressus schranki n.subsp. is characteristic of deep-water intervals of the Komstad Limestone and may there be the only *Nileus* present (Figs. 55–56). The subspecies is absent in the most shallow-water facies (see, however, remarks on *Nileus* sp. B) but occurs sparsely in the *Geragnostus* biofacies when developed on muddy substrate. *N. depressus schranki* n.subsp. does occur together with *N. orbiculatooides*, especially in the *M. polyphemus* Zone (Fig. 55), but the two species tend to be mutually exclusive higher in the sections.

N. exarmatus is uncommon in the Komstad Limestone, except in the Skelbro beds. It is inferred that the species preferred muddy substrate and therefore, indirectly, intermediate to greater depth. Apart from the occurrence in the transgressive Skelbro beds (Figs. 33, 55), only a few specimens of *N. exarmatus* have been found in the lower part of the Komstad Limestone in Scania, in what appears to be *Megistaspis* and *Symphysurus* biofacies.

N. latifrons n.sp. and *N. armadillo* tend to be mutually exclusive in the sections. *N. latifrons* was undoubtedly adapted to coarser substrate than *N. armadillo*. It is also likely that *N. depressus serotinus* n.subsp., *N. depressus glazialis*, and *N. d. depressus* were characteristic of fairly shallow water with coarser substrate, where they replace *N. orbiculatooides* and *N. armadillo*.

N. depressus serotinus n.subsp. has so far been found only in SE Scania, but it is probably closely related to *N. depressus depressus* and may be a marginal ecophenotype of that form. *N. d. serotinus* n.subsp. is typical of shallower-water settings

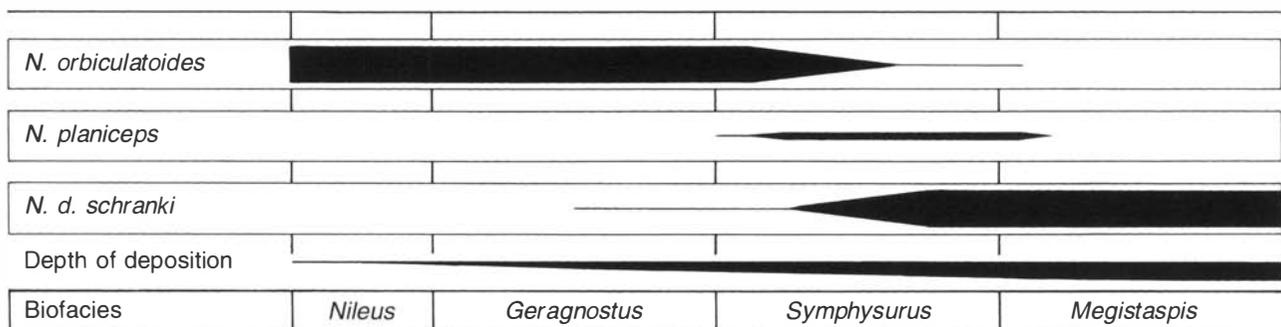


Fig. 54. Inferred depth distribution of nileid species on a muddy substrate in the *M. simon* and *M. limbata* Zones. When the substrate contained a higher proportion of skeletal grains, the species in the chart were replaced by representatives of the *Nileus depressus depressus* group (*N. d. depressus*, *N. d. glazialis*, *N. d. serotinus*, *N. d. subsp. A*).

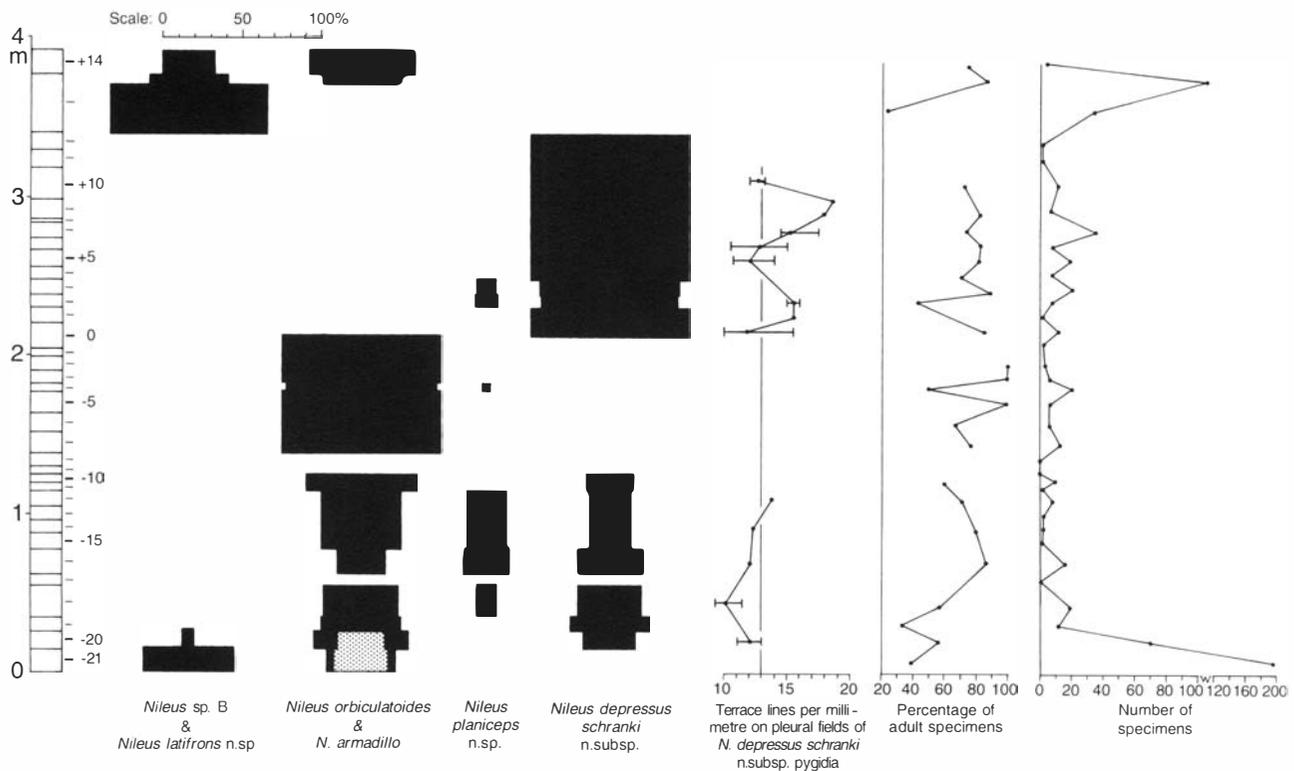


Fig. 55. Chart showing the relative abundance of various species of *Nileus* in the Komstad Limestone at Skelbro. All species of *Nileus* = 100%. *N. exarmatus* is included in *N. orbiculatoides* (shaded).

with moderately coarse substrate. In some beds the subspecies occurs together with *N. orbiculatoides* (Fig. 56), whereas *N. depressus schranki* n.subsp. and *N. d. serotinus* n.subsp. are mutually exclusive in the section.

The palaeoenvironmental distributions of *N. implexus* n.sp. and *N. depressus parvus* n.subsp. are unclear. With regard to the latter, it is striking that minute *Nileus* species recur in narrow horizons at several levels (*N. depressus parvus* n.subsp., *N. orbiculatus* Tjernvik, 1956, *N. sp. sensu* Wandås 1984), invariably connected to sea-level rises. These small nileids may have been pelagic, as also suggested by the unusually broad pygidial axis shown by *N. depressus parvus* n.subsp.

Terrace lines. – The surface sculpture as well as the presence or absence of a pygidial border have been strongly emphasized in taxonomic studies of *Nileus* (Schrank 1972; Tjernvik 1980). These eye-catching features should, however, be treated with caution, as they were obviously affected by the environment. For a general discussion of terrace lines, see Miller (1975), Schmalzfuss (1981) and Seilacher (1985).

The density and distribution of exterior terrace lines on *N. depressus* vary with palaeodepth in a puzzling way. The terrace-line density of the *N. d. schranki* n.subsp. pygidium is about 10–12 lines/mm on the pleural fields in deeper-water environments, whereas specimens from intermediate water

depth show about 18–19 lines/mm (Figs. 55–56; Table 30). Growth did not influence the terrace-line density significantly (Fig. 198C).

The same tendency is seen for *N. d. glazialis* and *N. d. depressus*, but the terrace-line density is overall lower, compared to *N. d. schranki* n.subsp. (Fig. 48). No quantitative data on sediment grain size is available, but the relationship of terrace-line density to environment is the opposite of what should be expected if the lines had some kind of sediment relation, as deeper-water sediment generally speaking is finer than that of shallower water. The inverse relationship seems to contradict that the lines had a sediment-catching function in connection with burrowing.

N. d. schranki n.subsp. and *N. d. glazialis* were apparently both able to develop cranidial terrace lines when living in shallower-water habitats. *N. d. glazialis* is then called *N. d. subsp. A* and is characterized by a high terrace-line density on the pygidium and terrace lines covering the entire cranidium. Furthermore, it appears that individuals of *N. depressus* living in very shallow water entirely lost the terrace lines, which obviously entails identification problems. Thus *N. depressus* specimens from beds A-4 and A-10–A-11 at Slemmestad show a very sparse terrace-line coverage (Fig. 48); *Nileus* sp. B from bed –21 at Skelbro is exceedingly similar to *N. d. schranki* n.subsp., except for the pygidial terrace-line pattern; and *N. latifrons* n.sp., from the top of *M. limbata*

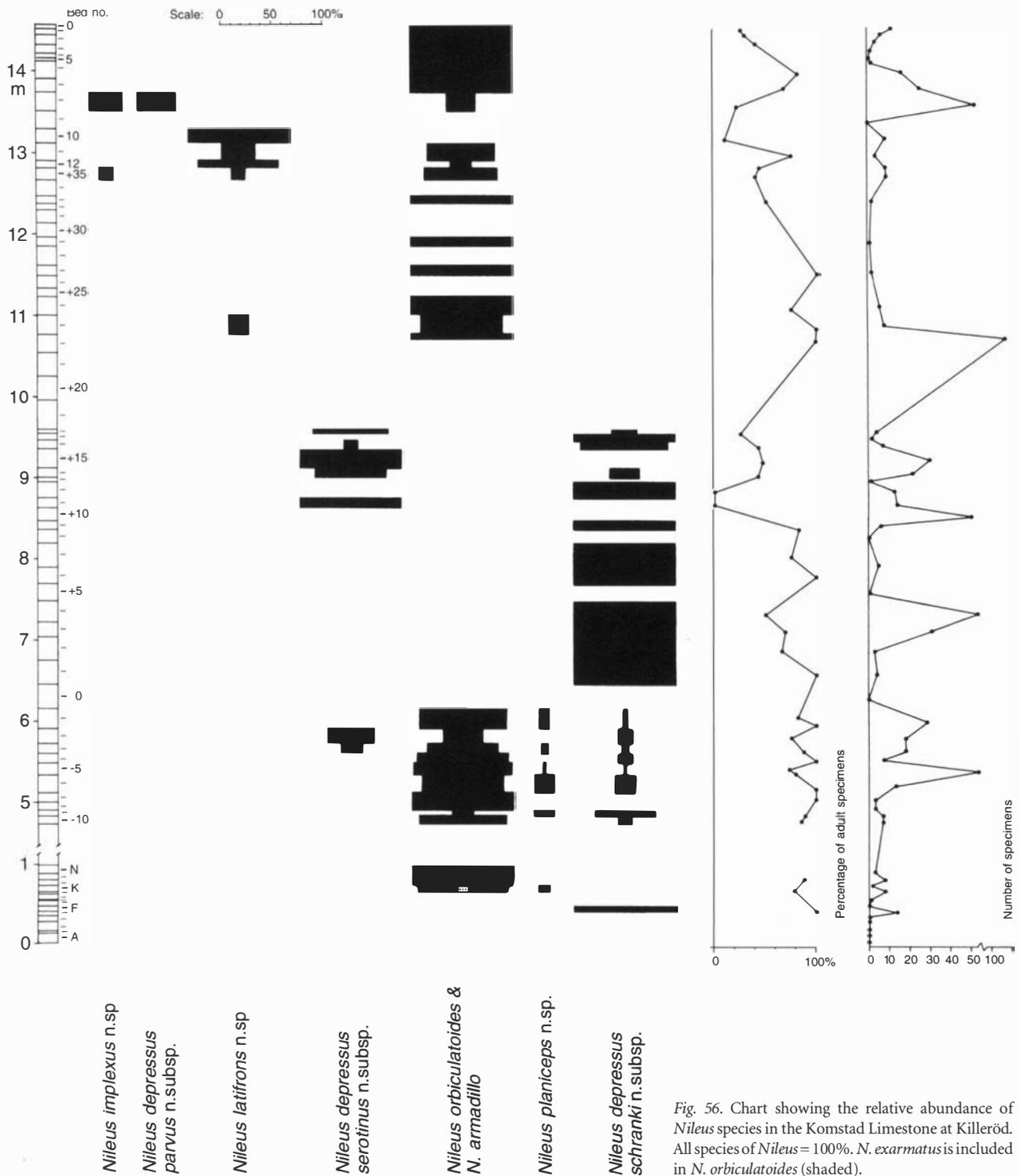


Fig. 56. Chart showing the relative abundance of *Nileus* species in the Komstad Limestone at Killeröd. All species of *Nileus* = 100%. *N. exarmatus* is included in *N. orbiculatooides* (shaded).

Zone and the *A. expansus* Zone of the Komstad Limestone, has a cephalon basically similar to that of *N. depressus*, but the pygidium is almost devoid of exterior terrace lines.

The presence or absence of a border also appears to have been influenced by the environment (see *N. latifrons* n.sp., *N.*

orbiculatooides, *N. depressus*, *N. sp. B*), with a tendency towards well-developed borders in deeper-water types and absence or feeble development in shallow-water types. There are exceptions to this trend, and the feature remains to be interpreted in functional terms.

General remarks. – Juvenile nileids are much more abundant in shallow-water facies (where they comprise about 60–70% of the *Nileus* material) than in deeper-water intervals (0–30% of *Nileus*) (Figs. 48, 55, 56). This trend, seen in all sections investigated, is actually valid for most trilobites in the Komstad Limestone and Huk Formation. Various biasing taphonomic factors may be considered to explain the distribution (such as differential preservation due to quick/slow burial etc.); if the rather persistent pattern has a biological background, it indicates that juvenile trilobites grew up predominantly in shallow-water environments (compare Sheldon 1988, pp. 295–299), which in turn entails migration during growth of those species typical of deeper-water environment. As juvenile nileids cannot be assigned to species, it is impossible to verify whether or not juveniles of species, characteristic of deeper-water environments, actually did grow up in shallow water. I am most inclined to interpret the uneven size distribution as related to preservational differences.

The trilobite composition of the fossil *Nileus* biofacies is undoubtedly distorted compared to the original biological communities. In this respect, bed +22 at Killeröd is atypical, as two-thirds of the specimens encountered are complete, and several of the remaining partly disarticulated specimens do still show contiguous thoracic segments, genae etc. The circumstances suggest a catastrophic death *en masse* (compare Speyer & Brett 1985). The fossil faunal composition is therefore probably fairly close to the true ratios between the living trilobite species (see Table 6). It cannot, of course, be excluded that the anomalous environmental event causing the death of the trilobites also altered the environment prior to the ‘catastrophe’, in which case the assemblage would not be entirely representative for a typical life assemblage. The bed can be recognized throughout the whole type area of the Komstad Limestone and is not a local event at Killeröd.

The mode of life of *Nileus* has briefly been commented upon by J. Bergström (1973) and Fortey (1986, Textfig. 12).

Table 6. List of trilobites encountered from the upper part of bed +22 at Killeröd, specified as number of complete specimens (mainly enrolled) and disarticulated skeletal parts. The faunule, which apparently died largely *en masse*, represents a *Nileus* biofacies.

	Entire	Single	%
<i>Nileus armadillo</i>	62	16	80
<i>Iliaenus fornicatus</i> n.sp.	2	1	3
<i>Ampyx nasutus</i>	1	2	3
<i>Cyrtometopus</i> sp.	1	1	2
<i>Iliaenus sarsi</i>	1	1	2
<i>Dysplanus centrotus</i>	1	1	2
<i>Geragnostus</i> (s.l.)	–	3	3
<i>Ptychopyge</i> (s.l.)	–	2	2
<i>Niobe tjernviki</i> n.sp.	–	1	1
Others	–	2	2
In total	68	30	100

NIOBE

Niobe is widely distributed in the Lower Ordovician of Baltoscandia and also occurs commonly in the Komstad Limestone and Huk Formation. The two most widespread subgenera, *N. (Niobella)* and *N. (Niobe)*, rarely occur together, and they obviously had dissimilar environmental preferences.

N. (Niobella) is frequent in the *M. dalecarlicus* and *M. estonica* Zones of Sweden (Tjernvik 1956), in the *M. polyphemus* to *M. simon* Zones of the Komstad Limestone, as well as in the lower part of the *M. limbata* Zone at Slemmestad. Only *N. (Niobella) laeviceps* occurs in the *A. expansus* Zone of Sweden. This distribution inevitably leads to the conclusion that the representatives of *N. (Niobella)* preferred a muddy substrate, and, hence, indirectly medium to deeper-water habitats. *Niobella* consistently plots close to *Symphysurus* in the correspondence analyses of the trilobite faunas of the Komstad Limestone and the lower members of the Huk Formation (Figs. 49, 51). A preference for muddy substrate is also in accordance with occurrences elsewhere (see, e.g., Whittington 1965; Fortey 1975a) and with the presence of *Niobella* in Upper Cambrian shales (e.g., Westergård 1939; Lake 1942).

It appears that the *N. (Niobella) imparilimbata* group, including *N. (N.) plana*, was adapted to slightly deeper water (or more muddy substrate) than the species plexus *N. bohlini–N. lindstroemi–N. laeviceps. N. obsoleta* may be a fourth member of the latter group. This deduction is in accordance with the much longer range of *N. (Niobella) imparilimbata* in the Komstad Limestone, compared to the Swedish mainland (see Tjernvik 1980), and also explains the common occurrence of *N. (N.) cf. plana* in the lower part of the *M. limbata* Zone at Slemmestad, whereas it is more scarce in the mainland of Sweden (Tjernvik 1980). It remains puzzling, though, that *N. imparilimbata* (s.l.) is so rare in the lower part of the *M. limbata* Zone in the Komstad Limestone.

The Komstad Limestone palaeoenvironment evidently did not suit *N. lindstroemi* during the *M. simon* Zone time interval, whereas this species is common in Sweden and Norway; only rare specimens have been found at Killeröd. The absence is perhaps due to too high a content of mud, as the contemporaneous sediment at Slemmestad, with frequent *N. lindstroemi*, contains a significantly higher proportion of skeletal grains. Instead, *N. imparilimbata* occurs through most of the *M. simon* Zone of the Komstad Limestone, being absent only in the upper part.

Niobe (Niobe) is virtually absent in Scandinavia during the Billingen and Volkhov time intervals, while the subgenus is known from the upper Tremadocian and the Hunneberg Stage (Tjernvik 1956, 1980) as well as the Kunda Stage (Bohlin 1955; Balashova 1976; Tjernvik 1980; this study, see Fig. 127). From this distribution emerges the conclusion that *N. (Niobe)* in some way was connected to shallow-water habitats (presumably more coarse-grained substrates). Cor-

respondence analyses (Figs. 49 and 51) place *Niobe* closest to *Geragnostus*, *Asaphus*, *Illaeus*, *M. (Megistaspidella)* and *Dysplanus*; except for the latter, all of these are inferred to have lived predominantly in shallow-water habitats.

ILLAENUS

Illaeids invariably seem to be associated with shallow-water environments (e.g., Fortey 1975b), and the occurrence of *Illaeus* in the Komstad Limestone and Huk Formation at Slemmestad is in excellent agreement with previous observations. *Illaeus* turns up in Baltoscandia at or just below the base of the *A. expansus* Zone, inferred to be a time with a very low sea-level. The two early species *I. fornicatus* n.sp. and *I. sarsi* tend to be mutually exclusive, at least in the sections at Skelbro and Slemmestad, which suggests that *I. fornicatus* n.sp. inhabited slightly deeper water (?more muddy substrate) than *I. sarsi*.

Illaeid classification makes use of cuticle terrace-line sculpture (cf. Jaanusson 1954, 1957), but illaeid individuals from very shallow-water intervals seem to exhibit much denser terrace-line coverage than individuals of the same species from slightly deeper water (e.g., Fig. 242D, G, H), and the case appears analogous to that of *Nileus*. More detailed studies are needed to throw light on this taxonomic problem.

DYSPLANUS

Dysplanus was almost certainly adapted to deeper water than *Illaeus*, although its rarity in the Komstad Limestone suggests that *Dysplanus* generally avoided very muddy substrates. This is supported by its sparse presence in the *M. simon* Zone of SE Scania, where *D. acutigenia acutigenia* is present in shallower-water intervals, i.e. beds with a slightly higher grain content.

D. acutigenia vetustus n.subsp. occurs in a *Symphysurus* biofacies in the upper part of the *M. polyphemus* Zone at Skelbro, taken to be deposited in fairly deep water, and *D. acutigenia acutigenia* is common in the lower half of the *M. limbata* Zone at Slemmestad, also inferred to represent relatively deep water.

D. centrotus is, like *D. acutigenia acutigenia*, infrequent in the Komstad Limestone and more common in the Slemmestad section. *D. centrotus* and *Illaeus sarsi* display a strong tendency towards being mutually exclusive in the section. *D. centrotus* is most common in the lower half of the *A. expansus* Zone, also containing *Megistaspis (M.) elongata*, but comparatively few *Asaphus expansus* (as well as *I. sarsi*), compared to the densities in beds A-28 and A-29 and above bed A-35 (see Fig. 48). This is taken to indicate that *D. centrotus* was adapted to slightly deeper water than *I. sarsi*.

At the species level, *D. acutigenia* seems adapted to deeper water than *D. centrotus*, which makes a combined analysis (Fig. 49) misleading.

Ptychopygids

Ptychopygids are common in the Komstad Limestone and the Huk Formation at Slemmestad, but the group is in need of a thorough revision. Ptychopygids as a whole seems to be most abundant in shallower-water habitats without any obvious ties to sediment type. Thus, ptychopygids are common in the Komstad Limestone in the lower part of the *M. polyphemus* Zone, in the upper part of the *M. simon* Zone, in the middle of the *M. limbata* Zone, and throughout the *A. expansus* Zone. Limestone beds inferred to have been deposited in very shallow water during the *A. expansus* Zone typically contain a profuse abundance of ptychopygids.

A shallow-water environmental preference is in accordance with the rich ptychopygid fauna described from the East Baltic area (Balashova 1964, 1976), but different species undoubtedly had dissimilar environmental preferences. For instance, the lower part of the *M. limbata* Zone at Slemmestad, assumed to represent relatively deeper water, is comparatively rich in ptychopygids (Fig. 48), and the same stratigraphical level in the Komstad Limestone also contains relatively frequent ptychopygids. *Ptychopyge (s.l.)* therefore plots close to *M. (Megistaspis)* in correspondence analyses (Figs. 49 and 51).

It is fairly common to find outstretched entire specimens, often with lowered thorax (cf. Balashova 1976, Pl. 3:2–3); this is inferred as a life position for ptychopygids, although the position alternatively may be interpreted as postmortem 'sacking'. The pronounced flatness of the exoskeleton, the broad border and the raised eyes presumably indicate that ptychopygids were shallow burrowers, leaving only the eyes above the sediment surface. The extraordinary wide doubleure may be an adaption for a burrowing habit.

ASAPHUS

Asaphids are, like ptychopygids, typical of shallow-water facies, actually more strictly so than ptychopygids. *Asaphus* has been found in the Komstad Limestone only in the *A. expansus* and *A. 'raniceps'* Zones, deposited during a sea-level lowstand, while *Asaphus* turns up slightly earlier in the Slemmestad section, but still in a shallow-water environment.

Asaphus is a typical 'East Baltic' genus, there occurring from the top of the BII α Zone, and it is stepwise migrating into the Scandinavian region, at first in the middle of the *M. limbata* Zone, and secondly, and more conspicuously, at the base of the *A. expansus* Zone.

The disjunct distribution of the asaphid species clearly indicates that water depth was not the only environmental factor of influence. In the section at Killeröd site b, *A. 'raniceps'* seems typical of slightly deeper-water intervals than *A. striatus*.

RAYMONDASPIS

Raymondaspis is moderately common in the Komstad Limestone. Broadly speaking, it appears that *R. (Raymondaspis)* spp. predominantly occurred in shallower water, whereas *R. (Turgicephalus)* representatives were characteristic of deeper water, which probably is a matter of substrate-fabric control. A similar distribution can be interpreted in the Valhallfonna Formation on Spitsbergen (cf. Fortey 1980a vs. Fortey 1975a). These inferences are in accordance with the correspondence analyses (Figs. 49 and 51), where *R. (Raymondaspis)* plots close to *Nileus* and *R. (Turgicephalus)* is closest to *Symphysurus*.

Raymondaspis is comparatively infrequent in the section at Slemmestad, probably caused by substrate conditions. A scarcity of raymondaspids in the East Baltic area is also documented by the monograph of Schmidt (1881–1907). Jaanusson & Bergström (1980) reported Middle Ordovician styginids to be restricted to the central confacies belt of Baltoscandia, as well as the Blount confacies belt of the Appalachians, which also suggests a preference for relatively muddy substrates.

CYRTOMETOPUS

Cyrtometopus is significantly more common in the Huk Formation than in the Komstad Limestone. This distribution points to a preference for coarser substrate, which is in accordance with its presence throughout the entire Volkhov Stage of Sweden (Tjernvik 1980) and the eastern Baltic area (Lamansky 1905; Schmidt 1907).

CYCLOPYGE

Cyclopyge is exceedingly abundant in some intervals of the Komstad Limestone, invariably associated with pulses of a rising sea-level. A similar occurrence is seen in the 'Transition Beds' at the base of the Billingen Stage (Tjernvik 1956, 1960, 1980). The genus is entirely absent in between these episodes, and not all sea-level rises were accompanied by invasion of cyclopygids.

A pelagic mode of life has been inferred for *Cyclopyge* because of its hypertrophied eyes (Fortey 1974a, 1985), and it was considered characteristic of the outer shelf environment by Fortey & Owens (1987). The cyclopygid biofacies *sensu* Fortey & Owens (1987, pp. 105–108), which besides cyclopygids are usually dominated by blind benthic trilobites, never invades shallow-water settings, and is thus very different from the *Cyclopyge* assemblage of the Komstad Limestone, which are always associated with shallow-water benthic trilobite assemblages. The evidence for a deep-water setting of the cyclopygid biofacies, presented by Fortey & Owens (1987), is compelling, and the contradictory presence

in the Komstad Limestone is most likely reflecting a combination of sea-level events and the marginal position of the Komstad Limestone domain on the East European Plate. The cyclopygid biofacies *s.str.* is not represented by the Komstad Limestone, even in the intervals with *Megistaspis* biofacies, and *Cyclopyge* was most likely living in the no longer preserved outer shelf environment along the southern fringe of the East European Plate. This conjecture is supported by the circumstance that *Cyclopyge* is far more common on Bornholm, situated nearer to the plate edge, than in Scania. The only event allowing *Cyclopyge* to advance far into the Baltic platform was the significant sea-level rise at the base of the Billingen Stage. The exact mechanism causing the 'invasion' of *Cyclopyge* remains enigmatic but may involve a change of palaeocurrents.

Raphiophorids

Fortey & Owens (1978) recognized a 'Raphiophorid community', inferred to represent a habitat intermediate between the shallow-water *Neseuretus* and the deep-water Olenid communities. Generally speaking, the distribution of raphiophorids within the Komstad Limestone matches this palaeoenvironmental position, which is also comparable to the distribution within the Valhallfonna Formation of Spitsbergen (cf. Fortey 1975b). *Rhombampyx* is most abundant in transitional *Geragnostus*–*Symphysurus* biofacies with muddy substrate, i.e. shallower intermediate water depth. This fits well with the higher abundance of *Rhombampyx* on Bornholm, compared to SE Scania, where raphiophorids (*Ampyx*) first become common in the *A. expansus* and *A. 'raniceps'* Zones. *A. nasutus* ranges throughout the *A. 'raniceps'* Zone at Killeröd site b but is certainly most common in the middle of the zone, which is inferred to represent slightly greater depth of deposition than the short intervals of *A. 'raniceps'* Zone below and above. *Rhombampyx* seems to be typical of more muddy substrates than *Ampyx*, an inference which, however, seems to be at odds with the occurrence in the Spitsbergen sections described by Fortey (1975a). The substrate preferences of *Lonchodomas* are unclear.

Ampyx is rare in the Slemmestad section, which again points to a preference for relatively muddy substrate, as other mud-bottom forms are rare or absent in the Slemmestad section as well. Cephalae of *Ampyx nasutus* lacking a glabella spine were reported from the East Baltic area by Schmidt (1894), whereas the specimens described herein are characterized by a long spine. The specimen with the longest spine reported so far is from the Killingen Member of southern Norway (Wandås 1984). It is possible that there is a relation between spine length and substrate. Fortey & Owens (1978) regarded the spines of *Ampyx* as adaptations for support on a soft bottom to prevent sinking into the muddy substrate.

Geragnostids

The *Geragnostus* assemblage is invariably tied to relatively shallow-water habitats in the Komstad Limestone, and I believe that the group was benthic. Agnostids are generally assumed to have been pelagic, but interpretations of life habits are disparate (see Robison 1972 and Müller & Walossek 1987 for reviews). The main reason for inferring a pelagic mode of living for agnostids is their wide distribution in the Middle and Upper Cambrian, with a typical occurrence in black-shale facies (e.g., Jago 1973). However, if they were adapted to low-oxygen facies, survival would benefit greatly by a high production of spat, and, even more advantageous, long lived spat. This would at the same time provide the agnostids with a potential for widespread occurrence, eliminating the need to assume a pelagic mode of life. A pelagic life mode for the Early Ordovician agnostids of Spitsbergen was not regarded likely by Fortey (1980a, p. 23).

Agnostids are uncommon in the Slemmestad section; judging from Schmidt (1894, 1907) they are also scarce in the East Baltic area while very abundant in the *A. raniceps* Zone of southern Öland (Moberg 1890). Tjernvik (1956, p. 191) remarked that agnostids occur far more sparsely in the Billingen Stage than in the underlying beds. This spatial distribution suggests that Ordovician agnostids of Baltoscandia (exclusive of *Micragnostus* and a few related genera) mostly preferred shallower water with muddy substrates (see also Ahlberg 1989a). This seems to be in contradiction to Lamont's (1967) hypothesis that agnostids were mimicking pebble and grit material.

Pek (1977, pp. 34–35) suggested that adult agnostids were epifaunal and lived attached to sea-weed, based on the findings of peculiar accumulations of enrolled specimens lying in rows (Pek 1977, Pls. 9–12). According to Pek's hypothesis, the *Geragnostus* assemblage of the Komstad Limestone could be taken to characterize a sea-weed belt. However, Müller & Walossek (1987) did not find any attachment structures in their extremely well-preserved material of *Agnostus pisiiformis*, but the specimens described were all juveniles, which may be significant. Pek (1977) emphasized that he saw only adult specimens in the 'row-accumulations', and he inferred a different mode of life for juveniles.

When evaluating agnostid ecology it should be kept in mind that different species or genera very likely had different modes of life (cf. Fortey 1980a; Jago 1973). The available material is dominated by *Geragnostella* and *Arthrorhachis*, of which the former appears to dominate in shallower-water habitats, while the latter is comparatively more abundant in somewhat deeper-water settings.

Systematic description of selected taxa

Species of *Asaphus*, *Megistaspis*, *Niobe* (including *Niobella*), *Nileus*, *Stygina*, *Raymondaspis* (including *Turgicephalus*), *Hallanta*, *Dysplanus*, *Platillaenus*, *Panderia*, *Ottenbyaspis*, *Ampyx*, *Rhombampyx*, *Lonchodomas*, *Cnemidopyge* and *Globampyx* are described. The families are arranged in the same order as in the *Treatise on Invertebrate Paleontology* (Moore 1959).

The material studied includes a few specimens from institutional collections (see Table 1). The code in brackets following the specimen number refers to the preservational state; a key to the abbreviations is listed below.

Ecophenotypes

A rigid morphological approach to taxonomy collapses at least in the classification of *Megistaspis* and *Nileus* – but probably also of other trilobite groups – as the species of these genera appear to have been rather 'plastic', with the phenotypic appearances controlled to some degree by environmental factors. This may be a more common phenomenon among trilobites than generally acknowledged (see similar cases described by Cisne *et al.* 1980, Hughes 1991, 1994, and Labandeira & Hughes 1994). Tjernvik (1980, p. 190) ascribed the variability displayed by Scandinavian Lower Ordovician trilobites to evolution, and he suggested that especially *Nileus*, *Niobella* and *Raymondaspis*, but also to a certain degree *Megistaspis*, formed series of more or less imperceptibly intergrading 'species'. This interpretation seems to be contradicted by the circumstances that the morphologies are recurrent, and, even more importantly, are not contemporaneous in different areas. The gradual morphological changes described, e.g., by Kaufmann (1933a, b, 1935; see also Hoffman & Reif 1994) and Sheldon (1987) are considered parallel examples of environmental control of phenotype, in effect mimicking evolution (see also remarks by Cisne *et al.* 1980, pp. 58–59).

The apparent environmental control of the phenotype raises taxonomical difficulties. Botanical nomenclature separates 'ecotypes' at the subspecies level, but in the case of *Megistaspis* such an approach entails that several subspecies coexisted (and the subspecies boundaries remain dubious). Alternatively the term 'variant' may be restored, or it could be argued that no distinction should be made, i.e. adopting a broad species concept. It is deemed necessary to adopt broader species scopes of the Scandinavian Lower Ordo-

vician megistaspids, but, on the other hand, not to distinguish ecophenotypes means loss of information. The formal classification problems are bypassed with regard to *Megistaspis* by employing an open nomenclature, whereas a distinction of ecophenotypes as subspecies works fairly well in *Nileus*, at least in the material at hand. However, a recognition of variants may prove the only way to tackle the problem looking at *Nileus* on a regional scale.

Terminology

The morphological terminology of Harrington (1959) is followed with a few exceptions and emendations (listed below). Hypostomes are described from the ventral side. The hypostomal terminology for asaphids introduced by Jaanusson (1953a, Textfig. 3, *non* Textfig. 2) is, with a few exceptions, adopted in English translation (Fig. 57).

Descriptive terms

Anterior and posterior branch of axial furrows. – Translations of *vorderer Teil der Dorsalfurche* and *hinterer Teil der Dorsalfurche* as used for illaenids by Jaanusson (1954 p. 552; 1957, Textfig. 7). The section of the axial furrow anterior to the lateral pit [*q.v.*] is referred to as the *anterior branch*; the section behind the pit is referred to as the *posterior branch*.

Bacculae. – Following Öpik (1967) and Fortey (1975a), this term is applied to inflated areas flanking the base of the glabella, previously termed *alae* or *basal glabellar lobes*. See Fortey (1975a, pp. 14–15) for further remarks.

Basal glabellar furrows. – Asaphid *Augengruben* (*sensu* Schmidt 1901).

Cranidial angle. – Sagittal curvature of illaenimorph cranidia, measured as angle between tangents of posterior part of glabella and anterior part of cranium (Jaanusson 1957, pp. 83–84, Textfig. 1).

Glabellar muscle area. – A segmental numbering, F0 to F4, is applied, counting from behind. When muscle impressions

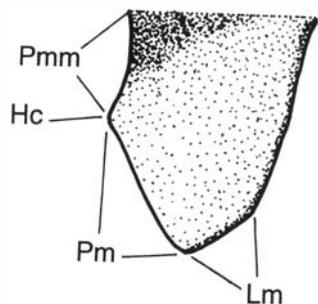


Fig. 57. Terminology of anterior hypostomal wing of *Asaphus* (from Jaanusson 1953a, Textfig. 3). Lm = Lateral margin; Pm = Posterolateral margin; Hc = Hind corner; Pmm = Posteromedian margin.

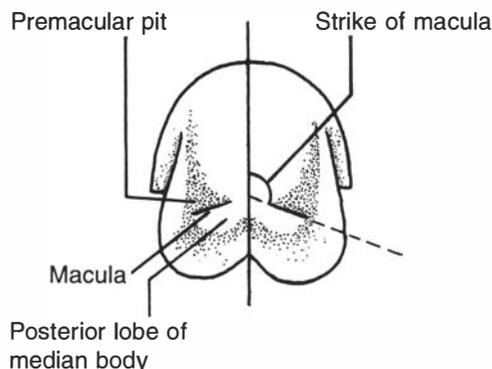


Fig. 58. Terminology, hypostome.

are partially effaced, no numbering has been used, as it might not refer to homologous muscle sites. Glabellar muscle insertion sites are termed *muscle areas*; if impressed they are referred to as *muscle scars*, and if the test is dark or light coloured the term *muscle markings* is applied.

Lateral pits of axial furrows. – Illaenid *Lateralgrube* (*sensu* Jaanusson 1954, p. 552). Virtually all illaenid species show a bend of cephalic axial furrows; the bending point is more or less distinctly impressed and is referred to as lateral pit of axial furrow.

Macula. – This hypostomal term has been used in different ways by previous authors. The term is here used in the sense of Lindström (1901), referring to the flat, steeply sloping surface bounding the premacular pit posteriorly.

Paradoublural furrow. – Furrow demarcating paradoublural line. English synonym of *Duplikaturfurschen* (Schmidt 1901).

Paradoublural line. – Dorsal position on exoskeleton of inner limit of doublure, which may or may not be indicated by the morphology.

Paradoublural ridge. – Elongate swelling of the librigena between paradoublural furrow and border furrow.

Postaxial ramp (new). – Descending axial ramp posterior to the terminal piece of niobinid pygidia. A ramp differs from a postaxial ridge by being broader and shorter.

Posterior lobe of median body. – The premacular pits and the maculae divide the median body of hypostomes into a large anterior lobe and a short, often weakly inflated posterior lobe. The posterior lobe of the median body was termed *consoles* by Lindström (1901) and *maculae* by Balashova (1976).

Premacular pits. – Following Balashova (1976), the term is applied to the deep pits in front of the hypostomal maculae. Called *Muscheleindrücken* by Brögger (1886).

Snout. – Cranidial term for the slender, elongate distal part of frontal area (Bohlin 1960).

Measurements

All measurements are maximum values with specimen in optimal position, if not otherwise stated. This condition is especially important with regard to the sagittal length of cranidia and pygidia, and in forms showing a strong convexity, such as illaenids. In the few cases where specimens are measured in 'life' position, 'dorsal projection' is specified. The stated glabellar length includes the occipital region. Width of glabella is measured between hind corners of palpebral lobes in nileids, in which the length of posterior fixigena is measured exsagittally between posterior margin of cranidium and inner posterior corner of palpebral lobe. The direction of the facial suture is measured in degrees clockwise from sagittal line. For hypostomes with posterior notch, a distinction is made between sagittal length and maximum length (ML), measured exsagittally to end of border lobe.

Strike of bacculae (niobinids). – Angle (clockwise) between long axis of bacculae and sagittal line. The feature is possibly size-related, with an increased alignment of bacculae to sagittal line during growth, but the material is too limited to confirm this.

Strike of maculae. – Angle (clockwise) between posterior crest of maculae and sagittal line (Fig. 58).

Length of pygidial axis. – Measured to the posterior edge of the terminal piece. This specification is especially important for niobinids, where a postaxial ramp is developed.

Abbreviations

- FW Width across posterior fixigenae of cranidium, usually expressed as ratio of cranial length (FW:L)
- L Sagittal length (skeletal part referred to obvious from context)
- ML Maximum length of hypostomes showing posterior notch, measured exsagittally to end of border lobe
- OD By original designation
- PW Greatest preocular width of cranidium, usually expressed as ratio of cranial length (PW:L)
- SD By subsequent designation
- W Maximum width (skeletal part referred to obvious from context)
- (c) Corroded test surface (the corrosion is due to small-scale pressure solution)
- (d) Doublure exposed
- (em) External mould
- (im) Internal mould

- (is) Ventral side of test
- (pim) Partly internal mould
- (pc) Partly corroded test surface
- (t) Test intact

Family Asaphidae Burmeister, 1843

Subfamily Asaphinae Burmeister, 1843

Genus *Asaphus* Brongniart, 1822

Type species. – *Entomostracites expansus* Wahlenberg, 1821 (SD Jaanusson 1956b).

Material of ASAPHUS. – Forty-two complete specimens, 9 cephalae, 51 cranidia, 11 librigenae, 23 hypostomata and 221 pygidia, of which 1 complete specimen, 1 librigena and 12 pygidia are too poorly preserved to be assigned to species.

Remarks on generic subdivision. – The definition of *Asaphus* has been subject to discussion and revision since the work of Angelin (1851), and the issue is still in a state of flux (cf. Balashova 1976).

Currently defined subgenera of *Asaphus* are *A. (Asaphus)* Jaanusson, 1953 (August) [= *A. (Schizophorus)* Balashova, 1953 (December)], *A. (Neoasaphus)* Jaanusson, 1953 (August) [= *A. (Trematophoris)* Balashova, 1953 (December)], *A. (Multiasaphus)* Balashova, 1976, *A. (Subasaphus)* Balashova, 1976, and *A. (Postasaphus)* Balashova, 1976. The distinction of the latter three taxa is considered dubious, and future revision will most likely result in a reassignment of the few species in these groups to *A. (Neoasaphus)*. Possible additional subgenera are *A. (Onchometopus)* Schmidt, 1898, which is separated at the generic level by some authors (Lamansky 1905; Schmidt 1907; Sigfried 1936; Balashova 1976), and *Ogmasaphus* Jaanusson, 1953, which perhaps should be separated only at the subgenus level (Henningsmoen 1960, pp. 235–236).

Asaphus (Asaphus) Jaanusson, 1953

The investigated material includes only *Asaphus (Asaphus)* Jaanusson, 1953. This subgenus contains the oldest representatives of *Asaphus* and is characterized by having comparatively small eyes, no genal spines, an open notch- or slit-like panderian opening in the thoracic doublure, and a rather wide pygidial doublure, typically provided with a limited number of fairly distinct terrace lines.

The species of *A. (Asaphus)* can be separated into two species groups (modified after Jaanusson 1953a and Balashova 1953):

The *A. EXPANSUS* group. – *A. expansus* (Wahlenberg, 1821), *A. fallax* Angelin, 1854, *A. lepidurus* Nieszkowski, 1859, *A. broeggeri* Schmidt, 1901, *A. raniceps* Dalman, 1827 [*nomen dubium*].

The *A. 'RANICEPS'* group. – *A. 'raniceps'* [*sensu* Angelin 1854 and Schmidt 1901; *non* Dalman 1827], *A. acuminatus* (Boeck, 1838), *A. striatus* (Boeck, 1838), *A. incertus* Brögger, 1882 [*nomen dubium*], *A. vicarius* Törnquist, 1884 [? = *A. 'raniceps'*] [*nomen dubium*], *A. maximus* Brögger, 1886 [*nomen dubium*], *A. lamanskii* Schmidt, 1901, *A. sp.* Johansson, 1980 [? = *A. incertus*], ? *A. sp.* A [? = *A. incertus*].

Invalid species of unknown affinity. – *A. princeps* Wiman, 1906 [*nomen nudum*], *A. superior* Wiman, 1906 [*nomen nudum*].

Balashova (1953, p. 396) firstly described the thoracic doublure of *A. major* (= *A. pachyophthalmus* var. *major* Schmidt, 1901) as similar to that of *A. raniceps* [*sensu* Schmidt, 1901], and the species was, accordingly, included in *A. (Schizophorus)* [= *A. (Asaphus)* Jaanusson, 1953]. However, Balashova (1976) later stated that the thoracic doublure of *A. major* shows panderian organs with aperture, not a slit, i.e. is of *A. (Neoasaphus)* type. Balashova did not comment on this change of interpretation, but it may reflect that the material

originally identified with *A. major* by Balashova (1953) was incorrectly assigned (cf. list of synonymy, Balashova 1976, p. 9).

Wiman (1906c, pp. 102, 105) listed *A. princeps* n.sp. and *A. superior* n.sp. from, respectively, the *Limbata* limestone and the Upper *Asaphus* limestone of southern Öland. The material that formed the basis of these invalid species names could not be located in the repository of the Geological Survey of Sweden, Uppsala.

The ASAPHUS EXPANSUS species group

The members of this group are characterized by a comparatively broad panderian opening in the inner margin of the thoracic doublure, widening adaxially (Balashova 1953); furthermore, most of the species have strongly impressed occipital and basal glabellar furrows, very well-developed vincular notch and hook, and a relatively broad hypostome with median body showing anterior lobe that is broader (tr.) than long, and an only slightly inflated posterior lobe, if inflated at all.

Asaphus priscus, described by Lamansky (1905, pp. 61–62, 169, 173), was stated to be characteristic of the BII α Zone. As



Fig. 59. Stratigraphical distribution of *Asaphus* (*Asaphus*) species in Baltoscandia (includes data from Balashova 1953, 1976; Tjernvik & Johansson 1980).

the original description was not accompanied by figures, Jaanusson (1953a, p. 392) declared *A. priscus* a *nomen nudum*, but Lesnikova (in Lesnikova & Weber 1949, Pl. 19:1a, b) had a few years earlier figured a specimen, originally collected by Lamansky. The species was transferred to *Ptychopyge* by Balashova (1953, p. 424) and later became the type species of *Protoptychopyge* Balashova, 1959.

A. broeggeri is for the time being the stratigraphically oldest known representative of *Asaphus*. This peculiar species, described by Schmidt (1901) and Balashova (1953), is characteristic of the East Baltic BII β Zone (Lamansky 1905; Schmidt 1907) but ranges from the upper part of BII α and into the lower part of BII γ (Balashova 1953, pp. 389, 424). Tjernvik (1956, p. 258) mentioned two poorly preserved pygidia, resembling *A. broeggeri*, from the upper part of the *M. estonica* Zone of Sweden, but subsequently the determination was changed to *Protoptychopyge*? (Tjernvik 1980, p. 188). *A. broeggeri* was assigned to the *A. 'raniceps'* species group by Jaanusson (1953a, p. 397), because of the indistinct occipital furrow and the diffuse basal glabellar furrows. However, prime importance is attached to doublural morphology in asaphid taxonomy, and as a consequence, *A. broeggeri* is here allocated to the *A. expansus* species group (see description by Balashova 1953).

A. raniceps was originally defined as a variant of *A. expansus*, characterized by the angulate anterior junction of the facial suture (Dalman 1827, Pl. 3:4). A species, identified with *A. raniceps*, was later described by Angelin (1854), Brögger (1886), Balashova (1953) and at length by Schmidt (1901), and this form defines the *A. raniceps* Zone of Lamansky (1905). *Asaphus raniceps sensu* Angelin (1854) [= *A. raniceps* as described by Brögger, Schmidt and Balashova] is not, however, identical to *A. raniceps* Dalman. This problem was hinted at already by Törnquist (1884, p. 63), but first discussed in detail by Jaanusson (1953a, p. 394), according to whom the specimen figured by Angelin (1854), and later by Brögger (1886), cannot belong to the original material collected by Dalman, despite contrary claims by Brögger (1886, pp. 26, 75). *A. raniceps (s.str.)* seems to be confined to the Zone of *A. expansus*, where it may be as frequent as *A. expansus* itself, according to Tjernvik & Johansson (1980, p. 190). These authors added that this was also the case in 'the corresponding unit of Norway', which, however, is not so at Slemmestad. Examination of material at the Swedish Museum of Natural History, Stockholm, has convinced me that Tjernvik & Johansson's (1980) identification of *A. raniceps (s.str.)* is correct (for details, see discussion of *A. expansus*). Consequently, it appears that the Zone of *A. 'raniceps'* is characterized by a misidentified species of *Asaphus*, and that *A. raniceps (s.str.)* probably is confined to the preceding Zone of *A. expansus*. This is the reason why the Zone of *A. raniceps* is referred to as the Zone of *A. 'raniceps'* (see Jaanusson & Mutvei 1953, p. 30). *A. raniceps (s.str.)* is clearly a member of the *A. expansus* group, characterized, e.g., by a fairly well-impressed occipital furrow.

The *ASAPHUS* '*RANICEPS*' species group

The members of this group are characterized by a narrow, slit-like panderian opening in the inner margin of the thoracic doublure; the opening may taper adaxially (Balashova 1953, 1976). The species typically also have a shallow occipital furrow (occasionally effaced mesially), shallow basal glabellar furrows, a moderately distinct vincular notch and hook, and an elongate hypostome, with an anterior lobe of median body that is as long as wide or longer, and with a somewhat inflated posterior lobe.

The first representatives the *Asaphus 'raniceps'* species plexus appear at the base of the *A. expansus* Zone and its eastern Baltic equivalent, BIII α . *A. lepidurus* is a plausible ancestor of the group.

A. 'raniceps', characterizing the *A. 'raniceps'* Zone, is rather different from the smaller *A. raniceps (s.str.)* (see discussion above), but the confusion, caused by the traditional misidentification, is now mainly nomenclatorial and not based on practical identification problems. Before a new name is given to *A. 'raniceps'*, the relations to *A. vicarius* should be clarified, as this species possibly is a valid synonym (see also Jaanusson 1953a, p. 394). *A. vicarius* is known only through the original description (Törnquist 1884, pp. 64–65; Pl. 2:18–20), but the accompanying figures are inaccurate, according to Brögger (1886, p. 30). *A. vicarius* appears to be characteristic of the interval corresponding to the *A. 'raniceps'* Zone of the Siljan Region (Jaanusson & Mutvei 1951); it has not been reported from other areas.

The East Baltic *A. lamanskii*, described by Schmidt (1901), Sigfried (1936), and Balashova (1953), has not been found in Scandinavia, but it is probably a close relative of the coeval *A. acuminatus*.

The *Asaphus (Asaphus)* group almost disappears at the beginning of *M. obtusicauda* Zone (BIII γ) and is replaced by the *Asaphus (Neoasaphus)* group. The earliest verified member of the *A. (Neoasaphus)* group is *A. major*, and this species is perhaps, as indicated by Balashova (1953), the ancestor of this prolific group. The ancestry of *A. major* is uncertain, but it may stem from *A. 'raniceps'*, as suggested by previous authors (Lamansky 1905; Balashova 1953). However, a more plausible ancestor to the *A. (Neoasaphus)* line is *A. striatus*, which is one of the most '*Neoasaphus*-like' members of *A. (Asaphus)*, having large eyes and a wide pygidial doublure with numerous terrace lines. Besides, it is the youngest representative of *A. (Asaphus)* yet recognized.

Asaphus was a typical element in shallow-water environments, and its marked radiation at the beginning of the Kunda Stage was most likely connected to the sea-level lowstand during the *A. expansus* Zone, where suitable shallow-water environments spread over a vast region of Baltoscandia. The lowstand period reached a culmination in the upper part of the *A. 'raniceps'* Zone. The shift from *A. (Asaphus)* to *A. (Neoasaphus)* appears connected with increasing water depth towards the close of Kunda Stage.

Asaphus (Asaphus) expansus (Wahlenberg, 1821)

Figs. 60–61, 65.

Synonymy. – (Key papers only; see Brögger 1882, Schmidt 1901, and Jaanusson 1956b for additional references.) □1821 *Entomostracites expansus* – Wahlenberg, pp. 25–27 (description, occurrence). □1827 *Asaphus expansus* – Dalman, pp. 240–242; Pl. 3:3a–d (description, occurrence, illustrations of complete specimens and cephalon). □1847 *Hemicrypturus expansus* – Hawle & Corda pp. 69–70, Pl. 4:37 (description, designation as type of *Hemicrypturus*). □1854 *Asaphus expansus*. Linn. ex. p. – Angelin, pp. 52–53; Pl. 28:1, 1a–b (brief diagnosis, occurrence, illustrations of complete specimen and cephalon). □v 1882 *Asaphus expansus*, Linn., Wahlenberg – Brögger, pp. 85–92; Pls. 7:1–5; 8:6 (description, occurrence, illustrations of complete specimens, hypostome, pygidium). □v 1886 *Asaphus expansus*, Linné – Brögger, pp. 29, 72–73; Pls. 1:2; 3:49–51 (description of hypostome and thoracic articulation; illustrations of hypostome and thorax). □v 1901 *Asaphus expansus*, L. – Lindström, pp. 39–40; Pl. 1:8–17 (description of hypostome and eye; illustrations of eye and hypostome). □v 1901 *Asaphus fallax* Dalm.? – Lindström, p. 41; Pl. 1:18–22 (brief comments on hypostome and eye; illustrations of eye and hypostome). □1901 *Asaphus expansus*, L. Dalm. – Schmidt, pp. 24–29; Textfigs. 14–16; Pls. 1:1–3, 5; 12:6 (description, occurrence, illustrations of complete specimens, hypostome, pygidia). □1905 *Asaphus expansus*, Dalm. – Lamansky, pp. 56, 168, 169 (listed). □1936 *Asaphus expansus* Dalm. – Sigfried, pp. 25–28; Textfigs. 1–5; Pl. 1:1–8 (description of doublure, illustrations of doublure and enrolled specimen). □1953 *Asaphus (Schizophorus) expansus* Dalman – Balashova, pp. 391–392; Pls. 1:2, 20, 32; 2:14 (supplementary description to Schmidt 1901, occurrence, illustrations of cephalon, hypostome, cephalic and thoracic doublure). □v 1956b *Asaphus expansus* (Wahlenberg) – Jaanusson, pp. 90–96; Pl. 1:1–5 (designation of lectotype; illustrations of complete specimen [lectotype]). □1976 *Entomostracites (Asaphus) expansus* (Wahlenberg) – Reymont, Fig. 29 (illustration of lectotype). □1980 *Asaphus expansus* (Linnaeus) – Tjernvik & Johansson, pp. 177, 194 (occurrence).

Lectotype. – Complete specimen, designated and figured by Jaanusson (1956b, Pl. 1:1–5); refigured by Reymont (1976, Fig. 29).

Material. – Thirty-three complete specimens, 5 cephalae, 5 cranidia, 4 librigenae, 6 hypostomata, and 28 pygidia.

List of material. – □Complete specimens A 440 (pim) [MGUH 22.376], A 456 (im), A 472 (im), A 476 (pim), A 477 (pim), A 478 (pim) [MGUH 22.379], A 487 (pim), A 489 (pim), A 491 (im), A 492 (im), A 495 (pim), A 497 (pim), A 501 (pim) [MGUH 22.378], A 503 (im), A 504 (im), A 505? (im), A 508 (im) [MGUH 22.372], A 512 (pim), A 514 (im/c), A 515? (im), A 517 (pim), A 518 (im), A 520? (im), A 521 (pim), A 523 (pim), A 525 (im), A 533 (im), A 539 (im), A 544 (im), A 565 (t) [MGUH 22.377], A 1102 (t) [MGUH 22.373], A 1124 (im), A 1128? (c). □Cephalae (all with some

contiguous thoracic segments) A 483 (im) [MGUH 22.375], A 535 (pim), A 541 (pim), A 578a (im), A 578b with hypostome (im). □Cranidia A 527 (im), A 528 (im), A 1115 (pim), A 1126 (im), A 1147 (pim). □Librigenae A 502 (im), A 509? (im), A 1122 (im), A 1136? (pim). □Hypostomata A 415 (pim), A 1135 (pim), A 1158a (pim) [MGUH 22.374], A 1160b (pim), (see also A 578b), PMO 142.595. □Pygidia A 413 (t), A 417 (im), A 425 (pim), A 439? (im), A 445 (im) [MGUH 22.380], A 446 (im), A 449 (pim), A 457? (im), A 473? (im), A 479 (im), A 493? (im), A 499 (im), A 522 (im), A 524? (im), A 540 with thoracic segments (im), A 542 (im), A 547 with thoracic segments (im), A 559? (im), A 562 with thoracic segments (im), A 1104? (im), A 1105? (im), A 1132 (t), A 1139? (pim), A 1140? (im), A 1149 (im), A 1152 (im), A 1154 (im), A 1155? (c).

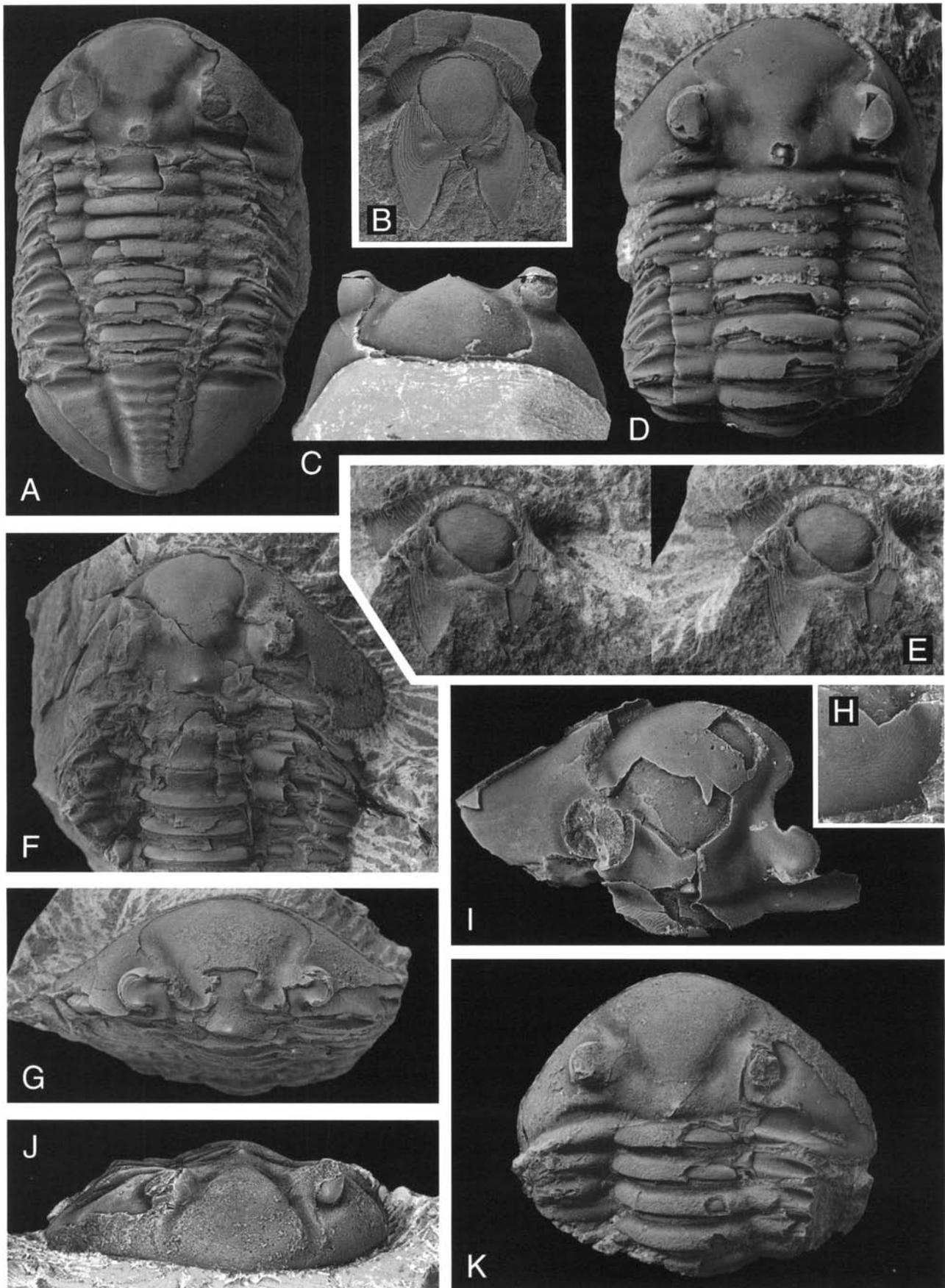
Occurrence. – *Asaphus expansus* is very frequent in the upper half of the Lysaker Member at Slemmestad, where it has been found in bed interval A-29 to A-56, constituting the *A. expansus* Zone; the species presumably continues into the basal part of the overlying Svartodden Limestone (Størmer 1953, p. 43; Brögger 1882, pp. 25, 90), surmised to represent the *A. 'raniceps'* Zone.

A. expansus, which does not occur in the Komstad Limestone, is characteristic of the *A. expansus* Zone of Sweden and the equivalent level in the eastern Baltic area (Tjernvik & Johansson 1980; Schmidt 1901; Balashova 1953). It appears, however, to range into the basal part of the *A. 'raniceps'* Zone, not only in the Oslo region, but also on southern Öland (Wiman 1906c, p. 105), and in the eastern Baltic area (Lamansky 1905, pp. 58, 62, 169).

Description. – See Brögger (1882), Schmidt (1901), and Balashova (1953). A few additional observations are discussed below.

Affinities. – *A. expansus* is close to *A. lepidurus*, but several distinguishing characters were pointed out by Schmidt (1901, pp. 30–32) and Balashova (1953, p. 392); see discussion of *A. lepidurus* below. Of these, the cephalic terrace-line ornamentation and the concavity of the pygidial doublure seem to be more variable characters than recognized by Schmidt (1901). His material of *A. expansus* showed a smooth cephalic test, but all well-preserved cephalae in the material at hand exhibit terrace lines at least on the glabella (see also Balashova 1953, p. 391). Small cephalae of *A. expansus* may show a very delicate terrace-line ornamentation on the glabella, palpebral areas and occipital ring, i.e. resemble the *A. lepidurus* condition, whereas adult specimens of *A. expansus* (Fig. 60H) are characterized by a coarser and less dense terrace-line pattern compared to adult specimens of *A. lepidurus*.

The primary criterion for distinction between pygidia of *A. lepidurus* and *A. expansus* is the external test ornamentation, but Schmidt (1901, p. 31) remarked that pygidia of *A. lepidurus* also differ by occasionally showing an outer concavity of the doublure, resembling a 'border'. However, the majority of the *A. expansus* pygidia available exhibit a similar, slightly concave doublure. On the other hand, it appears that the anterolateral part of the doublure in *A. expansus* has a distinct outer transverse ridge immediately behind the level



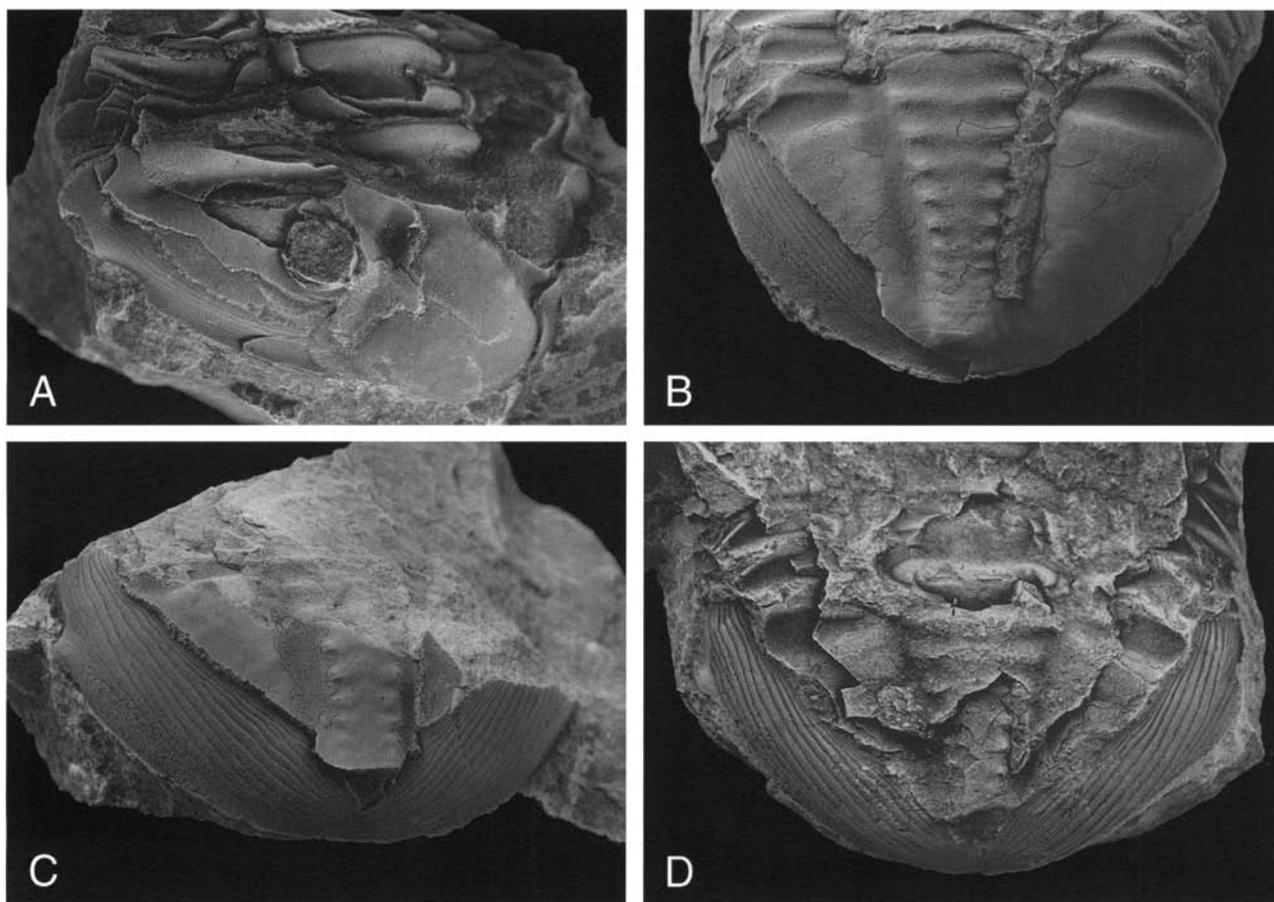


Fig. 61. *Asaphus (A.) expansus* (Wahlenberg, 1821). □A. Exfoliated cephalon showing doublure, $\times 3$. Oblique lateral view. Complete specimen MGUH 22.379 (A 478), bed A-40, Slemmestad. □B. Exfoliated pygidium of complete specimen shown on Fig. 60A, $\times 2$. MGUH 22.372 (A 508), bed A-43, Slemmestad. □C. Internal mould of pygidium showing doublure, $\times 2$. MGUH 22.380 (A 445), bed A-33, Slemmestad. □D. Internal mould of pygidium showing doublure, $\times 2$. Complete specimen MGUH 22.376 (A 440), bed A-33, Slemmestad.

of the articulating facet (see also Törnquist 1884, p. 65), not seen in *A. lepidurus*, and a slight incision in the inner margin at the same level; there are several short interspersed extra terrace lines on the doublure below the articulating facet.

The hypostomes of *A. lepidurus* and *A. expansus* are identical for all practical purposes, although the posterior lobe of

median body tends to be slightly more inflated in *A. lepidurus*. This feature, however, is more variable within *A. expansus* than recognized by Brögger (1886). In all six specimens at hand, the posterior lobe has a positive, albeit minimal relief, also in testaceous specimens (cf. Brögger 1886, p. 29). Balashova (1953, p. 392) claimed that the hypostome of *A. expansus* has a more vaulted median body and almost horizontal 'posterior wings' [posterior border lobes], diverging more strongly, compared to *A. lepidurus*. The posterior border is possibly more flat in *A. expansus*, compared to *A. lepidurus*, but the other differences are not evident in the few hypostomes available.

The differences between *A. expansus* and *A. raniceps* (*s.str.*) are discussed below.

Remarks. – The classical species name *expansus* dates back to Linné (1768), but it has been decided to suppress references to the name prior to Wahlenberg (1821) (ICZN opinion 296; see Jaanusson 1956b); this is the reason for the meandering authorship of *A. expansus*.

Fig. 60. *Asaphus (A.) expansus* (Wahlenberg, 1821). □A. Exfoliated complete specimen, $\times 1.5$. A close-up of the pygidium is shown in Fig. 61B. MGUH 22.372 (A 508), bed A-43, Slemmestad. □B. Hypostome, $\times 1.5$. PMO 142.595, upperpart of the Lysaker Member, Gjeitungholmen, Oslo. □C–D. Slightly distorted small complete specimen, frontal and dorsal views, $\times 3$. MGUH 22.373 (A 1102), bed A-32, Slemmestad. □E. Hypostome, stereo-pair $\times 3$. MGUH 22.374 (A 1158a), bed A-51, Slemmestad. □F. Cephalothorax, 'long' form, $\times 1.5$. MGUH 22.375 (A 483), bed A-40, Slemmestad. □G. Slightly compacted cephalon, 'short' form, $\times 1.5$. Complete specimen MGUH 22.376 (A 440), bed A-33, Slemmestad. (Pygidium shown on 61D). □H–I. Small early cephalon showing terrace lines, dorsal view, $\times 4$, and close-up of frontal glabellar lobe (frontal view), $\times 6$. MGUH 22.377 (A 565), Lysaker Member, Slemmestad. □J–K. Cephalothorax, frontal and dorsal views, $\times 1.5$. MGUH 22.378 (A 501), bed A-42, Slemmestad.

Brögger (1882, p. 90; Pl. 7:1, 2) distinguished a short and a long form of *A. expansus*. 'Long' specimens are by far the most common in the material studied, as among the specimens examined by Brögger (1882, p. 91), and the few 'short' specimens at hand cannot with certainty be ascribed to biological variation, as they equally well may have suffered from symmetrical shortening caused by compaction. The specimen figured as 'short form' by Brögger (1882, Pl. 7:2) is also slightly compacted, augmenting the shortness, but the specimen does represent the short end of variation range. There is, however, definitely no bimodal distribution of short and long forms (see also Schmidt 1901, p. 25).

Brögger (1882, p. 88; Pl. 7:4) mentioned that the facial sutures of *A. expansus* typically meet anteriorly in an ogive, whereas Schmidt (1901, p. 26) described the junction as forming a very blunt angle. The question is relevant, as the original diagnosis of *A. raniceps* (Dalman 1827, Pl. 3:4) primarily stressed the angulate outline of the anterior facial suture in comparison to *A. expansus*. The available material from Slemmestad contains 26 cranidia (including cephalon and complete specimens) with intact anterior margin, of which 10 show a faint to fairly distinctly angulate junction of facial sutures (Fig. 60C). The feature is present in 60% of the cranidia from bed interval A-32 to A-42; above this interval all specimens sampled exhibit a smooth anterior margin. Except for the angulate junction of the facial sutures, the early specimens in all other features correspond to *A. expansus*, and it is possible that the pointed outline of the facial suture is a relict morphology inherited from the assumed ancestor, *A. lepidurus*.

Tjernvik & Johansson (1980, Fig. 10A) figured a cephalon from Östergötland, identified as *A. raniceps* (*s.str.*) (herein shown on Fig. 75A–D). The criteria for identification were not discussed, but *A. raniceps sensu* Tjernvik & Johansson (1980) is fairly common in the Dalman collection from Östergötland (Swedish Museum of Natural History, Stockholm) along with *A. expansus*, and it appears to be the only qualified candidate for *A. raniceps* (*s.str.*) Comparing the original drawings of *A. expansus* and *A. expansus* var. β *raniceps* (Dalman 1827, Pl. 3:3 versus Pl. 3:4), it is evident that *A. expansus* has a relatively broader cephalon and the eyes in a more advanced position; the anterior parts of the facial sutures are not visible in Pl. 3:3d (Dalman 1827), indicating a higher sagittal convexity. The relatively advanced position of the eyes is augmented by the strong sagittal convexity of the cephalon. The second asaphid type in the Dalman collection, similar to the specimen figured by Tjernvik & Johansson (1980, Fig. 10A), matches the figure of var. *raniceps* well (Dalman 1827, Pl. 3:4). The cephalon differs from that of *A. expansus* by being relative longer, semicircular in outline with narrower librigenae; the sagittal convexity is less strong and the glabella is less vaulted (*tr.*), the axial furrows are less strongly impressed, the facial suture meet at front in a mesial boss, the posterior border furrow is narrower (*exsag.*), and the posterior fixigena is overall narrower (*exsag.*), so the eye is relatively closer to the posterior margin.

Tjernvik & Johansson (1980, p. 190) mentioned that *A. raniceps* (*s.str.*) occurs in the *A. expansus* Zone of Norway, but it has not been found at Slemmestad, and no specimens have been seen in museum collections. The cephalic convexity of *A. expansus* changes markedly during growth, and smaller specimens are more vaulted (both ways) and therefore have narrow librigenae in dorsal view (Fig. 60D). Some of the early, small specimens from Slemmestad, up to about 15–20 mm long (*sag.*), with pointed facial sutures and narrow librigenae, superficially resemble *A. raniceps*, but at closer inspection they differ by being significantly more convex (*sag.*), and the glabella is clearly stronger vaulted (*tr.*).

Asaphus (*Asaphus*) *fallax* Angelin, 1854

Fig. 62

Synonymy. – □ 1854 *Asaphus fallax*. Dalm. – Angelin, p. 53; Pl. 28:1e, 3, 3a–c (brief diagnosis, occurrence, illustrations of complete specimen, cephalon, hypostome, pygidium). □ v 1886 *Asaphus expansus*, Linné, var. *fallax*, Dalm. – Brögger, pp. 27–29; Pls. 1:3; 3:46 (description of hypostome and thoracic articulation; illustrations of hypostome and thorax). □ v non 1901 *Asaphus fallax* Dalm.? – Lindström, p. 41; Pl. 1:18–22 [= *A. expansus*]. □ v 1953a *Asaphus fallax* Ang. – Jaanusson, pp. 380, 397, Textfigs. 3:2 and 5:1 (remarks on species limits and details of hypostome, illustrations of anterior wing of hypostome and pygidial doublure). □ v 1959 *Asaphus fallax*, Angelin – Jaanusson, p. O336, Fig. 248:1b (drawing of cephalic doublure and hypostome).

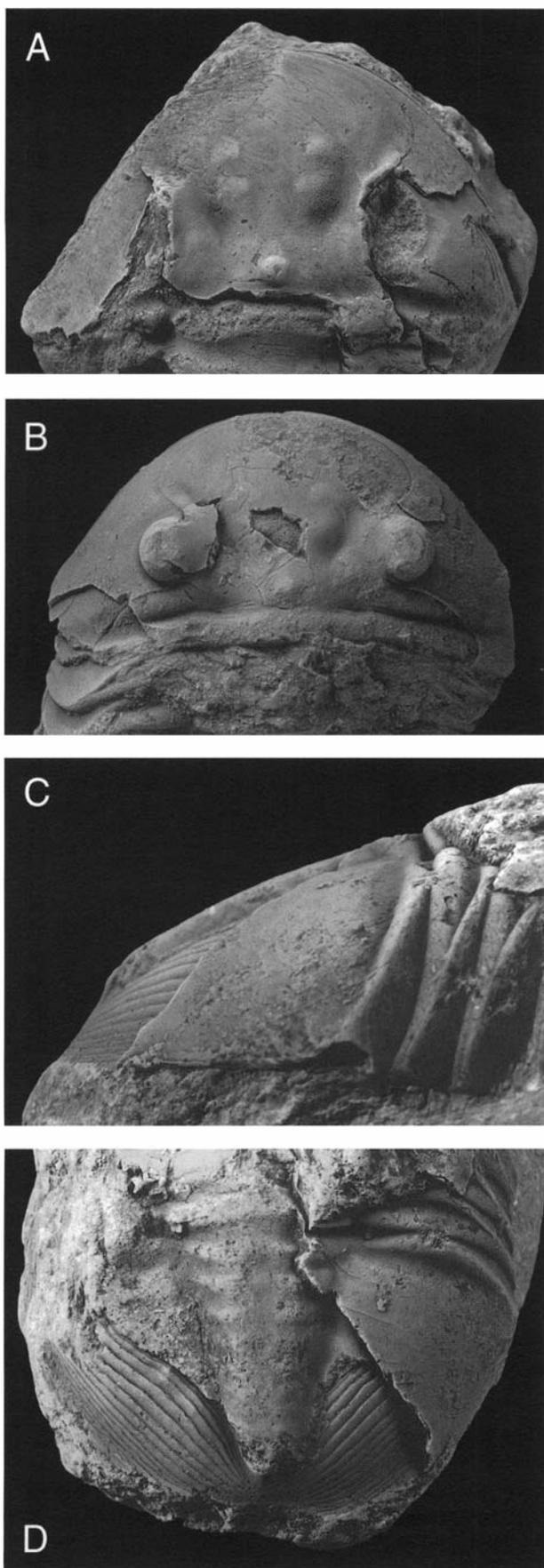
Lectotype. – Complete specimen Ar 16515, figured by Brögger (1886); herein shown on Fig. 62B–D. Designated by Jaanusson (1953a).

Material. – Two complete specimens, including the lectotype.

List of material. – □ Complete specimens Ar 16151 (t), MGUH 22.381 (im).

Occurrence. – Presumably the *A. expansus* Zone of Östergötland, Sweden. The rare species is, so far, known only from the locality Husbyfjöl (Angelin 1854).

Affinities. – By comparison to *A. expansus*, the cephalon of *A. fallax* differs by being only moderately strongly convex (*sag.*), subsemicircular in outline, the glabella is comparatively little vaulted (*tr.*), the facial sutures meet at front in a little point, and two pairs of comparatively distinct muscle insertion sites are situated on the posterior part of the glabella (cf. Angelin 1854, Pl. 28:3a), which appears to be an important diagnostic feature. Furthermore, the eyes are only moderately raised and situated relatively closer to the posterior margin, compared to typical specimens of *A. expansus* (see Angelin 1854, Pl. 28:3b versus 1b); several cephalon of *A. expansus* have, however, similar moderately raised eyes. The unusually short posterior fixigenae (*tr.*) indicated by Angelin (1854, Pl. 28:3, 3a) are not accurately portrayed; in reality



they are longer (cf. Fig. 62B). The posterior border furrow, however, is distinctly narrower (exsag.) than in *A. expansus*. The hypostomal differences indicated by Jaanusson (1953a, Textfig. 3:1 versus 3:2) are not entirely real, as the apparent lack of terrace lines is due to rough preparation of the specimen; distinct terrace lines can actually be seen on the left anterior wing (ventral view) in the same hypostome. The thoracic segments of *A. fallax* have distinctly truncate ends, whereas *A. expansus* segments are more rounded. It is at present not possible to point out any obvious pygidial differences, but *A. fallax* is likely to have a more semicircular pygidium with a higher L:W ratio (see, however, Fig. 65). The pygidial features of *A. fallax*, emphasized by Angelin (1854, p. 53), are not real (see also remarks by Brögger 1886, pp. 27–28); patches of intact test show fine, scattered terrace lines.

Asaphus (Asaphus) lepidurus Nieszkowski, 1859

Figs. 63–65

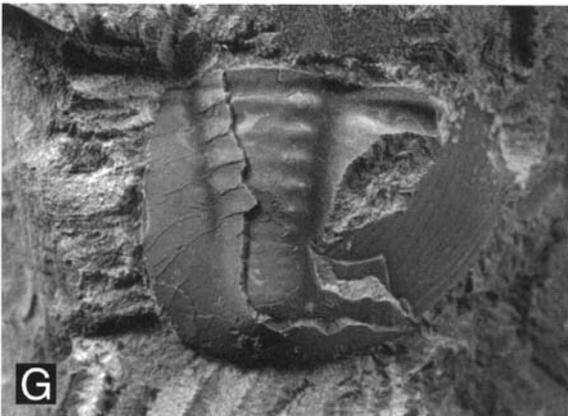
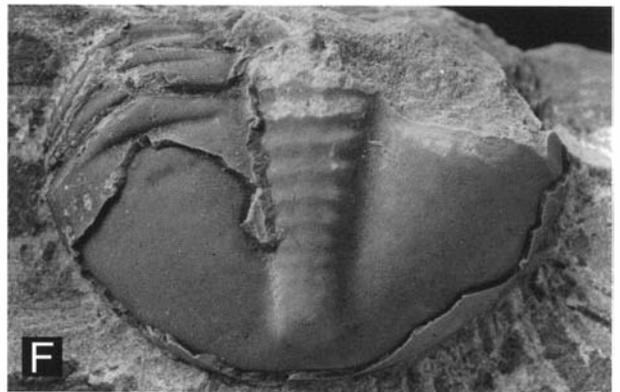
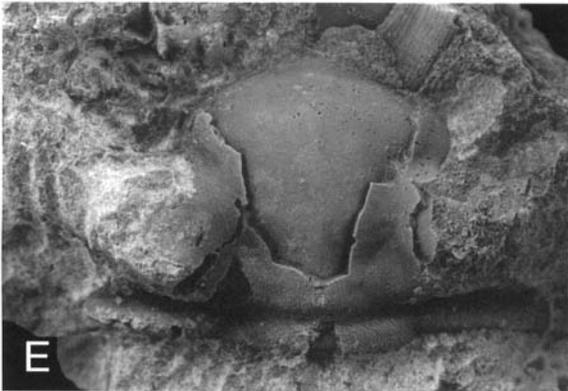
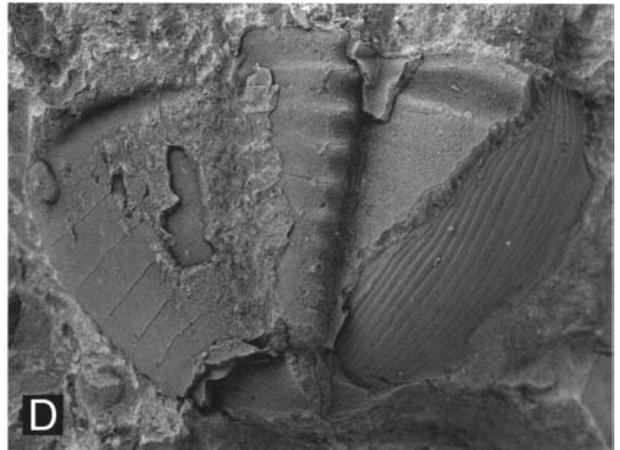
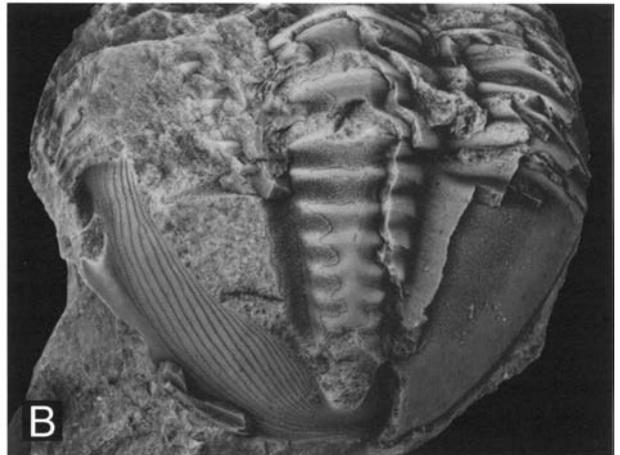
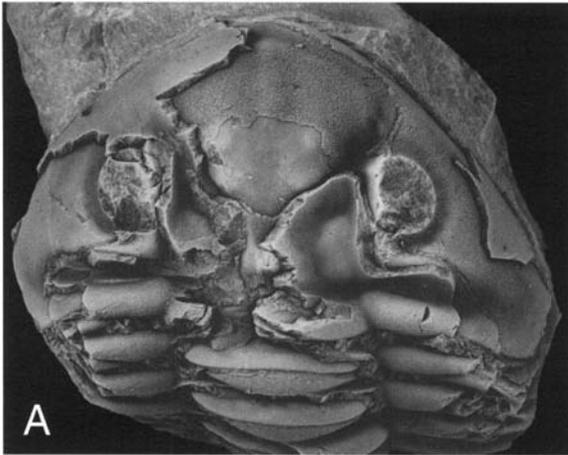
Synonymy. – □1859 *Asaphus lepidurus* m. – Nieszkowski, pp. 360–362 (diagnosis, description). □1901 *Asaphus lepidurus* Nieszk. – Schmidt, pp. 29–32; Textfigs. 17–19; Pls. 1:4, 6, 7; 12:7 (description, occurrence, illustrations of complete specimens, hypostome, pygidia). □1905 *Asaphus lepidurus* Nieszk. – Lamansky, pp. 55, 169 (listed). □1936 *Asaphus lepidurus* Nieszk. – Sigfried, p. 28; Pl. 2:1–4 (notes on thoracic doublure, illustrations of thoracic doublure). □1953 *Asaphus (Schizophorus) lepidurus* Nieszkowski – Balashova, pp. 389–391; Pls. 1:3, 31; 2:3 (description, occurrence, illustrations of complete specimen, hypostome, thoracic doublure). □1960 *Asaphus lepidurus* Nieszkowski – Balashova, Pls. 5:1; 7:3 (illustrations of complete specimen, thoracic doublure). □1971 *Asaphus lepidurus* Nieszkowski – Neben & Krueger, Pl. 4:1–3 (illustrations of complete specimens, pygidium). □v 1980 *Asaphus lepidurus* – Tjernvik & Johansson, pp. 189, 192; Figs. 3, 9I (occurrence, illustration of cranidium).

Lectotype. – Complete specimen figured by Schmidt (1901, Pl. 1:7), designated by Balashova (1976).

Material. – Six complete specimens, 1 poorly preserved cephalon, 4 cranidia, 4 librigenae and 24 pygidia.

List of material. – □Complete specimens A 212 (pim) [MGUH 22.385], MGUH 22.382 (pim), PMO 1641 (im), PMO 2101 (im), PMO 83677 (im), PMO 83679 (im). □Cephalon A 233b? with thoracic segments (im). □Cranidia A 194a (pim), A 232b (im), A 252 (c), A 310 (im) [MGUH

Fig. 62. *Asaphus (A.) fallax* Angelin, 1854. Both specimens are probably from the *A. expansus* Zone. □A. Cephalon, slightly distorted, showing distinct muscle insertion sites, $\times 2$. MGUH 22.381, Östergötland. □B–D. Complete specimen (lectotype), $\times 2$. Ar 16 515, Husbyfjöl, Östergötland. Cephalon and pygidium (lateral and dorsal view); lateral view also shows posterior thoracic segments with truncate terminations.



22.383]. □Librigenae A 214 (im), A 229 (im), A 240? (im), A 278? (im). □Pygidia A 155 (im), A 165a (im), A 177 (im), A 194b with thoracic segments (pim), A 202? (im), A 221a (im), A 221b (pim), A 223 (pim), A 224 (pim), A 225 (pim), A 230a (t) [MGUH 22.388], A 230b (pim), A 230c (im), A 232a (im), A 245 (im), A 248? (im), 255? (pim), A 276? (pim), A 279 (pim) [MGUH 22.386], A 285 (t) [MGUH 22.387], A 324 (pim) [MGUH 22.384], A 338? (im), A 339 (im), A 387? (im).

Occurrence. – *A. lepidurus* is fairly frequent in bed interval A-7–A-20 of the Lysaker Member at Slemmestad; a poorly preserved pygidium from bed A-26½ presumably also belongs to this species. The range defines an upper subzone of the *M. limbata* Zone. *A. lepidurus* does not occur in the Komstad Limestone.

The species is characteristic of the BIIγ Zone in the eastern Baltic area (Lamansky 1905), and it is also common in the so-called *Lepidurus* Limestone of northern Öland (Bohlin 1949; Jaanusson 1951; Tjernvik 1972), whereas it occurs only sporadically in the middle part of the *M. limbata* Zone of mainland Sweden (Tjernvik 1980, pp. 189, 192). The BIIγ Zone (Langevojan Substage of Orviku 1958) seems to equal only the upper part of the western *M. limbata* Zone and not the entire zone (cf. Tjernvik 1972, 1980).

Description. – See Schmidt (1901) and Balashova (1953); diagnostic characters are discussed below.

Affinities. – *A. lepidurus* is a plausible ancestor of *A. expansus*, but the two species are readily separated. By comparison, the cephalon of *A. lepidurus* has acute genal angles and a rhombic glabella, the anterior facial sutures meet at an angle, the axial furrows and the basal glabellar furrows are shallower, the mesial tubercle is distinctly smaller, the anterior border is wider and the doublural vincular notch less well-developed, and well-preserved cephalons show fine concentric terrace lines on the glabella and occipital ring; the thorax of *A. lepidurus* has truncate extremities, and the pygidium is primarily characterized by a different external terrace-line pattern (Fig. 64), where the lines on the axis typically are connected across the sagittal line by bow-shaped connectives, and the pleural fields commonly show numerous short lines, in particular distally, in addition to the raised, gently curved lines outlining the segmentation (seen also in *A.*

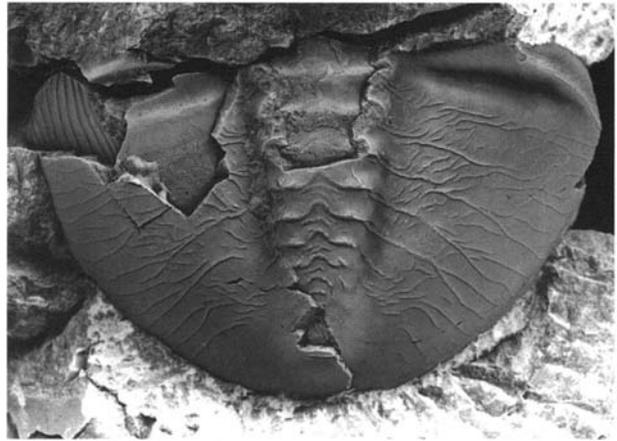


Fig. 64. *Asaphus* (*A.*) *lepidurus* Nieszkowski, 1859. Well-preserved pygidium with intact cuticle showing distinctive terrace-line sculpture, $\times 2$. MGUH 22.388 (A 230a), bed A-13, Slemmestad.

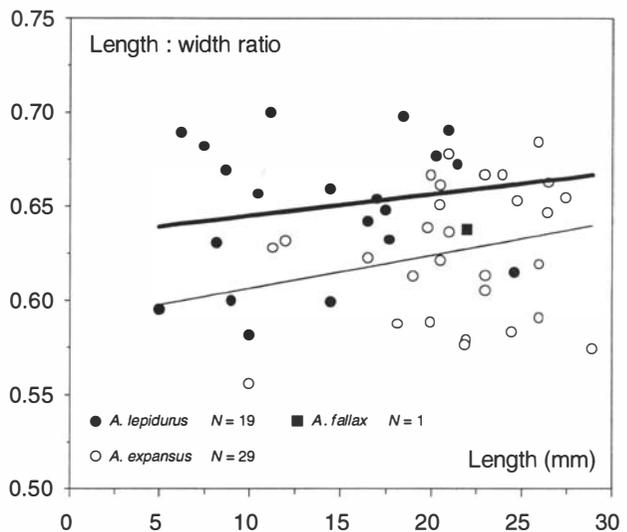


Fig. 65. Pygidia of *Asaphus* (*A.*) *expansus* (Wahlenberg, 1821), *A.* (*A.*) *lepidurus* Nieszkowski, 1859 and *A.* (*A.*) *fallax* Angelin, 1854. Pygidial L:W ratio plotted against length. Regression lines shown for *A. expansus* (upper) and *A. lepidurus* (lower).

Fig. 63 (opposite page). *Asaphus* (*A.*) *lepidurus* Nieszkowski, 1859. □A–B. Largely exfoliated complete specimen; the pygidium shows doublure and axis, $\times 3$. MGUH 22.382, Lysaker Member, unknown locality of Oslo area. □C. Partly exfoliated cranium, $\times 4$. MGUH 22.383 (A 310), bed A-19, Slemmestad. □D. Partly exfoliated pygidium showing doublure and dorsal terrace lines, $\times 3$. MGUH 22.384 (A 324), bed A-20, Slemmestad. □E. Cranium with patches of intact test showing fine terrace lines, $\times 4$. Complete specimen MGUH 22.385 (A 212), bed A-11, Slemmestad. Pygidium shown on F. □F. Internal mould of pygidium showing axis, $\times 4$. Complete specimen MGUH 22.385 (A 212), bed A-11, Slemmestad. □G. Partly exfoliated pygidium showing doublure, internal mould of axis, and exterior terrace lines, $\times 4$. MGUH 22.386 (A 279), bed A-14, Slemmestad. □H. Small, well-preserved pygidium with intact cuticle showing terrace-line sculpture, $\times 5$. Compare Fig. 64. MGUH 22.387 (A 285), bed A-18, Slemmestad.

expansus). A few additional differences were discussed by Balashova (1953, p. 392).

The cephalic terrace-line ornamentation and the concavity of the pygidial doublure is of less diagnostic value than indicated by Schmidt (1901) (see discussion of *A. expansus* above). Balashova (1953, p. 392) stated that the 'primary' terrace lines on the pygidium of *A. expansus* do not reach the outer margin as in *A. lepidurus*; this difference appears to be inconsistent.

The majority of the available pygidia are internal moulds, not covered by Schmidt's diagnosis or the supplementary remarks of Balashova (1953). It appears (at least in the

present material) that pygidia of *A. lepidurus*, compared to *A. expansus*, have a relatively narrow axis with a slightly more expanded terminal piece, and the doublure shows fewer short lines below the articulating facet and a visibly less pronounced outer swelling and inner incision below the anterior half rib. Besides, the pygidia of *A. lepidurus* tend to be marginally more elongate than those of *A. expansus* (Fig. 65), but it is important to compare specimens of the same size, as the ratio changes with size. The available material of *A. lepidurus* pygidia >6 mm long show L:W ratios between 0.58 and 0.70 (mean 0.65; $N = 19$), whereas *A. expansus* pygidia >10 mm long show L:W ratios between 0.57 and 0.68 (mean 0.63; $N = 29$). The juvenile pygidia of *A. lepidurus* at hand (Fig. 63H) do not show the characteristic short terrace lines on the pleural fields in between the raised, slightly curved, continuous lines indicating the segmentation (compare Balashova 1953, p. 390).

Remarks. – The available material is poorly preserved in general but matches *A. lepidurus* as described by Schmidt (1901) and Balashova (1953) in all details. The identification is vital, as *A. lepidurus* has been the source of much stratigraphical controversy (cf. Jaanusson 1951, 1955, 1956a, 1957, 1960; Tjernvik 1972, 1980), and the species was believed absent in the Oslo Region (Tjernvik 1980, p. 189). The collection of the Paleontological Museum, Oslo, contains several specimens of *A. lepidurus*, labelled *A. expansus*. Four of them have been included in the present study.

Asaphus expansus var. *incerta* Brögger was regarded a synonym of *A. lepidurus* by Schmidt (1898, 1901), an interpretation later rejected by Jaanusson (1953a, p. 395). I agree with Jaanusson.

Asaphus (Asaphus) acuminatus (Boeck, 1838)

Figs. 66–69

Synonymy. – □1838 *Trilobites acuminatus* – Boeck, p. 142 (brief diagnosis). □1854 *Asaphus acuminatus*, Boeck – Angelin, pp. 53–54; Pl. 29:2–2a (short description, occurrence, illustrations of cranium and pygidium). □non 1857 *Asaphus acuminatus* – Niezskowski, p. 552. □non 1858 *Asaphus acuminatus* – Hoffman, p. 48; Pl. 5:1 [assigned to *Ptychopyge tecticaudata* by Schmidt 1898]. □non 1859 *Asaphus acuminatus* Boeck sp. – Niezskowski, pp. 363–364; Pl. 1:2–6 [= *A. niezskowskii* s.l.]. □v 1882 *Asaphus acuminatus*, Boeck – Brögger, pp. 93–94; Pl. 8:5, 5a–b (description, occurrence, illustrations of cranium, librigena, pygidium). □cf. 1901 *Asaphus raniceps* var. *acuminata* Boeck sp. – Schmidt, pp. 33–36; Pl. 2:1 (description of *A. raniceps* including *acuminatus*, occurrence, illustration of cranium with disarticulated librigena and thoracic segments). □v 1936 *Megalaspis limbata* Sars & Boeck [partim] – C. Poulsen, pp. 48, 50 (listed). □1941 *Asaphus raniceps* Dalman, var. *acuminatus*

(Boeck) – Størmer, p. 141 (designation of neotype). □cf. 1953 *Asaphus (Schizophorus) acuminatus* Boeck – Balashova, pp. 394–395; Pls. 1:4; 5:3? (description, occurrence, illustrations of hypostome, ?pygidium).

Lectotype. – Here designated, specimen PMO 20214, figured by Brögger (1882, Pl. 8:5a, b); the pygidium is refigured on Fig. 68. According to Brögger's label, the specimen is probably the original specimen studied by Boeck (1838).

Material. – Three complete specimens, 1 cephalon, 21 cranidia, 1 librigena, 4 hypostomata and 40 pygidia.

List of material. – □Complete specimens PMO 1830 (pim), PMO 20214 (im) [original, Brögger 1882, Pl. 8:5–6], PMO 143.498. □Cephalon PMO 1827 (pim) (with thoracic segments). □Cranidia S 1472 (im) [MGUH 22.389], S 1523 (im), S 1524 (im), S 1736 (im), S 1745 (im), F 183 (pim), K 1214 (im), K 1217 (im), K 1244? (im), LU 34 (c), LU 57b (im) [LO 7095], LU 57d (im), LU 62 (is), LU 64 (im) [LO 7099], LU 65a (pim) [LO 7100], LU 70 (im), LU 75 (im), LU 87 (im), LU 101a (im), LU 121 (c), LU 139 (im, juvenile) [LO 7122]. □Librigena S 1740a (im) [MGUH 22.390]. □Hypostomata S 1600 (im) [MGUH 22.391], S 1639 (pim) S 1707 (im), LU 65b (im) [LO 7101]. □Pygidia S 1521? (im), S 1536 (im), S 1608? (im), S 1614? (im), S 1634 (im), S 1635 (pim) [MGUH 22.392], S 1711 (pim), S 1727 (im), S 1740b (c), S 1768 (im), GM 1871.979 (im), GM 1869.874 (im) [MGUH 22.395], F 69 (im) [MGUH 22.393], F 81 (im), F 197 (im), F 199? (im), F 201 (pim), F 306a (im), F 306b (im), K 415a (im), K 415b (pim), K 1213a (pim), K 1213b (im), K 1215 (im), LU 33 (im/c), LU 38a (pim), LU 38b (im), LU 54a? (im), LU 54b (im), LU 57a with thoracic segments (im), LU 57c (im) [LO 7096], LU 62b (im), LU 67 (im), LU 70 (im), LU 78 (im), LU 94 (t) [LO 7107], LU 101b (im), LU 126 (em), LU 157 (im), MGUH 22.394 (im).

Occurrence. – *A. acuminatus* is regarded indicative of the *A. expansus* Zone in the Komstad Limestone area, although it seems to range into the very basal part of the *A. 'raniceps'* Zone, at least elsewhere (see discussion below). The species has been found in the uppermost part of bed +13 and in bed +14 at Skelbro, in beds 18, 20, and 21 at Fågelsång, in the uppermost limestone bed at Limensgade and Gislövshammar, and in the lower half of bed 9 at Killeröd site b. The latter occurrence has been taken to define the local top of the *A. expansus* Biozone, but the lower half of bed 9 is probably of *A. 'raniceps'* Chronozone age (see discussion below).

The museum material studied is mainly from Fågelsång. The bulk, if not all, of the Fågelsång material comes from an interval corresponding to beds 18–23, representing the basal part of the *A. expansus* Zone. Additional museum specimens originate from loose boulders at Andrarum, one juvenile cranium is from Röstånga, and a few specimens (Funkquist coll.) are from the uppermost limestone bed at Tommarp, which is also within the *A. expansus* Zone. Pygidium GM 1871.979 is from the Soldatergård quarry of Bornholm (from the uppermost part of bed +13 or from bed +14).

A. acuminatus has not been found at Slemmestad during the present investigation (see discussion below); the Norwegian specimens listed above (PMO nos.) are from the Svartodden Limestone Member of the Oslo Region, i.e. presumably from the *A. 'raniceps'* Zone. According to Brögger (1882,

p. 93) the museum material in all probability originates from the so-called *Porambonites* Bed (basal Svartodden Limestone).

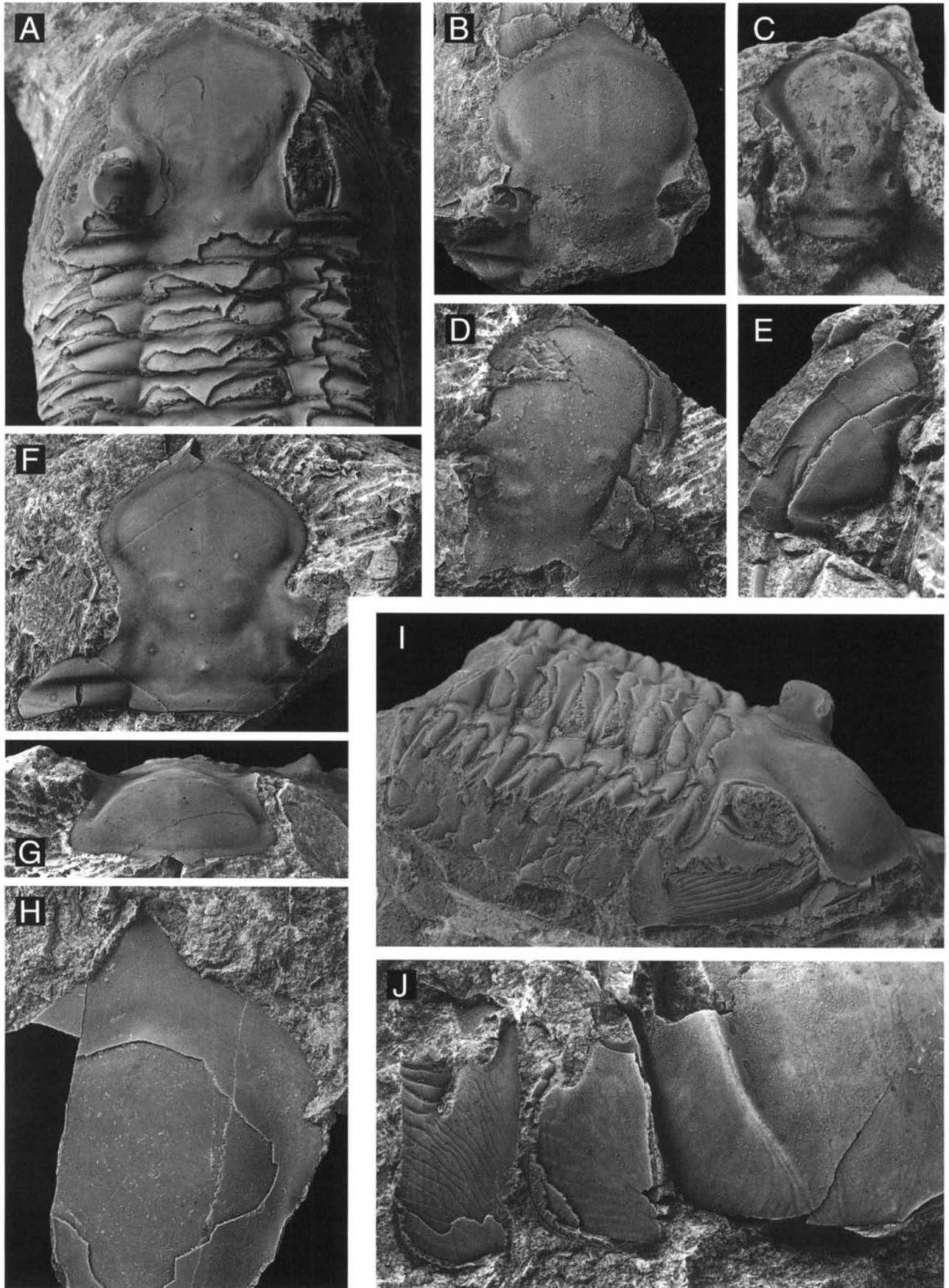
A. acuminatus has, so far, been found with certainty only in the western facies belt (Oslo–Scania–Bornholm), where the species is confined to very shallow-water facies, but perhaps it occurs rarely in the eastern Baltic area as well (Schmidt 1901; Lamansky 1905; Balashova 1953). The identification of the eastern Baltic material is discussed below. Wiman (1906c, p. 105) listed *A. acuminatus* from the 'Upper *Asaphus* limestone' of southern Öland, but his material could not be located in the repository of the Geological Survey of Sweden, and the identification remains in doubt.

Diagnosis. – Anterior branches of facial suture meet 'en ogive', and the cranium is distinctly pointed and has a wide preglabellar area; sagittal cranial convexity low in adults; occipital furrow faint; eyes small. Pygidium strongly vaulted, subtriangular; axis narrow, tapering evenly rearwards; pygidial doublure with 11–16 (typically 12–14) coarse, openly spaced terrace lines across widest part. [Emended from Boeck 1838.]

Description. – Medium-sized to fairly large for an *Asaphus*, largest cranidium 36 mm long, largest pygidium 48 mm long. Cephalon subtriangular in outline, L:W ratio about 2:3. Cranidium of moderate to low convexity (sag.); sagittal curvature diminishes with increasing size, and small cranidia are distinctly more convex than adults (Fig. 66C). Greatest width of cranidium at posterior margin, FW:L ratio varies between 1.34 and 1.42 (mean 1.38; $N=6$), a single specimen shows a ratio of 1.24; greatest preocular width equivalent to slightly more than half of maximum cranial width (mean 0.58; $N=7$). Glabella of low relief, degree of inflation even decreases with increasing size; it is delimited by wide and rather shallow axial furrows and a still shallower preglabellar furrow. All furrows are most deeply impressed in smaller specimens, and the preglabellar furrow is ill-defined in the largest specimens studied. A depression (anterior pit *sensu* Jaanusson 1953a), most obvious on internal moulds, is present in the axial furrow just behind the level of maximum glabella width. Maximum glabella width is midway between eyes and anterior margin and corresponds to about 1.8 times the minimum glabella width, which is between the eyes. Anterior glabella lobe pyriform, with slightly pointed front; it stretches for about 0.7 of the cranial length and occupies the major antero-central part of cranidium; lobe W:L ratio 0.90–1.00 (mean 0.94; $N=10$). On level with the palpebral lobes the axial furrows continue into a pair of basal glabella furrows, shallowing adaxially but with a faint connection across glabella. The furrows, which decrease in distinctness with increasing size, mark the posterior limit of the glabella but must be homologous to transverse lateral glabella furrows; however, the glabella contour is effaced rearwards. A characteristic, low glabella median keel stretches forwards from midpoint (or just behind) of anterior lobe to its front

(Fig. 66B, F), although the foremost part usually is somewhat effaced. The keel is most distinct on internal moulds, but visible also on testaceous specimens; it is divided by a longitudinal furrow in well-preserved cranidia. Two pairs of low nodes, most distinct on internal moulds, but usually also faintly outlined on outside of test, are present on posterolateral part of glabella behind the median keel (Fig. 66B, D, F). The anterior nodes are curved, comma-shaped, transverse; the posterior nodes are straight, oblique. Well-preserved specimens have one or two additional indistinct pairs of smaller nodes situated behind the two larger pairs. Mesial tubercle situated immediately in front of occipital furrow, 0.17–0.19 of the cranial length from posterior margin (mean 0.18; $N=7$). A pair of low, elongate baculae stretches between the basal glabella furrows and occipital furrow; their distinctness decreases during growth. The axial furrow, delimiting the bacula on the outside, continues rearwards into a moderately incised articulating socket, best defined on internal moulds. Occipital furrow faint, almost effaced on testaceous material, delimiting an ill-defined occipital ring; the furrow is better defined in small specimens. Anterior fixigena and preglabellar area narrow and almost of equal width all the way. Palpebral lobes unusually small, raised well above glabella, situated far from posterior margin; length (exsag.) equivalent to 0.16–0.17 ($N=3$) of the cranial length, distance to posterior margin corresponds to about 1.6 times the length of the palpebral lobe. Posterior fixigena comparatively broad, width (exsag.) behind eyes 0.21–0.27 (mean 0.25; $N=5$) of the cranial length; transected by deeply impressed posterior border furrow. Posterior margin of cranidium almost straight, turned slightly backwards in distal half. Internal moulds show a very shallow transverse furrow, which probably is a paradoublural furrow, commencing at the bend of the posterior margin, thence running to the distal end of fixigena. Facial suture converge anteriorly at an angle of about 55–65° to sagittal line (mean 60°; $N=13$), to change direction shortly before sagittal line and join in an acute angle (80–100°; $N=7$), thereby forming the characteristic ogival anterior margin of cranidium. The largest cranidia show the most acute junction of sutures and, consequently, the most prominent anterior 'snout' (Fig. 66H). Posterior branches of facial suture turn sharply outwards behind the eyes, run perpendicular to sagittal line for half the length (tr.) of the posterior fixigenae, then turn gently in posterior direction, and finally turn sharply backwards to intersect posterior margin almost at a right angle.

Many specimens show small patches of preserved test covering different parts of the cranidium. The entire test surface of the cranidium is finely and very densely punctate, but this sculpture is obliterated by even the faintest corrosion. Scattered terrace lines, following the glabella contour, are present anterolaterally on the anterior glabella lobe in the Bornholm–Scanian specimens (Fig. 66H), while the Norwegian cephalons show no such lines. Slightly coarser, more discontinuous and wavy terrace lines are present on the



palpebral area and palpebral lobe, with a general trend parallel to the sagittal line, and single, fine terrace lines occur on the anterior proximal part of the posterior fixigena and on the posterior border, especially distally, orientated roughly parallel to the posterior margin. The Norwegian material generally shows fewer terrace lines than the cranidia from the Komstad Limestone.

Librigena are without spine, but genal angle is acute; posterior border furrow continues onto librigena (Fig. 66E), but shallows up at level with panderian opening in doublure; eye socle well-developed; visual surface small. Internal moulds show very shallow paradoublural furrow; the external expression, if any, is unknown. External test ornamentation unknown.

Doublure of cephalon gently convex, steeply inclined, especially anteriorly and laterally, with a narrow concave strip along the outer margin; the doublure extends inwards along the posterior margin below the posterior border. It is covered with 10–12 coarse, continuous terrace lines (counted laterally); a slit-like panderian opening is incised in the inner margin close to the posterior margin (Fig. 66I); the terrace lines are irregular adjacent to the opening and are only faintly impressed behind, curving inwards.

Hypostome large, length of largest specimen 17 mm. Hypostomal W:ML ratio about 1:1; greatest width is across anterior wings; width across posterolateral borders equivalent to about 0.85 of hypostomal maximum length. Anterior lobe of median body rounded subrectangular in outline, reaching the curved anterior margin; anterior lobe delimited posteriorly by subtriangular premacular pits; W:L ratio of anterior lobe about 0.85. Posterior lobe of median body almost undefined, and the term ‘consoles’ (Lindström 1901) is more appropriate. Maculae elliptical, flat, small, sloping moderately (about 45°) in anterior to anterolateral direction. Each macula rests on a small inflated ‘console’. Anterior wings ascend in dorsal direction at an angle of about 50° from horizontal; the wings join the lateral furrows at base of median body. Dorsal termination of anterior wing resembles the hypostome of *A. fallax*, as figured by Jaanusson (1953a,

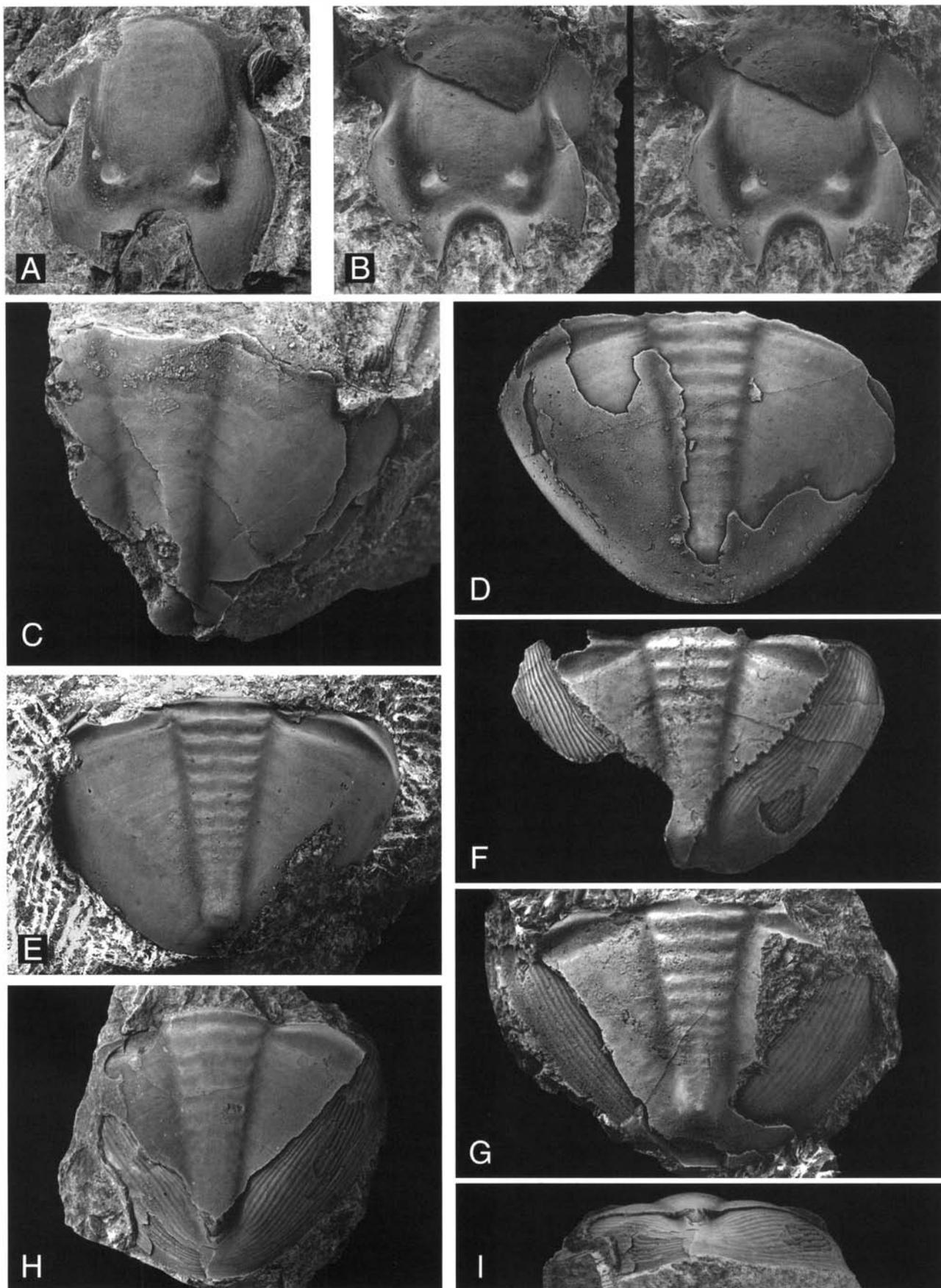
Textfig. 3:2); Jaanusson’s terminology is used here in English translation (Fig. 57). Lateral margin short, half the length of posterolateral margin; hind corner slightly pointed; postero-medial margin ca. 0.75 times as long as posterolateral margin. Lateral border starts at about 0.3 of maximum hypostomal length from anterior margin and widens backwards into a wide, flat posterior border; lateral and posterior borders confluent. Posterior border divided by deep mesial incision stretching inwards for about 0.3 of the maximum hypostomal length. Lateral border furrows moderately impressed, confluent with premacular pits and joined posteriorly via slight depression between the bipartite ‘posterior lobe’ of median body.

The internal moulds show impressions of terrace lines (Fig. 67A, B). Continuous, rather coarse terrace lines are present at least laterally on the anterior lobe of main body, following the contour, and on the main outer part of the lateral and posterior borders, running subparallel to outer margin, while inner part of posterior border lacks terrace lines. Short, discontinuous, coarse terrace lines cross the anterior wings. No terrace lines are impressed on the central part of the median body.

Thoracic axis bounded by distinct axial furrows; it occupies slightly less than 0.4 of the thoracic width (tr.) and is basically of the same width all the way, although a faint expansion is seen from the anterior segment to the fifth segment, behind which the axis barely tapers. Inner half of pleura flat, level with inner limit of articulating facet there is a sharp bend, and distal half of pleura slants rather steeply; termination truncate. Pleural area crossed by deep pleural furrow, running from axial furrow to stop behind articulating facet midway down the steep distal half of the pleura. Articulating facet delimited rearwards by a low crest. Articulating process situated at inner termination of the articulating facet; an additional process is presumably situated at the base of axis. Patches of intact test are finely punctate. Sporadic fine terrace lines occur close to the base of the axis in a Scanian specimen (LU 57a), whereas the pleural fields show only a single transverse line behind the pleural furrow. A posterior, narrow doublural wedge extends all the way to the outer articulating socket (Fig. 66J); the main part of the doublure stops just outside the bending zone between the inner and outer pleural parts. Slit-like panderian opening deeply incised; inner part of doublure slightly lowered in front of incision. Fine terrace lines run obliquely downwards–backwards across main part of doublure; the small lowered area in front of the panderian opening shows coarse, transverse lines (Fig. 66J).

Pygidium typically strongly vaulted, subtriangular in outline; L:W ratio varies between 0.67 and 0.78 (mean 0.72; $N = 28$; Fig. 69A–B). A few specimens are clearly less vaulted than the remaining pygidia. Axis moderately long and narrow, stretching for 0.80–0.92 of pygidial length (mean 0.86; $N = 21$; Fig. 69C–III) and accounting for 0.26–0.32 of pygidial width at anterior margin (mean 0.29; $N = 21$; Fig. 69C–I).

Fig. 66. *Asaphus (A.) acuminatus* (Boeck, 1838). □A. Cephalothorax, ×2. Note fine terrace lines on palpebral lobes. PMO 1827, Lysaker Member, Stensberggaten, Oslo (Kiær coll.). See also I. □B. Internal mould of cranidium showing glabellar muscle insertion sites, ×1.5. LO 7095 (LU 57b), Fågelsång, loc. E21b. □C. Internal mould of juvenile cranidium, ×9. LO 7122 (LU 139), Röstånga. □D. Internal mould of cranidium showing posterior glabellar muscle insertion sites, ×2. MGUH 22.389 (S 1472), bed +13, Skelbro. □E. Internal mould of librigena showing doublure, ×2. MGUH 22.390 (S 1740a), bed +13, Skelbro. □F–G. Exfoliated well-preserved cranidium, dorsal and frontal views, ×2. LO 7099 (LU 64), Fågelsång, loc. E21. □H. Anterior part of large cranidium showing distinct median point; the patches of intact cuticle exhibit openly spaced, fine terrace lines, ×3. LO 7100 (LU 65a), Fågelsång, loc. E21b. □I. Same specimen as in A, left lateral side showing doublure, ×2.5. □J. Close-up of thoracic doublure, posterior two segments and anterior part of pygidium, ×4. PMO 20214 (lectotype), unknown locality, Oslo region. The pygidium is figured on Fig. 68.



Axis slightly raised above pleural fields anteriorly and posteriorly, and approximately of equal height in the middle; it tapers almost evenly in posterior direction but is barely funnel-shaped; minimum posterior width (tr.) is half of the anterior width (mean 0.48; $N = 23$; Fig. 69C-II). Axial segmentation indistinct and normally effaced posteriorly. The segmentation is more distinct in small pygidia, showing 11 axial rings in addition to anterior half-ring and terminal piece, which is gently expanded into a low knob; it is, however, inconclusively indicated by the material that a slightly shorter, broad form has 11 rings and a long form has 12. Anterior 5–7 axial rings, as seen on internal moulds, are true rings; posterior segmentation is indicated by lateral swellings, if not effaced. Axial furrows wide, moderately impressed. Pleural fields fairly strongly convex; no border. Internal moulds show faint traces of pleural ribs (Fig. 67E), up to 9 pairs in a few specimens. Anterior half rib prominent, forming a sharp crest between articulating facet and pleural fields; it is separated from pleural fields by wide, shallow furrow. Articulating facet triangular, slanting forwards, but less so than in many asaphids; anterolateral corner acute. Articulating facets together account for about 0.4 of pygidial width at anterior margin.

Dorsal test surface largely without terrace lines, but a few transverse terrace lines are present anterolaterally on pleural fields; very fine, discontinuous transverse lines cross the axis, and 6–8 pairs of short, oblique lines (matching the segmentation) may occur in anterior part of the axial furrow (Fig. 67C). Entire test surface very finely and densely punctate.

Doublure reaches axis only in posterior end; slight bulge marks position of articulating facet, and narrow concave strip present along outer margin. Doublure covered with 11–16 (mean 13; $N = 16$; most specimens show 12–14) coarse, widely spaced, continuous terrace lines across widest part.

Affinities. – *Asaphus acuminatus* is characterized, among other things, by small eyes, slit-like panderian openings, and a wide pygidial doublure with coarse terrace lines, and the species clearly belongs to *A. (Asaphus)*. The pointed cranidium, the indistinct occipital furrow, and the shallow basal glabellar furrows suggest an assignment to the *A. 'raniceps'* species group. As several authors have questioned the valid-

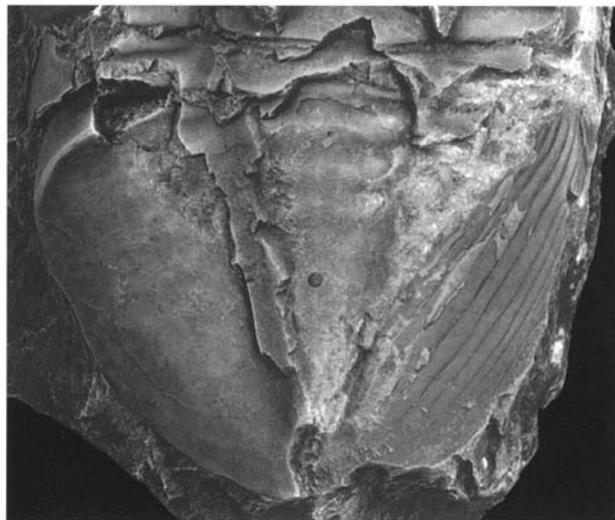


Fig. 68. *Asaphus (A.) acuminatus* (Boeck, 1838). Exfoliated pygidium showing very coarse terrace lines on doublure, $\times 2$. Complete specimen PMO 20214 (lectotype), unknown locality, Oslo area; probably basal part of the Svartodden Limestone. Previously figured by Brögger (1882, Pl. 8:5a). See also Fig. 66J.

ity of *A. acuminatus* (e.g., Schmidt 1901; Jaanusson 1953a), its distinguishing characters are critically assessed.

Compared to the somewhat older *A. broeggeri*, *A. acuminatus* has a slightly higher glabellar relief, better impressed basal glabellar furrows, better defined bacculae, smaller eyes, a more prominent hypostomal median body, and a more strongly vaulted, relatively elongate pygidium with significantly fewer terrace lines on the doublure. The cephalic surface sculpture also seems to be different.

The eastern Baltic *A. lamanskii* is contemporaneous with *A. acuminatus*. *A. lamanskii* is, according to Schmidt (1901, pp. 33–36) and Balashova (1953, p. 393), distinguished from *A. 'raniceps'* by the unusually small eyes, situated far from posterior cephalic margin, the better impressed occipital and basal glabellar furrows, the better impressed and narrower posterior border furrow (occipital furrow *sensu* Schmidt & Balashova), the more strongly backwards-directed posterior branches of the facial suture, and the more distinct segmentation of the pygidial axis, outlined even on testaceous specimens. However, the distinctness of furrows and segmentation diminishes markedly during growth, and the specimens of *A. lamanskii* are typically smallish (Schmidt 1901). It is therefore not possible to point out any reliable cephalic differences between *A. acuminatus* and *A. lamanskii*, except that the latter presumably lacks external terrace lines (cf. Balashova 1953), but the significance of this difference is unknown. Judging from Balashova (1953, Pl. 2:7) the cranidium of *A. lamanskii* may also be less pointed anteriorly, but this character is influenced by size, too. On the other hand, there seem to be some differences between the hypostomes and pygidia of *A. acuminatus* and *A. lamanskii*, ac-

Fig. 67. *Asaphus (A.) acuminatus* (Boeck, 1838). □A. Exfoliated hypostome showing imprints of exterior terrace pattern, $\times 3$. LO 7101 (LU 65b), Fågelsång, loc. E21b. □B. Stereo-pair of exfoliated, partly repaired hypostome, $\times 3$. MGUH 22.391 (S 1600), bed +13, Skelbro. □C. Fragmentary pygidium with intact cuticle showing a sparse terrace-line sculpture, $\times 2$. LO 7107 (LU 94), Fågelsång area. □D. Partly exfoliated pygidium, $\times 1.5$. MGUH 22.392 (S 1635), bed +14, Skelbro. □E. Exfoliated pygidium showing axis and faint segmentation of pleural fields, $\times 1.5$. MGUH 22.393 (F 69), bed 18, Fågelsång. □F. Internal mould of pygidium showing doublure, $\times 1.5$. MGUH 22.394, Fågelsång. □G. Internal mould of pygidium showing doublure, $\times 1.5$. MGUH 22.395 (GM 1869.874), Fågelsång. □H–I. Internal mould of pygidium showing doublure, dorsal and posterior views, $\times 1$. LO 7096 (LU 57c), Fågelsång, loc. E21b.

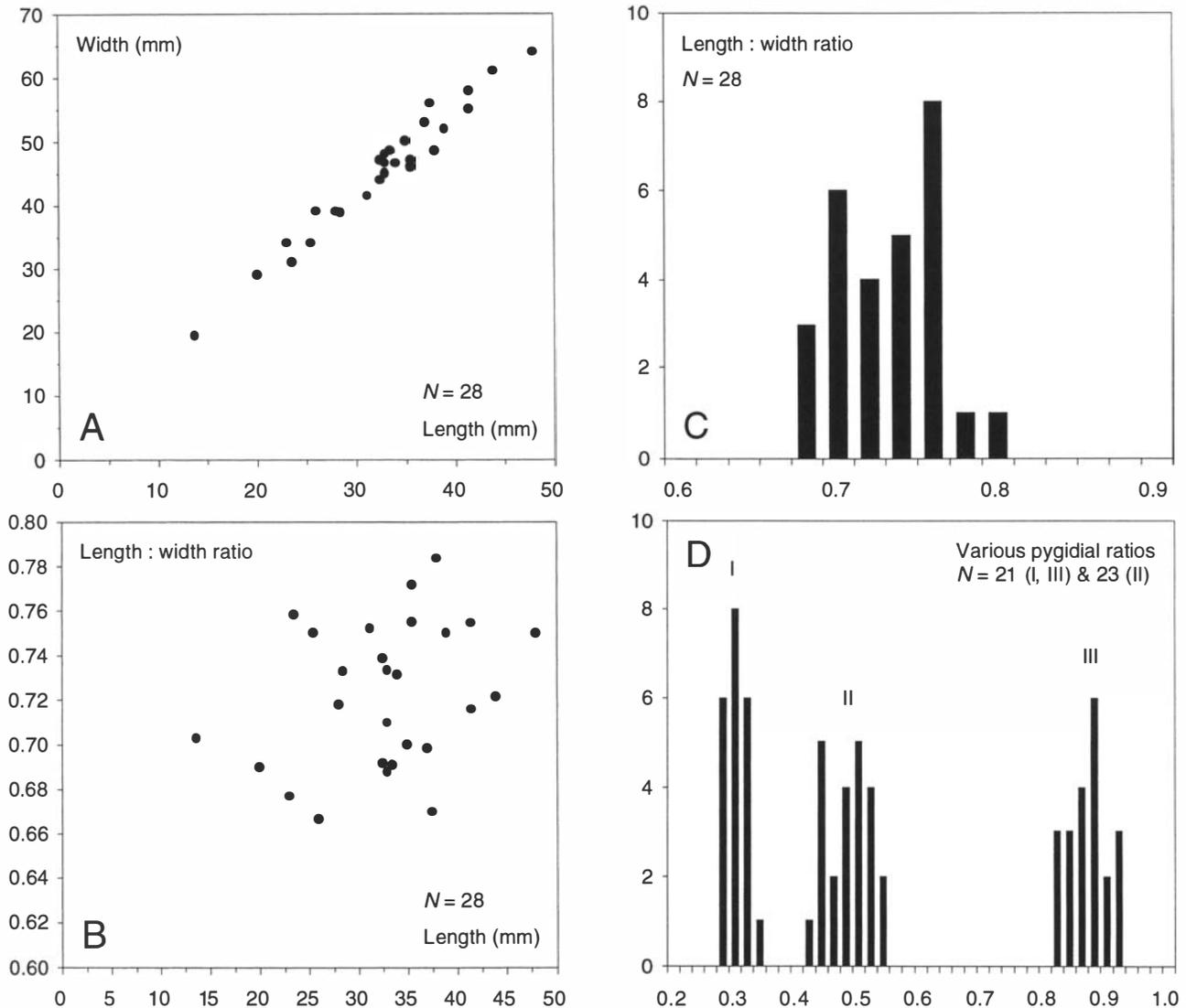


Fig. 69. Pygidia of *Asaphus (A.) acuminatus*. □A. Length (sag.) plotted against maximum width. □B. Pygidial L:W ratio plotted against pygidial length. □C. I: Ratio between anterior axial width and maximum pygidial width. II: Ratio between posterior and anterior axial width. III: Ratio between axial length and pygidial length.

cepting Balashova's (1953, p. 393, Pl. 5:9–10) identification and description of the latter species. Thus the hypostome of *A. lamanskii* has a much longer posterior border (exsag.) and a short median body, compared to *A. acuminatus*, and the pygidium of *A. lamanskii* is proportionally shorter, less triangular, with terrace lines on the pleural fields and a more distinct axial segmentation. It also appears that the density of terrace lines on the pygidial doublure is higher in *A. lamanskii* than in *A. acuminatus* (cf. Balashova 1953, p. 393).

Compared to *A. raniceps* (*s.str.*) (see discussion of *A. expansus* for remarks on identification), the cephalon of *A. acuminatus* is elongate and triangular in outline, less strongly convex (sag.), with a more distinct angulate junction of the facial suture at front, a relatively narrower glabella (tr.), a much shallower occipital furrow, smaller eyes, and a fairly

indistinct posterior outline of glabella. The pygidium of *A. acuminatus* is more elongate, subtriangular in outline, more strongly vaulted, and has nearly no external terrace-line ornamentation.

Compared to *A. raniceps* (*sensu* Angelin 1854), *A. vicarius*, and *A. striatus*, the cranidium of *A. acuminatus* is more pointed, with a prominent angulate anterior junction of the facial suture, the preglabellar area is wider, the glabella is narrower (tr.), and the eyes are smaller. Furthermore, dorsal terrace lines have not previously been reported from the cephalon of any of these species, but some specimens of *A. striatus* from SE Scania actually do show terrace lines on the palpebral lobes. The pygidium of *A. acuminatus* is comparatively elongate, subtriangular in outline, highly vaulted, and with fewer and coarser terrace lines on the doublure. It is,

furthermore, characteristic for *A. 'raniceps'* that the posterior cephalic border furrow does not stop at the intersection with the axial furrow, as in *A. acuminatus*, but is slightly backwards-deflected and continues into the occipital furrow. Compared to *A. acuminatus*, the hypostome of *A. 'raniceps'* has a comparatively slightly smaller median body, the posterior lobes of the median body are significantly less inflated, the anterior wings are shorter (exsag.), beginning ca. 0.2 of the hypostomal maximum length from the anterior margin, and the inner margin in front of the posterior mesial notch is slightly swollen, which is not the case in *A. acuminatus*.

Compared to *A. 'maximus'*, *A. acuminatus* attains smaller maximum sizes, and the pygidium is markedly narrower (tr.) and has fewer terrace lines on the doublure.

Remarks. – The status of *A. acuminatus* has been discussed by Brögger (1882), Schmidt (1901), and Jaanusson (1953a, pp. 394–395); the latter author declared it a *nomen dubium* and held it likely that *A. acuminatus* and *A. striatus* may prove synonymous. *A. acuminatus* is, however, distinctly different from *A. striatus* as well as from *A. 'raniceps'* [*sensu* Angelin 1854 & Schmidt 1901] and appears to be older than both, although its top range may overlap.

Schmidt (1901, p. 33) remarked that var. *acuminatus* is difficult to separate from *A. raniceps* var. *typica*, except for showing a more pointed pygidium, but material from Fågelsång led him to suggest an overlap of this character. Sample LU 57 contains two pygidia and two cranidia of *A. acuminatus*, which according to the label have been examined by Schmidt. Both pygidia are regular, quite triangular representatives of *A. acuminatus* (one is shown in Fig. 67H–I), and they do not resemble the broader *A. 'raniceps'*. Schmidt also wrote that pygidia of *A. acuminatus* with intact test typically show faint pleural ribs and an axial segmentation marked by lateral swellings even on the posterior part, a description reiterated by Balashova (1953, p. 394). These accounts are not in accordance with Brögger's (1882) description and the material studied herein. The pygidium of *A. 'acuminatus'* figured by Balashova (1953, Pl. 5:3) (previously identified with *A. raniceps* by Schmidt 1901, Pl. 1:10) matches Schmidt's and Balashova's descriptions, but the specimen does not represent *A. acuminatus*. It is thus questionable whether *A. acuminatus* (*s.str.*) actually does occur in the eastern Baltic area – and Balashova (1976) did not mention the species. However, the cephalon figured by Schmidt (1901, Pl. 2:1) strongly resembles *A. acuminatus*.

Nieszkowski (1857, 1859) described material, erroneously identified with *A. acuminatus*, and which later caused Schmidt (1898, 1901, 1907) considerable troubles (cf. Schmidt 1907, p. IX); see Jaanusson (1953a, pp. 404–408) for a detailed discussion.

No new material of *A. acuminatus* was found at Slemmestad in connection with the present work. Sparse material of *A. acuminatus* in the Paleontological Museum, Tøyen, including the specimen figured by Brögger (1882, Pl. 8:5),

seems to originate from the Svartodden Limestone. An occurrence in the '*Porambonites* bed', as suggested by Brögger (1882, p. 93), would be similar to the conditions in the Killeröd area of SE Scania, where the lower part of bed 9 is included in the *A. expansus* Biozone, actually because of the occurrence of *A. acuminatus*, but it is entirely possible that all of bed 9 in fact belongs to the very base of the *A. 'raniceps'* Chronozone.

Asaphus (Asaphus) striatus (Boeck, 1838)

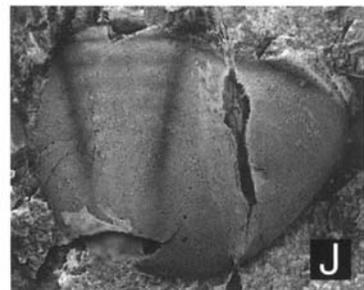
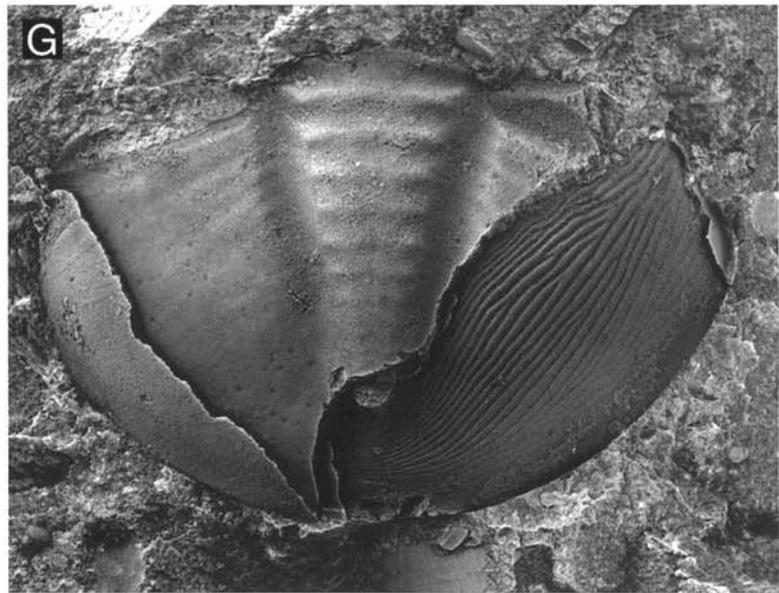
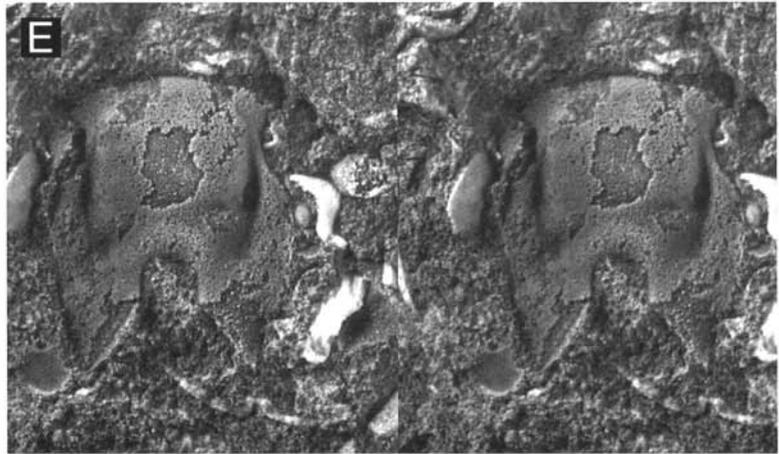
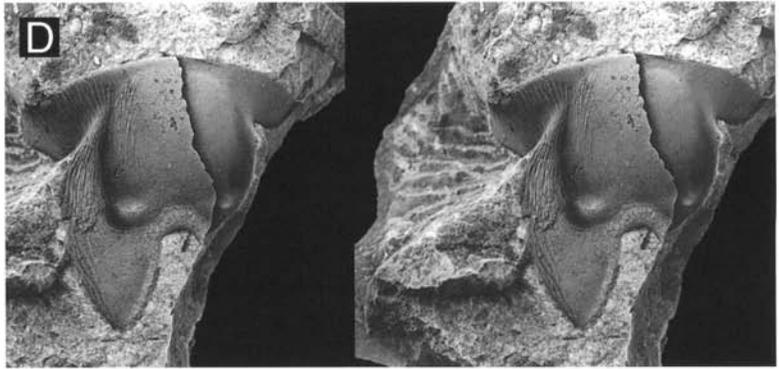
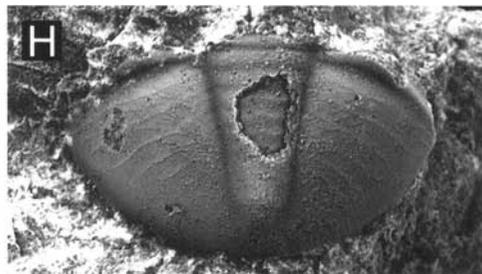
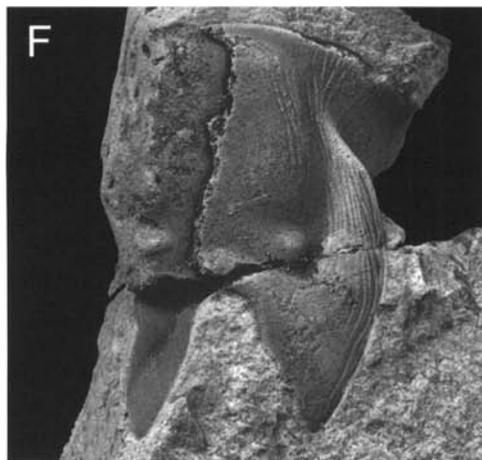
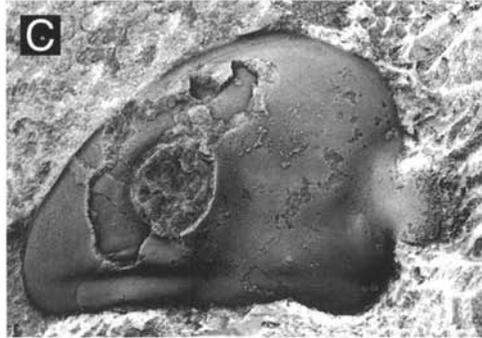
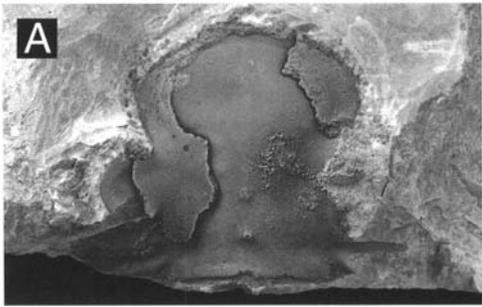
Figs. 70–73

Synonymy. – (See also Wandås 1984.) □1838 *Trilobites striatus* Sars & Boeck Mscr. – Boeck, p. 142 (short diagnosis). □v 1882 *Asaphus striatus*, Sars. var. *Sarsi* – Brögger, pp. 94–95; Pl. 8:1, 1a, 2, 2a, 3, 3a–b (description, occurrence, illustrations of entire specimen, cephalon, pygidium). □v 1882 *Asaphus striatus*, Sars & Boeck, form. *typica* – Brögger, p. 95; Pl. 8:4, 4a (occurrence, illustration of Boeck's original pygidium [holotype], hypostome). □1886 *Asaphus striatus*, Boeck – Brögger, pp. 28, 30; Pl. 1:9 (hypostome refigured; reservations concerning Pl. 8:4a in the 1882 publication). □1941 *Asaphus striatus* (Sars et Boeck MS) – Størmer, pp. 141–142; Pl. 3:12–15 (designation of lectotype, illustrations of cephalon and pygidium). □v 1984 *Asaphus (Asaphus) striatus* (Boeck, 1838) – Wandås, pp. 218–219; Pls. 1H–I; 2A–F, H, K–L (description, discussion of species, occurrence, illustrations of entire enrolled specimen, cephalon, pygidia including lectotype pygidium, pygidial doublure). □v cf. 1984 *Asaphus (Asaphus?)* sp. – Wandås, pp. 218–219; Pl. 2G, J, M. (occurrence, illustrations of entire specimen [included in *A. (N.) bottnicus* by Jaanusson 1953b, p. 498], pygidia).

Holotype. – By monotypy, pygidium PMO H2634, figured by Wandås (1984, Pl. 1H).

Material. – One cephalon, 18 cranidia (including 10 juvenile specimens), 1 librigena, 7 hypostomata, and 59 pygidia (including 18 juvenile specimens).

List of material. – □Cephalon K 1141 (t) [MGUH 22.398]. □Cranidia K 888 (im), K 1005 (im), K 1066c (pim, fragment), K 1096 (pim) [MGUH 22.396], K 1131b (im), K 1153 (im), K 1208a (im), K 1345b (im). □Juvenile cranidia K 1035 (pim), K 1048a (t) [MGUH 22.397], K 1050a (t), K 1050b (t), K 1064 (t), K 1097a (t), K 1125 (t), K 1131c (t), K 1136a (pim), K 1179 (t), K 1199a (t). □Librigena K 1123 (im). □Hypostomata K 1023 (im), K 1038 (pim), K 1048b (im) [MGUH 22.401], K 1060 (pim) [MGUH 22.399], K 1067b (im), K 1132 (im), K 1357 (t) [MGUH 22.400]. □Thoracic segment K 1097b. □Pygidia K 821 (im), K 829 (pim), K 877 (im), K 879 (im), K 882 (im), K 1004a (im) [MGUH 22.402], K 1004b (im), K 1006a (pim) [MGUH 22.406], K 1006b (im), K 1027 (im), K 1028 (im), K 1037 (im), K 1062 (im), K 1066a (pim) [MGUH 22.407], K 1073 (pim), K 1089 (im), K 1108 (im), K 1119 (im), K 1121 (im), K 1132a (pim), K 1132b (t) [MGUH 22.405], K 1132c (im), K 1133 (im), K 1134 (im), K 1135a (im) [MGUH 22.408], K 1135b? (pim), K 1135c? (im), K 1136b (pim), K 1138 (im), K 1144? (im), K 1174 (im) [MGUH 22.409], K 1203 (im), K 1208b (im), K 1212a (im), K 1212b (pim), K 1212c (pim), K 1213b (pim), K 1347? (pim), K 1354 (im), LU 39? (im), LU 42? (im). □Juvenile pygidia (i.e. <10 mm long) [Tentatively assigned; see discussion] K 827 (im), K 1004c (im),



K 1009 (t) [MGUH 22.404], K 1015 (t), K 1040 (t), K 1047 (im), K 1129a (t), K 1145 (t), K 1150 (t) [MGUH 22.403], K 1160 (t), K 1164 (em), K 1172b (im), K 1199b (pim), K 1210 (pim), K 1211 (im), K 1212d (t), K 1345a (im), LU 35 (im).

Occurrence. – *Asaphus striatus* is frequent in bed interval 9 (upper half) to 0 of Killeröd site b, and defines the *A. 'raniceps'* Zone. A single, tentatively assigned pygidium was found at the same locality in bed 11, which belongs to the uppermost part of the *A. expansus* Zone.

Three isolated pygidia from Andrarum and Tommarp (LU 35, LU 39, and LU 42) may belong to *A. striatus*, but the identification is questionable. An occurrence at Tommarp is noteworthy, since the top level of the Komstad Limestone at that locality is within the *A. expansus* Zone, and the possible association with *A. acuminatus* may resemble bed 11 at Killeröd site b (see further discussion below).

A. striatus has not been found *in situ* by me at Slemmestad, but the species has been reported from the Svartodden Limestone of the Oslo region (Brögger 1882; Wandås 1984) and from the overlying Killingen Member (Størmer 1953; Wandås 1984), where it is occasionally very frequent. The Svartodden Limestone corresponds largely or entirely to the *A. 'raniceps'* Zone, whereas the Killingen Member of the Elnes Formation represents the *M. gigas* – *M. obtusicauda* Zones. *A. striatus* is the youngest known representative of *A. (Asaphus)*.

Description. – The description is complementary to the one published by Wandås (1984). Medium-sized species, largest cranidium 28 mm long, largest pygidium impaired but is ca. 35 mm long. Sagittal convexity of cranidium and transversal convexity of glabella decrease with increasing size; preglabellar area very narrow in adults, and even narrower and steeper in juveniles, in which glabella extends almost to anterior cranial margin (Fig. 70B). Internal moulds show two pairs of fairly distinct nodes posterolaterally on glabella, as described for *A. acuminatus*, and a low mesial glabellar keel is usually also present. Basal glabellar furrows developed as fairly distinct lateral impressions in juveniles; they are markedly shallower in adults, but then joined across sagittal line. Mesial tubercle in front of occipital furrow distinct, but small (cf. Wandås 1984, p. 218), visible on internal moulds as well

as on testaceous material. Eyes large and well raised above glabella. Posterior border furrow deep and rather sharply incised on posterior fixigena, wider on internal moulds; the furrow becomes shallower on the librigena but continues all the way to outer margin.

Hypostome exceedingly like that of *A. acuminatus*; the only established difference is that the posterior notch is deeper in *A. striatus*, stretching for 0.4 of the hypostomal maximum length, and the inner margin of the notch is gently swollen. The hypostome of the associated *A. 'raniceps'* is also very similar to *A. striatus*, but the latter has more deeply incised lateral border furrows and premacular pits, and the 'consoles' (*sensu* Lindström 1901) are more inflated, so the maculae are slightly larger. Two juvenile hypostomes of *A. striatus*, 2.5 mm and 4 mm long, have a distinctly more vaulted central part (notably the median body), and a dorsally depressed lateral and outer posterior border (Fig. 70E).

Pygidium more or less parabolic in outline with a rounded posterior margin; L:W ratio varies between 0.56 and 0.70 in specimens more than 15 mm long (mean 0.64; $N = 29$), whereas smaller pygidia, 3.1 to 15 mm long, are relatively shorter, wider, showing L:W ratios between 0.50 and 0.63 (mean 0.56; $N = 21$; see Fig. 72B). Posterior segmentation of axis indistinct, but all adult specimens have 9 or 10 axial segments in addition to terminal piece and anterior half-ring; the variability possibly reflects dimorphism. Brögger (1882) wrote that the pygidial axis shows 12 segments, but the anterior half-ring as well as the terminal piece are included in this number (the specimens figured by Brögger have been examined). Small adult specimens have fewer axial rings (the smallest specimens available do not seem to be transitory pygidia), as two pygidia 3.4 and 3.9 mm long show only 7 axial rings, while pygidia 4.4–15 mm long appear to have 8 axial rings. The axis is considerably more inflated in small pygidia than in larger specimens. The pleural fields of internal moulds may show a vestigial segmentation, in particular inside paradoublural line, but most specimens have smooth pleural fields.

Among the few pygidia with intact test, some specimens exhibit an entirely smooth surface (Fig. 71A), as described by Wandås (1984), whereas others, including all juveniles, certainly do possess terrace lines. Juvenile pygidia display up to 7 pairs of raised lines, running across the pleural fields almost from axial furrow to stop at some distance from outer margin (Fig. 70H–I); the lines reflect the segmentation. A similar pattern is present in a couple of adult specimens (Fig. 71B), which also show additional short, fine, wavy terrace lines on the inner part of the pleural fields.

Doublure of pygidium wide, with 18–24 terrace lines (counted across the widest part; see Fig. 73), which are well-impressed and distinct on the inner part of the doublure, becoming gradually shallower outwards. It is characteristic, especially of the later pygidia, that the terrace lines of the inner part downlap on the outer continuous terrace lines on the posterior middle part of the doublure.

Fig. 70. *Asaphus (A.) striatus* (Boeck, 1838). □A. Partly exfoliated cranidium, ×2. MGUH 22.396 (K 1096), bed 6, Killeröd b. □B. Fragmentary juvenile cranidium, ×10. MGUH 22.397 (K 1048a), bed 0, Killeröd site b. □C. Cephalon, ×2. MGUH 22.398 (K 1141), bed 7, Killeröd site b. □D. Stereo-pair of hypostome, ×2. MGUH 22.399 (K 1060), bed 0, Killeröd site b. □E. Stereo-pair of juvenile hypostome, ×16. MGUH 22.400 (K 1357), bed A, Killeröd Canal. □F. Partly exfoliated hypostome, ×3. MGUH 22.401 (K 1048b), bed 0, Killeröd site b. □G. Internal mould of pygidium showing axis and doublure, ×2. MGUH 22.402 (K 1004a), bed 0, Killeröd b. □H. Small pygidium with almost intact cuticle showing terrace-line sculpture, ×5. MGUH 22.403 (K 1150), bed 7, Killeröd site b. □I. Fragment of juvenile pygidium with intact cuticle showing terrace-line sculpture, ×10. MGUH 22.404 (K 1009), bed 0, Killeröd site b. □J. Small pygidium with smooth cuticle, ×2. MGUH 22.405 (K 1132b), bed 7, Killeröd site b.

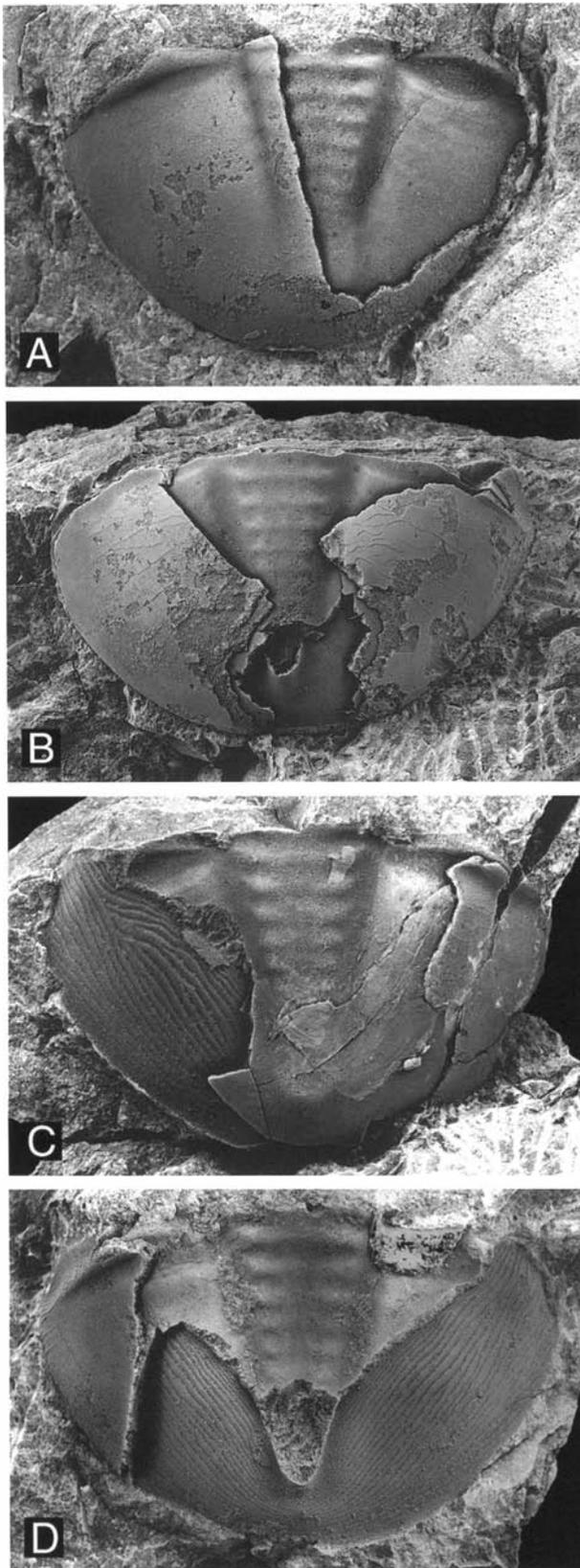


Fig. 71. Pygidia of *Asaphus* (*A.*) *striatus* (Boeck, 1838). □A. Partly exfoliated specimen, $\times 1$. The preserved cuticle has a smooth surface except for sporadic short terrace lines adjacent to the axis. Exfoliated half shows segmentation of axis, and, faintly, of pleural fields. MGUH 22.406 (K 1106a), bed 6, Killeröd site b. □B. Specimen with partly preserved cuticle carrying fine terrace lines, $\times 2$. MGUH 22.407 (K 1066a), bed 0. Killeröd b. □C. Internal mould showing axis and doublure, $\times 1.5$. MGUH 22.408 (K 1135a), bed 7, Killeröd b. □D. Internal mould showing axis and doublure, $\times 2$. MGUH 22.409 (K 1174), bed 8, Killeröd b.

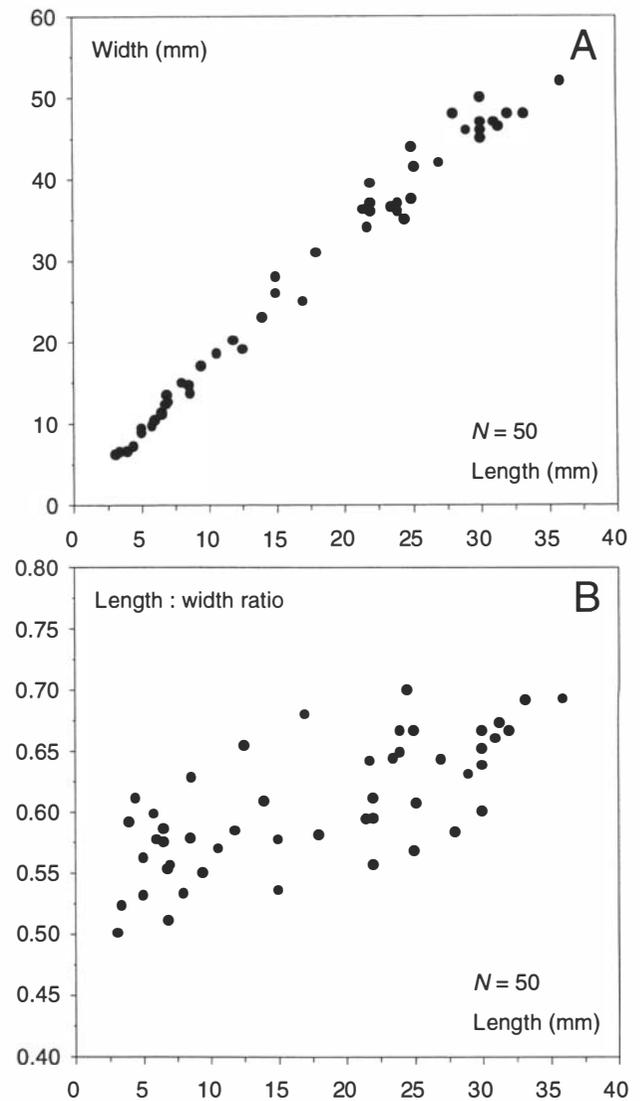


Fig. 72. Pygidia of *Asaphus* (*A.*) *striatus*. □A. Length plotted against maximum width. □B. Pygidial L:W ratio plotted against length.

Affinities. – *A. striatus* has rather large eyes and numerous terrace lines on the pygidial doublure, and, accordingly, resembles the *A. (Neoasaphus)* group, but the morphology of the thoracic doublure suggests an assignment to *A. (Asaphus)*, as indicated by Wandås (1984). *A. striatus* is a member of the *A. 'raniceps'* species group.

The differences between *A. striatus* and *A. acuminatus* seem consistent, and these species are hardly closely related (cf. Jaanusson 1953a, p. 395). Thus *A. striatus* is broader and

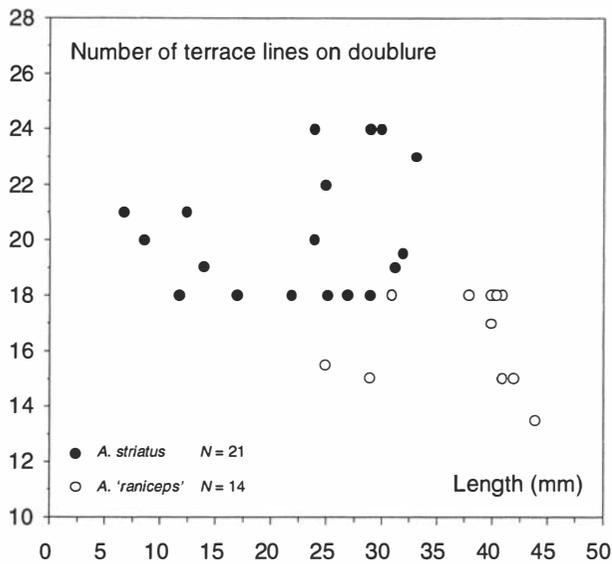


Fig. 73. *Asaphus* (*A.*) *striatus* versus *A.* (*A.*) '*raniceps*'. Total number of terrace lines on the pygidial doublure is plotted against pygidial length.

with a proportionally wider axial region (i.e. glabella, thoracic and pygidial axes are broader); the cephalon has a much less ogival anterior cranial margin, a narrower and more ill-defined preglabellar area, a better impressed posterior border furrow, a better impressed occipital furrow laterally, distinctly larger eyes, and, presumably, no or only a few dorsal terrace lines; the pygidium is less vaulted and more rounded posteriorly, the axis is more funnel-shaped and with fewer axial rings, and the doublure is wider and with finer and more numerous terrace lines. For hypostomal differences, see description above.

Compared to the coeval *A. 'raniceps'* [sensu Angelin 1854], *A. striatus* is usually broader, the eyes are significantly larger, the surface of the eye-socket is punctate, the nodes on posterior part of glabella (int. moulds) are better defined, the posterior cephalic border furrow is presumably more deeply incised, and the pygidium has finer and more numerous terrace lines on the doublure (Fig. 73). Besides, *A. striatus* attains a smaller maximum size than *A. 'raniceps'*. For hypostomal differences, see description above.

Remarks. – Brögger (1882) distinguished *A. striatus* var. *Sarsi*, described as being comparatively longer than *A. striatus* (*s.str.*) and with a more triangular cephalon, and the doublure of the pygidium was claimed to show fewer terrace lines (18–20 versus 22–24). The museum material of *A. striatus* from the Oslo region was examined by Wandås (1984), and he concluded that there is no basis for a distinction of two variants. The new material of *A. striatus* from the Komstad Limestone supports this conclusion.

Wandås (1984, p. 219, Pl. 2J, G) rejected a couple of terrace-line-bearing pygidia from *A. striatus*. A few adult pygidia in the material at hand exhibit external terrace lines,

arranged in a similar pattern (Fig. 71B), but those specimens are otherwise like *A. striatus* and occur associated with typical smooth individuals, and a separation appears artificial.

The juvenile pygidia described above are mainly from intervals with sole presence or dominance of *A. striatus*, but it cannot be excluded that a few specimens actually belong to *A. 'raniceps'*, which occurs in parts of the interval. However, the juvenile pygidia are all very similar, and there are no indications suggesting that the material is mixed.

Isolated pygidia from bed 11 at Killeröd site b and from the uppermost bed at Tommarp may belong to *A. striatus*; both occurrences are within the *A. expansus* Zone. The exfoliated specimens do not show the doublure, so the identification cannot be affirmed. Alternatively, but less likely, the specimens represent *Asaphus* sp. A.

Asaphus (*Asaphus*) cf. *incertus* Brögger, 1882

Synonymy. – □ cf. 1882 *Asaphus expansus*, Linn., var. *incerta* – Brögger, pp. 91–92 (short description, occurrence). □ cf. 1980 *Asaphus* n.sp. – Tjernvik & Johansson, p. 194, Fig. 9J (occurrence, illustration of cephalon).

Type material. – Not designated.

Material. – Fragmentary cephalon A 1158b with damaged hypostome *in situ*.

Occurrence. – The specimen is from bed A-51 of the Lysaker Member at Slemmestad, Zone of *A. expansus*. The range of *A. (Asaphus) incertus* is unknown, but it may prove characteristic of the upper part of the *A. expansus* Zone of southern Norway (Brögger 1882) and Sweden (compare *Asaphus* n.sp. sensu Tjernvik & Johansson 1980). The sparse material from the upper part of *A. expansus* Zone at Fågelsång, referred to as *Asaphus* sp. A, may also belong to *A. incertus*.

Remarks. – The cephalon is quite different from *A. expansus*, showing a less prominent mesial tubercle, a shallower occipital furrow, distinctly shallower basal glabellar furrows, an overall less vaulted glabella (tr.), more acute genal angles, and a flattened posterior cephalic margin (which is more raised, rounded in *A. expansus*); the anterior branches of the facial suture meet in a distinct point. Dorsal terrace lines are presumably present only on the palpebral area. The visible part of the hypostome show a more inflated posterior lobe of median body and much finer terrace lines on the lateral border and anterior wings, compared to *A. expansus*.

The specimen most likely represents *A. expansus* var. *incerta* Brögger, 1882; especially the acute genal angles, originally emphasized by Brögger (1882), points to such an identification, but a positive identification is hampered by the insufficient knowledge of *A. incertus* (see Jaanusson 1953a, p. 395). A cursory examination of the collections of the Palaeontological Museum, Oslo, failed to locate the two speci-

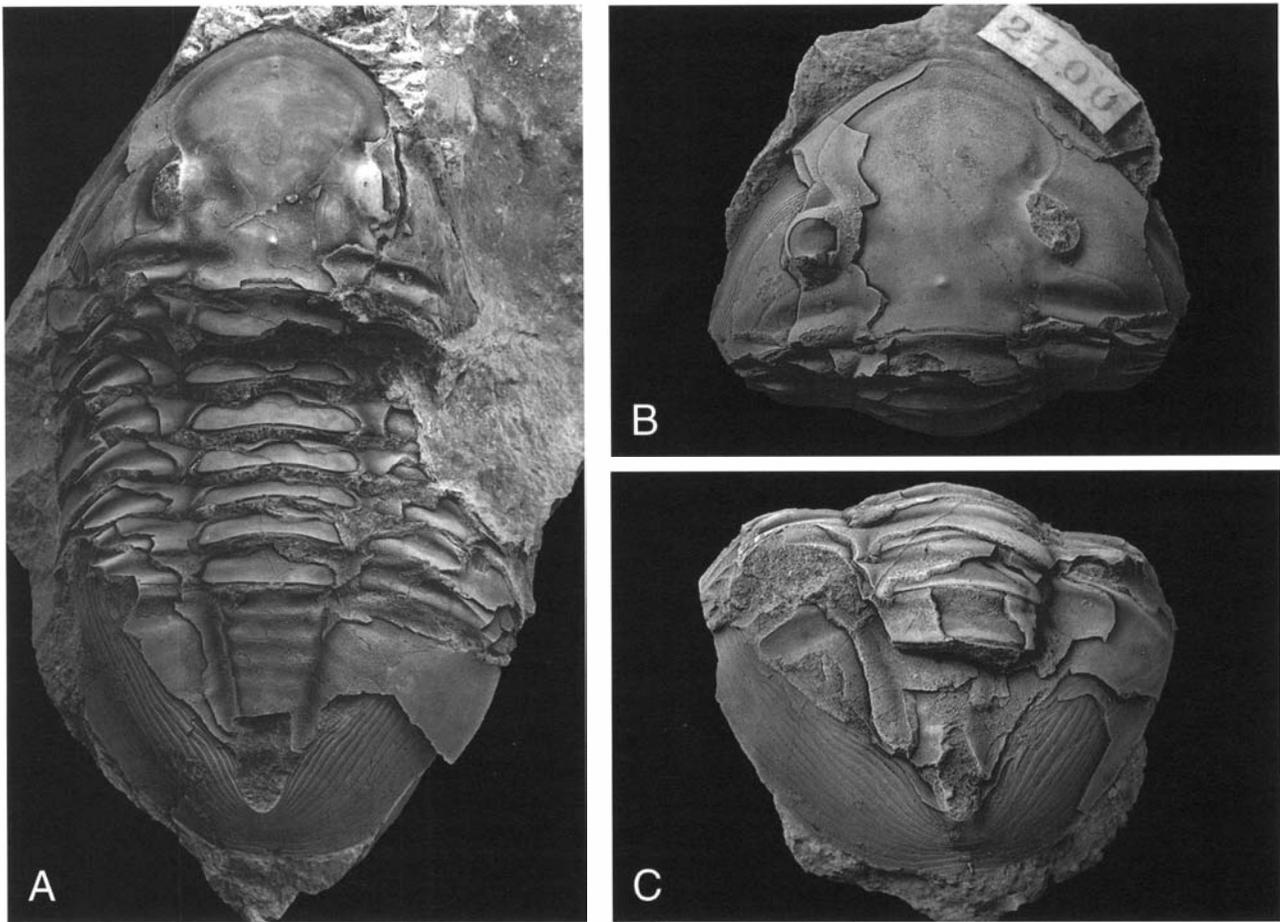


Fig. 74. *Asaphus (A.) incertus* Brögger, 1882. □A. Internal mould of complete specimen, $\times 1.5$. PMO 66408, Lysaker Member, Slemmestad (Henningsmoen coll.). □B–C. Cephalon and pygidium of enrolled specimen (internal mould showing doubleure), $\times 2$. PMO 2100, Lysaker Member, Huk, Bygdøy, Oslo (Kiaer coll.).

mens of *A. incertus*, referred to by Jaanusson (1953a), but additional specimens, which must represent the species, were found (Fig. 74). A redescription is in preparation. It is possible that *Asaphus* n.sp. Johansson, 1980, and *Asaphus* sp. A, described below, in fact are identical to *A. incertus*.

Schmidt (1898, 1901) regarded *incerta* synonymous with *A. lepidurus*, despite the fact that it does not precede *A. expansus* in the Oslo Region; Brögger (1882) repeatedly stated that var. *incerta* occurs in the upper part of the 'Expansus Shale'.

Asaphus (Asaphus) 'raniceps' sensu Angelin, 1854

Figs. 75E–F, 76

Synonymy. – □non 1827 *Asaphus expansus* Var. β : *raniceps* – Dalman, Pl. 3:4 (brief diagnosis, illustration of cephalon). □1854 *Asaphus raniceps*. Dalm. Boeck – Angelin, p. 53; Pl. 28:2, 2a–c (brief diagnosis, occurrence, illustrations of com-

plete specimen, cephalon, hypostome). □cf. 1884 *Asaphus vicarius* n.sp. – Törnquist, pp. 64–65; Pl. 2:18–20 (description, occurrence, illustrations of cranium, pygidia). □1886 *Asaphus raniceps*. Dalm. Boeck – Brögger, p. 28, Pl. 1:4 (brief notes on hypostome, illustration of hypostome). □1901 *Asaphus raniceps* Dalm. – Schmidt, V-II, pp. 32–36; Textfigs. 20–21; Pls. 1:8–11; 2:2–3; non Pl. 2:1 [= *A. acuminatus*] (description, occurrence, illustrations of complete specimens, cephalon, hypostome, pygidial doubleure). □1905 *Asaphus raniceps* Dalm. – Lamansky, pp. 58, 62–63, 168, 169 (occurrence). □cf. 1951 *Asaphus vicarius* Törnq. – Jaanusson & Mutvei, pp. 633, 634 (occurrence). □1953a *Asaphus (Asaphus) 'raniceps'* – Jaanusson, pp. 394, 396 (discussion of species). □1980 *Asaphus 'raniceps'* – Tjernvik & Johansson, pp. 190, 194; Figs. 1, 2, 10B (occurrence, illustration of cranium).

Type material. – Not designated. *A. 'raniceps'* is not identical to *A. raniceps* Dalman, 1827.

Material. – One cranium, 5 hypostomata, and 29 pygidia.

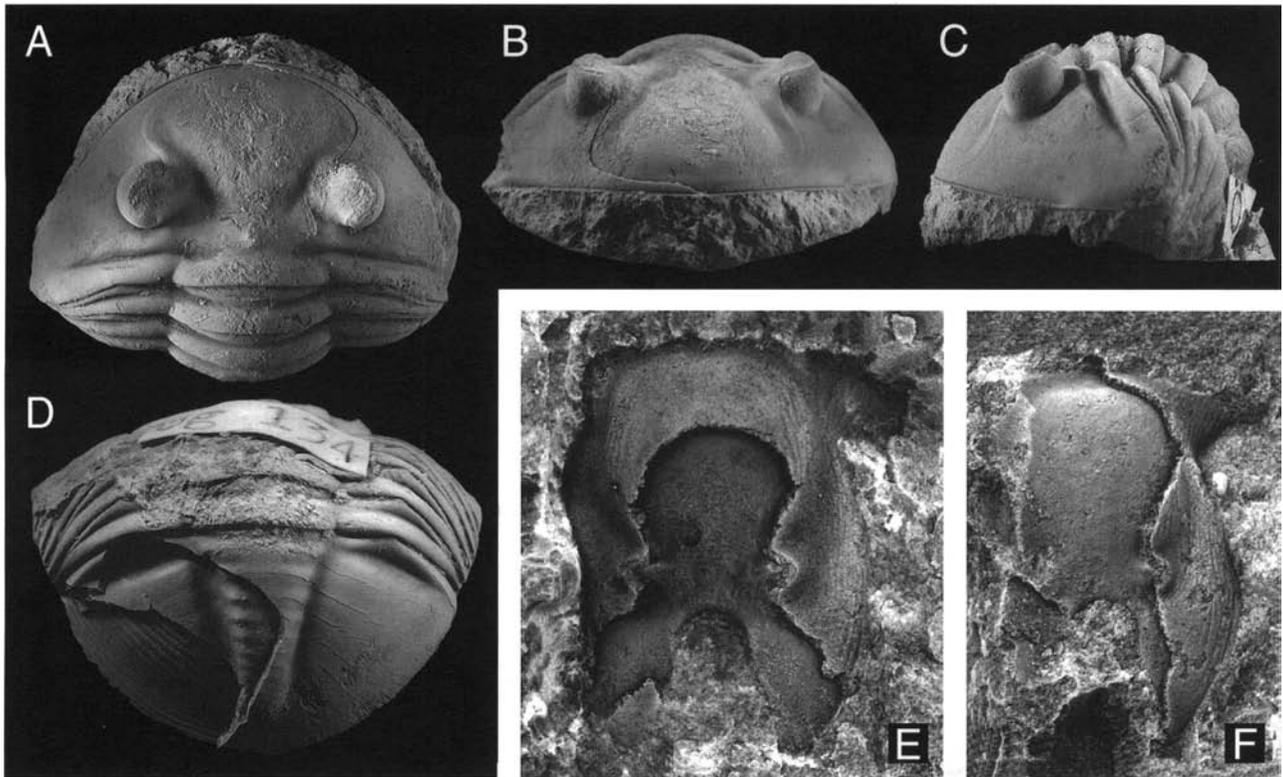


Fig. 75—A. □A–D. *Asaphus (A.) raniceps* (Dalman, 1827) (*s.str.*), $\times 2$. Dorsal, frontal, side and posterior views of complete specimen Ög 134 from Borensberg, Östergötland. Previously figured by Tjernvik & Johansson (1980, Fig. 10A). □E–F. *Asaphus (A.) raniceps*. □E. Partly exfoliated hypostome, $\times 4$. MGUH 22.410 (K 1111), bed 6, Killeröd site b. □F. Partly exfoliated hypostome, $\times 4$. MGUH 22.411 (K 887), bed 6, Killeröd site b.

List of material. — □Cranidium K 1190 (pim). □Hypostomata K 836 (t), K 874 (im), K 887 (pim) [MGUH 22.411], K 1111 (pim) [MGUH 22.410], K 1172a (im). □Pygidia K 810 (im), K 830? (im), K 850 (im) [MGUH 22.412], K 856 (im/c), K 861 (im) [MGUH 22.414], K 863 (im), K 864? (c), K 871 (im), K 890a (im/c), K 890b (im/c), K 890c (im/c), K 1085 (im), K 1090 (im) [MGUH 22.413], K 1095 (im), K 1102 (im), K 1122 (im), K 1129b (im), K 1131a (im), K 1137 (im), K 1152 (im), K 1172c? (im), K 1173a (im), K 1177 (im), K 1209 (im), K 1355a (c), K 1355b (c), K 1356a (c), K 1356b (c), K 1356c (c).

Occurrence. — *A. raniceps* is fairly frequent in bed interval 1 to 8 of Killeröd site b; it is an indicator of the *A. raniceps* Zone. The species has also been found in beds A and D in the Killeröd Canal; this interval most likely succeeds the limestone exposed at Killeröd site b. *A. raniceps* also occurs sparsely in the Svartodden Limestone of the Oslo area (see discussion below).

A. raniceps is widely distributed in Baltoscandia, and characterizes the *A. raniceps* Zone (Lamansky 1905; Balashova 1953; Jaanusson 1953a).

Description. — See Schmidt (1901).

Affinities. — Compared to the contemporaneous *A. striatus*, *A. raniceps* attains larger sizes (largest available pygidium is 45 mm long), the cephalon is usually more elongate, the cranidium is relatively narrower (preocular width), the posterior glabellar nodes, as seen on internal moulds, tend to be

less distinct, the eyes are significantly smaller, the test surface of the eye socle is smooth, the genal angles are more acute, the hypostome has less impressed lateral border furrows and smaller maculae, the pygidium is usually slightly more elongate (adult L:W ratio 0.61–0.72 [mean 0.67; $N = 21$] versus 0.56–0.70 [mean 0.64; $N = 29$] in *A. striatus*), and the axial segmentation is less distinct. The best distinguishing feature of the pygidia is, however, the doublure, which shows only 13–18 comparatively coarse terrace lines in *A. raniceps* and 18–24 fine lines in *A. striatus* (Fig. 73).

Compared to *A. raniceps (s.str.)* (see discussion of *A. expansus*), *A. raniceps* is larger, more elongate, with no preglabellar area, the occipital and lateral glabellar furrows are indistinct, the eyes are in a more advanced position, and the pygidium is usually smooth and with obsolescent axial segmentation.

The differences from *A. acuminatus* is discussed in the section on that species.

Remarks. — *A. raniceps sensu* Angelin (1854), Schmidt (1901), Lamansky (1905), and Balashova (1953), is not identical to *A. raniceps* Dalman (see Jaanusson 1953a, p. 394; Tjernvik & Johansson 1980, p. 190). Hence, the *A. raniceps* Zone of Lamansky (1905) is characterized by a species, misidentified with *A. raniceps*, while *A. raniceps (s.str.)* seems to occur in

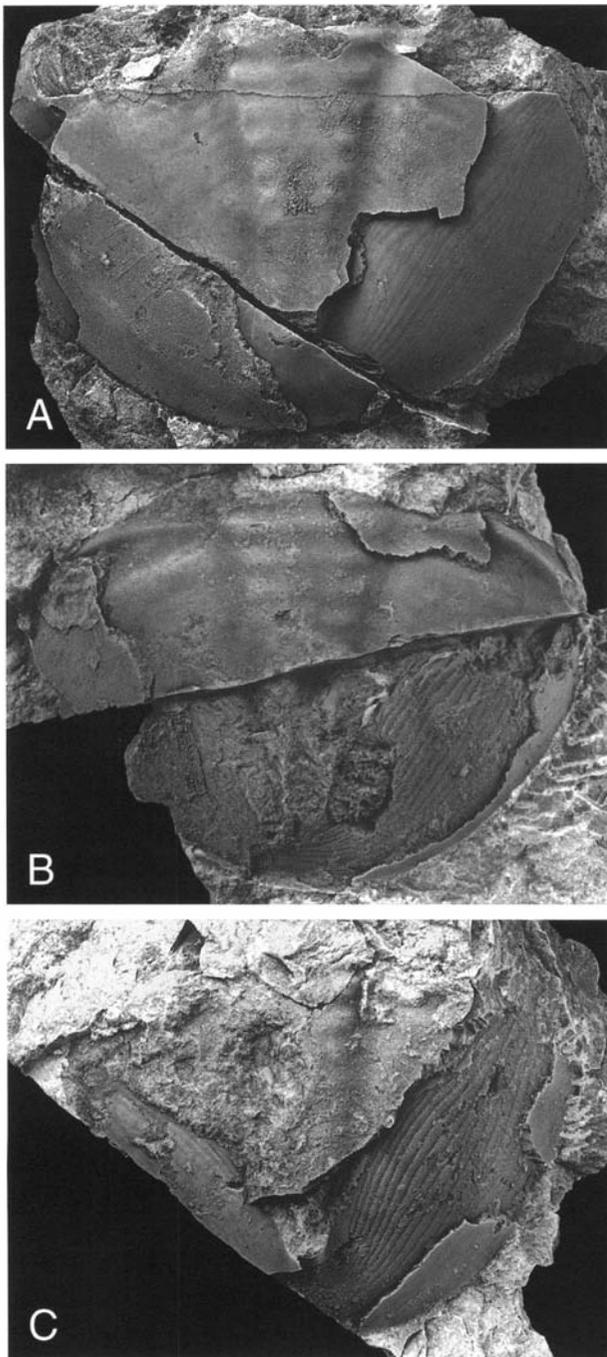


Fig. 76. *Asaphus* (*A.*) *'raniceps'*. □A. Internal mould of pygidium showing axis and doubleure, $\times 1.5$. MGUH 22.412 (K 850), bed 3, Killeröd site b. □B. Internal mould of pygidium showing the doubleure, $\times 1.3$. MGUH 22.413 (K 1090), bed 6, Killeröd site b. □C. Internal mould of pygidium showing doubleure, $\times 1.3$. MGUH 22.414 (K 861), bed 4, Killeröd site b.

the *A. expansus* Zone (Tjernvik & Johansson 1980). This is the reason why the *A. raniceps* Zone has been cited as the *A. 'raniceps'* Zone since Jaanusson & Mutvei (1953). The nomenclatorial and associated stratigraphical confusion appears intricate, but the problem is now essentially of for-

mal character, as little doubt can be raised against Tjernvik & Johansson's (1980) interpretation of *A. raniceps* (*s.str.*) (see discussion of *A. expansus* herein). It is possible that *A. 'raniceps'* is identical to *A. vicarius* Törnquist, 1884, but if not, a new name may be given to *A. 'raniceps'*, and thereby to the trilobite zone.

A single specimen of *A. 'raniceps'* (PMO 1816) was noticed in the collections of the Paleontological Museum, Oslo. It originates from the Svartodden Limestone, which supports the idea that at least a part of this unit corresponds to the *A. 'raniceps'* Zone. *A. striatus* appears to be much more common in the Svartodden Limestone than *A. 'raniceps'*, just as in the Komstad Limestone at Killeröd site b.

Asaphus (*Asaphus*) *'maximus'* Brögger, 1886

Figs. 77–78

Synonymy. – □1886 *Asaphus raniceps*, Dalm. var. *maxima* – Brögger, p. 30; ?*non* Pl. 1:6 (short description, occurrence, illustration of hypostome [identification questionable]). □*non* 1890 *Asaphus platyurus* var. *maximus* n.v. – Moberg, p. 15. [*Nomen nudum*]. □? 1937 *Megalaspis limbata* [partim] – Ekström, p. 15 (occurrence).

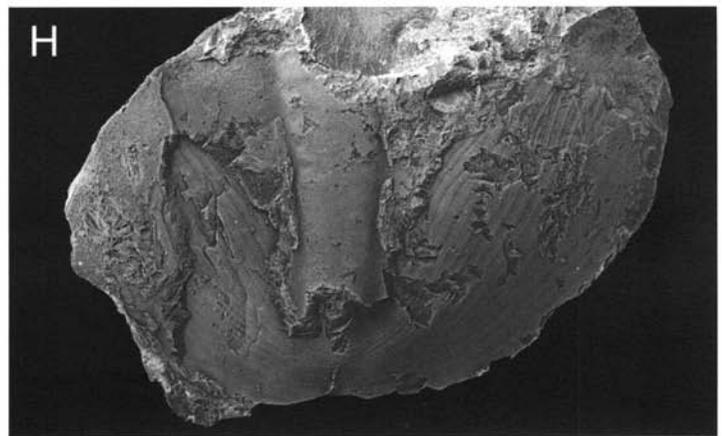
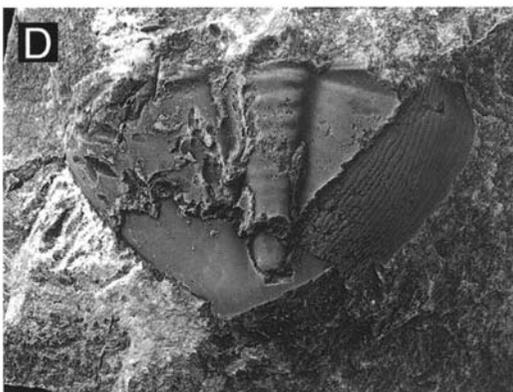
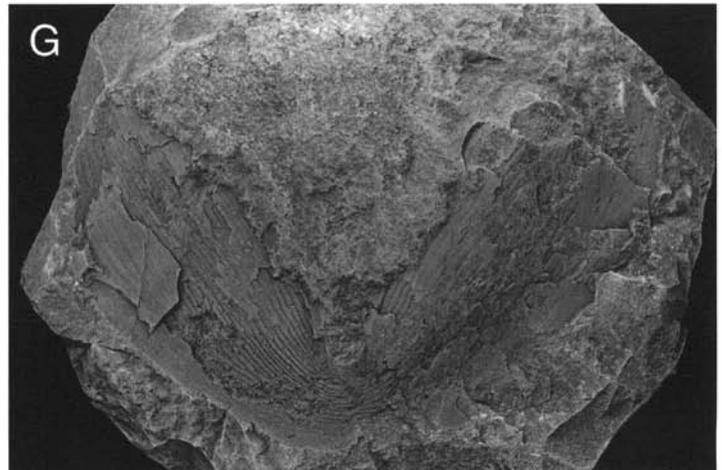
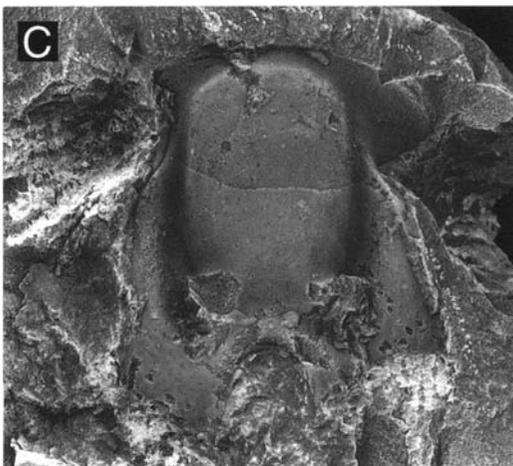
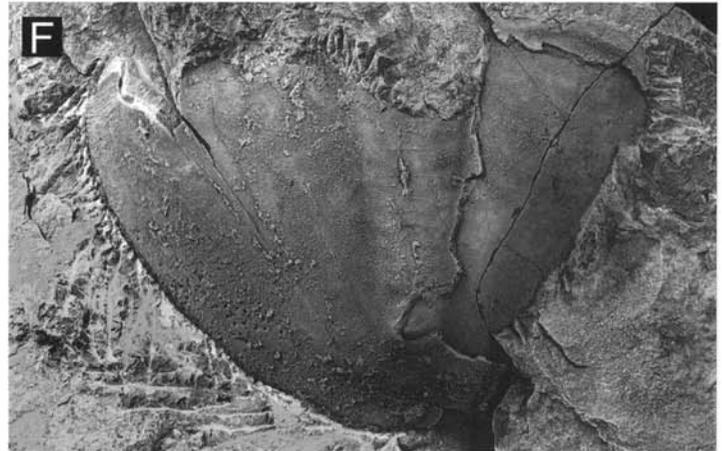
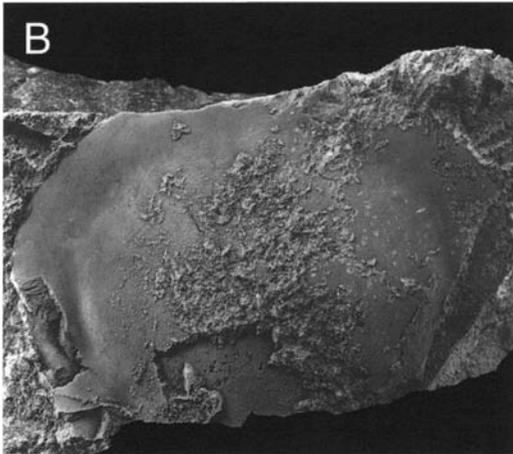
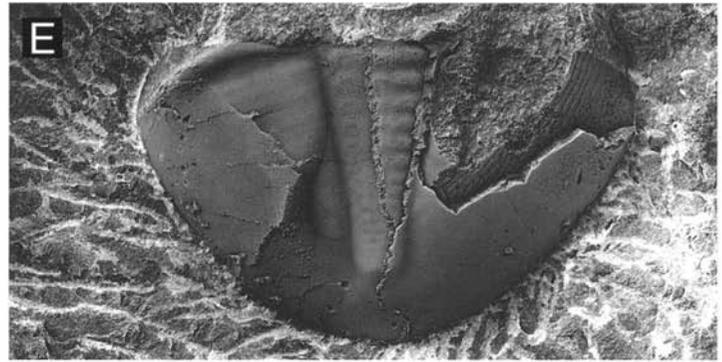
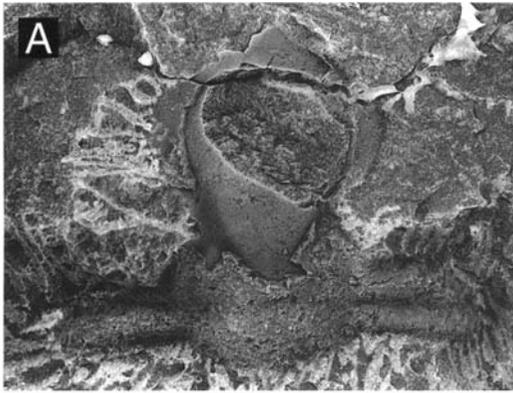
Type material. – Not designated.

Material. – Two cranidia, 1 hypostoma? and 21 pygidia. The material is generally poorly preserved, and more or less fragmentary.

List of material. – □Cranidia F 235 (im) [MGUH 22.415], F 249 (t) [MGUH 22.416]. □Hypostoma (Tentatively assigned) LU 110 (im) [LO 7116]. □Pygidia F 232 (pim) [MGUH 22.418], F 238? (pim), F 242 (pim), F 252? (im), F 253 (pim) [MGUH 22.419], F 255 (pim), F 256 (pim), F 263? (im), F 268 (im), F 273 (im), F 289? (im) [MGUH 22.420], F 297 (im), F 304 (pim) [MGUH 22.417], F 305a (pim), F 305b? (c), LU 68a (pim) [LO 7102], LU 68b (im), LU 107a (im) [LO 7113], LU 107b (im) [LO 7114], LU 107c (im), LU 111? (im).

Occurrence. – *Asaphus* (*A.*) *'maximus'* occurs in bed interval 25 to 29 at Fågelsång; a juvenile pygidium from bed 30 is tentatively assigned. The range is suggested to equal the lower part of the *A. 'raniceps'* Zone. The available museum material is from Fågelsång, but cannot be referred precisely to level, although the lithology of the samples suggests a provenance from bed interval 24–29.

Fig. 77 (opposite page). *Asaphus* (*A.*) *'maximus'* Brögger, 1886. □A. Badly preserved cranidium, partly exfoliated, $\times 2$. MGUH 22.415 (F 235), bed 29, Fågelsång. □B. Fragment of large cranidium, $\times 2$. MGUH 22.416 (F 249), bed 29, Fågelsång. □C. Internal mould of large, tentatively assigned hypostome, $\times 3$. LO 7116 (LU 110), Fågelsång, loc. E21b. □D. Internal mould of small pygidium, $\times 2$. LO 7102 (LU 68a), Fågelsång area. □E. Slightly compacted, partly exfoliated pygidium, $\times 2$. MGUH 22.417 (F 304), bed 29, Fågelsång. □F. Fragmentary large pygidium, $\times 1$. MGUH 22.418 (F 232), bed 27, Fågelsång. □G. Internal mould of pygidium showing doubleure, $\times 1$. LO 7114 (LU 107b), Fågelsång area. □H. Internal mould of pygidium showing doubleure, $\times 1$. LO 7113 (LU 107a), Fågelsång area.



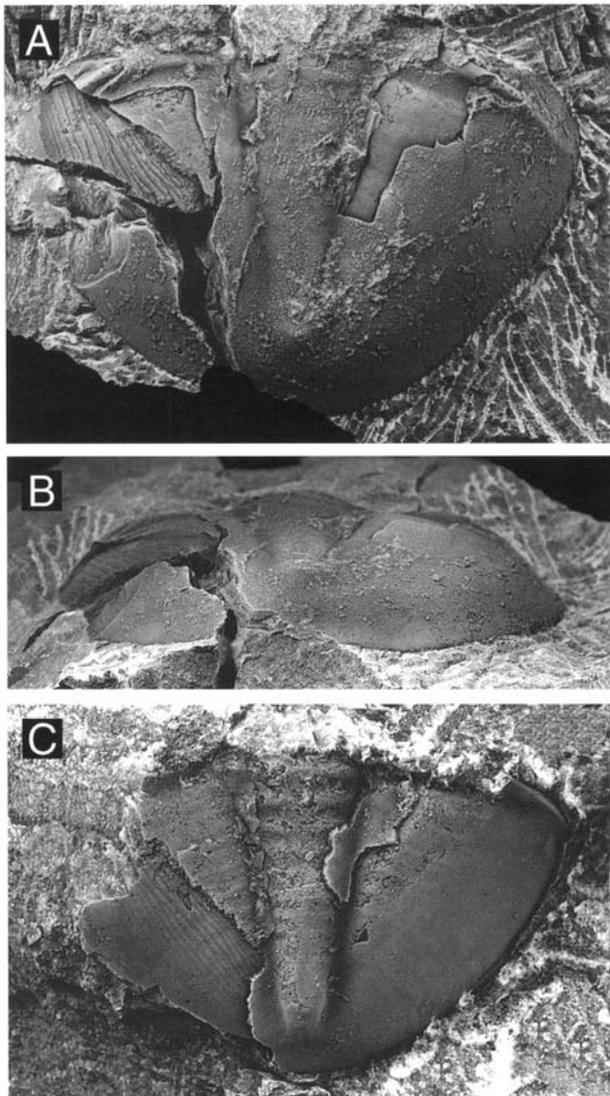


Fig. 78. *Asaphus* (A.) '*maximus*' Brögger, 1886. □A–B. Large pygidium, dorsal and posterior views, $\times 1$. MGUH 22.419 (F 253), bed 2, Fågelsång. □C. Internal mould of tentatively assigned small pygidium, $\times 4$. MGUH 22.420 (F 289), bed 31, Fågelsång.

Brögger (1886, p. 30) reported *A. 'maximus'* from the upper part of the 'lower grey orthoceratite limestone' of Öland, which presumably corresponds to a position within the *A. 'raniceps'* Zone, and later Holm (1901, p. 48) listed the form from the grey 'täljsten' of Kinnekulle, province of Västergötland. According to Johansson (1979) this level is within the *A. 'raniceps'* Zone. The materials referred to by Brögger (1886) and Holm (1901) have not been available for study.

Description. – Large for an *Asaphus*, preocular width of largest cranidium is 33 mm (specimen damaged, length presumably about 40–45 mm), largest pygidium almost 60 mm long. The preserved parts of the two fragmentary cranidia available (Fig. 77A–B) closely resemble *A. acuminatus*

and *A. 'raniceps'*. The sagittal convexity is low to moderate, a quite wide prelabellar field is present, wider than in *A. 'raniceps'* and comparable to *A. acuminatus*, and the facial sutures meet angularly, forming a distinctly pointed cranidium as in *A. acuminatus*. No nodes are present posterolaterally on glabella (internal mould; see *A. acuminatus*), and the posterior fixigenae are unusually short (tr.), so the FW:L ratio is only about 1.3; the short posterior fixigenae indicate that the unknown librigenae are very broad.

The hypostome (Fig. 77C) is tentatively assigned (see discussion below); original length about 20 mm. It is of '*raniceps*'-type with elongate median body and maculae situated on small inflated areas; the most striking feature is the pronounced elongation. Hypostomal W:ML ratio about 0.8; posterior mesial notch comparatively deep. Anterior lobe of median body has W:L ratio of about 3:4. Compared to *A. acuminatus*, the median body is clearly more elongate, the lateral border is longer (exsag.), commencing at about one third the length (sag.) of the median body (compared to about half in *A. acuminatus*), and the lateral border furrow is more strongly impressed. It also appears that the terrace lines are shallower in the specimen (internal mould), compared to *A. acuminatus*, but this may relate to preservation.

Pygidium broadly parabolic in outline, L:W ratio slightly below 2:3. Axis stretches for about 0.8 of the pygidial length, and anteriorly occupies about 0.25 of the pygidial width. It tapers backwards, most pronouncedly so in the anterior 2/3; posterior width (tr.) about half of anterior width; it is slightly elevated above pleural fields throughout. Axial segmentation vestigial on testaceous material and marked only by indistinct low lateral swellings on internal moulds, deflating rearwards. There seems to be about 12–13 axial segments in addition to the anterior half-ring and the terminal piece. The smallest pygidium available, about 11 mm long and tentatively assigned, has a more inflated axis with a better defined segmentation, showing about 12 segments in addition to the terminal piece and the anterior half-ring. Axis bounded by wide axial furrows. Pleural fields mostly smooth also on exfoliated specimens, with a well-defined, centrally raised anterior half rib, delimited rearwards by a wide furrow. Rarely 7–8 pairs of nebulous ribs can be discerned on the pleural fields, especially on internal moulds (compare Fig. 77F); the pleural segmentation is slightly better defined on smaller specimens. The largest pygidia show a slight change of slope 3–5 mm from the posterior margin, which may be taken as a faint indication of a border (Fig. 77F). Articulating facet stretches for half the distance from pygidial corner to sagittal line. All specimens are more or less corroded, but the test surface appears smooth, except for faint transverse ridges crossing the axis, presumably matching the segmentation.

Pygidial doublure wide; main part slightly convex and follows the curvature of dorsal test, with a gentle concave bend along outer margin; anterolateral corners flexed a little downwards. Doublure provided with 16–20 (mostly 18) continuous coarse terrace lines across widest part.

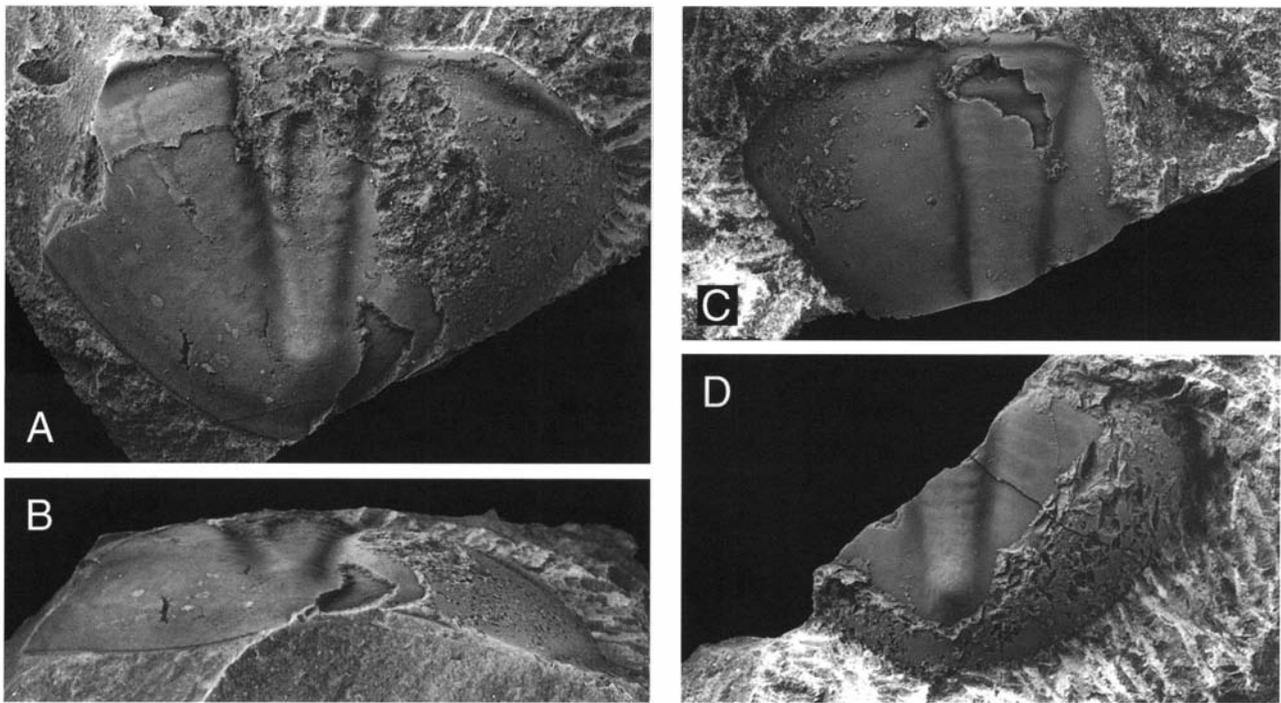


Fig. 79. *Asaphus* (A.) sp. A. □A–B. Partly exfoliated pygidium, dorsal and posterior views, $\times 2$. LO 7094 (LU 56), Fågelsång area. □C. Fragmentary pygidium, $\times 4$. MGUH 22.421 (F 211), bed 22, Fågelsång. □D. Partly exfoliated fragmentary pygidium, $\times 2$. MGUH 22.422 (F 215), bed 29, Fågelsång.

Affinities. – The sizable *Asaphus* ‘*maximus*’ is surpassed in size by the younger *A.* (*Neoasaphus*) *platyurus platyurus* (see Jaanusson & Mutvei 1953, Textfig. 2; Jaanusson 1953b, pp. 470–473), which also is characterized by the general lack of dorsal terrace lines on the pygidium. By comparison, the pygidium of *A.* ‘*maximus*’ has a wider doublure, a more effaced segmentation (pleural fields and axis), and a higher pygidial L:W ratio.

Moberg (1890, p. 15) briefly described a so-called *A. platyurus* var. *maximus* from the ‘transition beds’ between the ‘*Platyurus* Limestone’ and ‘*Centaurus* Limestone’ of southern Öland. This variant, which must be regarded a *nomen nudum* (Jaanusson 1953a), is not identical to *A. raniceps* var. *maxima* Brögger, as indicated by Moberg’s short description (pygidia characterized by distinct pleural ribs) and the high stratigraphical position.

A. ‘*maximus*’ seems close to *A.* ‘*raniceps*’ (*sensu* Schmidt 1901), but attains larger sizes, has a proportionally narrower pygidial axis, and does not show terrace lines on the pleural fields of the pygidium (cf. Schmidt, 1901). However, it is very likely that *A.* ‘*maximus*’ in fact merely represents a deep-water ecophenotype of *A.* ‘*raniceps*’.

Remarks. – *A. raniceps* var. *maxima* is, according to Brögger (1886, p. 30), characterized by attaining very large size, and by possessing an almost entirely smooth pygidium with a narrow posterior border. The hypostome, assigned to var. *maxima* by Brögger (1886, Pl. 1:6), is not similar to the

hypostome described here. The available rather large specimen is certainly from an *Asaphus* of ‘*raniceps*’ type, and an association with the described pygidia is likely.

The exceptional large size of the pygidia from Fågelsång, and especially the presence of a narrow, although admittedly ill-defined posterior border are taken to indicate that they represent *A. raniceps* var. *maxima*. The smaller pygidia without border are difficult to assign (which regards specimens F 289, LU 68a, LU 68b, LU 111), but the very wide doublure is also important for identification. Besides, a suite of pygidia of different size makes the identification of the smallest specimens plausible. *A. raniceps* var. *maxima* is, however, a *nomen dubium*, and its status is especially dubious, if the hypostome figured by Brögger (1886, Fig. 6) was erroneously combined with the large pygidia; Jaanusson (1953a, p. 392) regarded *A. r.* var. *maxima* a *nomen nudum*. It has not been possible to locate the material of var. *maxima* in the collections of Riksmuseet, Stockholm, the Geological Survey of Sweden, Uppsala, or the Paleontological Museum, Oslo. For this reason the name ‘*maximus*’ is applied informally.

The sizable pygidia are somewhat *Megistaspis*-like, and the bewildering report of *M. limbata* in bed g [= bed 31] at Fågelsång locality E 21a (Ekström 1937, p. 15; referred to by Størmer 1953, p. 131; Jaanusson 1960, p. 343; Tjernvik 1972, p. 308), most likely stems from confusion of *A.* ‘*maximus*’ with *M. limbata*. It has not been possible to locate the specimen in question, but a 2.5 m thick interval is faulted out

between Ekström's sections I and II (cf. Ekström 1937, Textfig. 3). This missing part comprises the top of the *M. limbata* Zone, as well as the Zone of *A. expansus*, and, accordingly, Ekström's statement 'The conditions ... thus prove that the zone of *Didymograptus bifidus* is underlain by the zone of *Megalaspis limbata*' (Ekström 1937, p. 49) is in error.

Asaphus (*Asaphus*) sp. A

Fig. 79

Synonymy. – □cf. 1882 *Asaphus expansus*, Linn., var. *incerta* – Brögger, p. 92 (brief description, occurrence). □cf. 1980 *Asaphus* n.sp. – Johansson, p. 194, Figs. 2, 9J (occurrence, illustration of cephalon).

Material. – Eight poorly preserved pygidia (all fragmentary internal moulds).

List of material. – □Pygidia (all internal moulds) F 206?, F 211 [MGUH 22.421], F 215 [MGUH 22.422], F 250, F 269, LU 56 [LO 7094], LU 111, LU 143.

Occurrence. – *Asaphus* sp. A occurs in bed interval 22 to 24 at Fågelsång, correlated with the upper part of the *A. expansus* Zone. The museum material studied appears to originate from the same interval, judging from the lithology of the samples.

Remarks. – By comparison to *A. acuminatus* the sp. A pygidia have a lower relief, a narrower and more vaulted axis, and a wider doublure with about 15–16 terrace lines. Sp. A is also relatively narrower and has a more vaulted axis than *A. 'maximus'* (comparing pygidia of equal size). Compared to *A. expansus*, sp. A pygidia have a higher L:W ratio (just above 2:3), a narrower axis, and a wider doublure with a few extra terrace lines.

Sp. A is tentatively assigned to *A. (Asaphus)*, because of the outline of the doublure (wide and with coarse terrace lines). The material is strongly similar to specimens from the Oslo area, which must represent *A. incertus* Brögger (cf. Fig. 74); it is actually not possible to point to any differences, but without cephalic material a detailed comparison is impossible. The relation to *Asaphus* sp. Johansson, 1980, reported from the upper part of the *A. expansus* Zone, is uncertain, but also this form may turn out to represent *A. incertus* Brögger.

Subfamily Isotelinae Angelin, 1854

Genus *Megistaspis* Jaanusson, 1956

pro *Megalaspis* Angelin, 1851; non *Megalaspis* Bleeker, 1851

Type species. – (OD) *Trilobites limbatus* Boeck, 1838.

Megistaspis material. – Eleven complete specimens, 5 cephalala, 148 cranidia, 46 librigenae, 12 hypostomata and 602

pygidia, of which 4 cranidia, 4 librigenae and 47 pygidia were too poorly preserved to be assigned to species. The bulk of the material belongs *Megistaspis (Megistaspis)*.

Remarks on genus and generic subdivision

Megalaspis Angelin, 1851 [June?] unfortunately appeared to be a homonym of *Megalaspis* Bleeker, 1851 [May?], and the replacement name *Megistaspis* was introduced by Jaanusson (1956a), to whom the reader is referred for details.

Jaanusson (1956a) divided the plexus of species assigned to *Megistaspis* among a *M. planilimbata* group, a *M. (Megistaspis)* group, and a *M. (Megistaspidella)* group, essentially in accordance with Schmidt (1906), whose *M. polyphemus* group was encompassed within *M. (Megistaspis)*. The *planilimbata* group had previously been assigned to *Plesiomegalaspis* Thoral by Tjernvik (1956). Bohlin (1960) discussed the *M. (Megistaspidella)* group, and excluded a few species, tentatively assigned by Jaanusson (1956a); those were subsequently separated as *M. (Heraspis)* by Wandås (1984). Balashova (1966) maintained an assignment of the *M. planilimbata* group *sensu* Jaanusson (1956a) to *Plesiomegalaspis*; *M. pogrebowi* Lamansky, 1905 was referred to a new subgenus, *P. (Popovkiaspis)*. Příbyl & Vaněk (1965, 1969) erected *Megistaspis (Nerudaspis)* and *M. (Klabavia)*, and suggested that at least the latter is present also in Baltoscandia. Tjernvik (1980) established *M. (Varvaspis)* to contain the *planilimbata* group, but *M. (Varvaspis)* Tjernvik, 1980 is an objective synonym of *Paramegistaspis* Balashova, 1976.

Balashova (1976) proposed a new 'split up' classification of *Megistaspis* comprising:

Ekeraspis Tjernvik, 1956

Paramegistaspis Balashova, 1976

Megistaspis Jaanusson, 1956

M. (Megistaspis) Jaanusson, 1956

M. (Megistaspinus) Balashova, 1976

Rhinoferus Balashova, 1976

R. (Rhinoferus) Balashova, 1976

R. (Lawiaspis) Balashova, 1976

R. (Ropschiaspis) Balashova, 1976

R.? (Popovkiaspis) Balashova, 1966

Megistaspidella Jaanusson, 1956

M. (Megistaspidella) Jaanusson, 1956

M. (Spinopyge) Balashova, 1976

M. (Megistaspinus) Balashova basically accommodates the *M. polyphemus* group of Schmidt (1906); the distinguishing characters from *M. (Megistaspis)* are listed in Table 7. However, these differences are inconsistent, and even the descriptions presented by Balashova herself are partly conflicting with the proposed subgeneric division, e.g., with regard to the pygidial border (cf. description of *M. (Megistaspis) lata* by Balashova 1976, p. 82). Also, the lectotype of *M. limbata*,

Table 7. Tabulation of differences between the two subgenera of *Megistaspis* Jaanusson, 1956 according to Balashova (1976, pp. 80, 85). Furthermore, the preocular width of cranium was stated to be smaller than the width across palpebral lobes in *M. (Megistaspis)*, and equal to the width across palpebral lobes in *M. (Megistaspinus)*. See text for discussion.

	<i>M. (Megistaspis)</i>	<i>M. (Megistaspinus)</i>
Lateral glabellar furrows	Distinct	Effaced
Baculae	Distinct	Effaced
Occipital ring	Well-defined	Effaced
Cephalic post. border furrow	Present	Absent
Preocular width of cranium	Small	Large
Depression in frontal area	Usually vestigial	Well-defined
Anterolateral border, pygidium	Absent	Present

which is the type species of *M. (Megistaspis)*, in fact lacks a posterior cephalic border (see Jaanusson 1956a), and *M. polyphemus* (the type species of *M. (Megistaspinus)*) has for instance no anterolateral pygidial border. The material at hand indicates that the distinctness of the lateral glabellar furrows, baculae, occipital ring, and mesial impression in frontal area varies considerably even within a species, and certainly can not serve as distinguishing characters between subgenera. *M. (Megistaspinus)* Balashova is therefore abandoned and the majority of species is instead attributed to *M. (Megistaspis)* Jaanusson.

Rhinoferus Balashova is a synonym of *Rhinaspis* Remelé, 1885 (*nomen nudum*; non *Rhinaspis* Perty, 1830—see Jaanusson 1956a). The taxon approximately embodies the *M. hyorrhina* [*hyorrhina*] species group of Schmidt (1906), which was included in *M. (Megistaspis)* by Jaanusson (1956a). The *M. hyorrhina* group appears to represent a natural entity of closely related species, and *Rhinoferus* is here ranked as a subgenus of *Megistaspis*, whereas the subdivision of *Rhinoferus*, proposed by Balashova (1976), is not adopted. *R. (Lawiaspis)* contains, according to Balashova, two species, *M. gibba* Schmidt, 1906 and *M. knyrkoi* Schmidt, 1906. Only two pygidia of the latter species are known (see Balashova 1976, pp. 112–113), and the pygidium of *M. gibba* does not show any obvious similarity to those specimens. The stated diagnostic features of *Lawiaspis*, which with regard to the pygidium focus on the doublure, are so general that they fit most megistaspids (cf. Balashova 1976, p. 111). Accordingly, *R. (Lawiaspis)* at most comprises only the peculiar type species, *M. gibba*, but which here is attributed to *Megistaspis (Rhinoferus)*. *M. knyrkoi* possibly belongs to a new, as yet undefined subgenus of *Megistaspis* (see below).

R. (Ropschiaspis) was also proposed by Balashova to contain two species, *M. lawrowi* Schmidt, 1906, and *R. petrowtschinensis* Balashova, 1976. The status of the latter species in relation to *M. lawrowi* cannot be settled from the description and figures presented by Balashova (1976); it is possibly a synonym. *M. lawrowi* is a rather peculiar species (see Balashova 1976; Bohlin 1960; Schmidt 1906), but the faint poste-

rior glabellar inflation may indicate an affinity to the *M. hyorrhina* group, as suggested by Balashova (1976, p. 114). However, although *M. lawrowi* differs somewhat from the remaining members of the *M. hyorrhina* group, a distinction at the subgenus level appears unwarranted. Wandås (1984) assigned *M. lawrowi* to *M. (Heraspis)*; the species is quite different from the remaining members of *M. (Heraspis)* and I do not support such an assignment.

M. pogrebowi Lamansky is known only from a single pygidium (Lamansky 1905; Schmidt 1906, 1907; Balashova 1966, 1976), which cannot serve as basis for defining a subgenus. Balashova (1976) tentatively moved *M. ('Popovkiaspis')* *pogrebowi* to *Rhinoferus*, from its previous assignment to *Plesiomegalaspis* (see Balashova 1966). Schmidt (1907) also remarked that *M. pogrebowi* may be related to the *M. hyorrhina* group. An assignment based solely on pygidial features is difficult and uncertain, and more material is needed to establish the affinities of the species.

The differences separating *Megistaspidella (Spinopyge)* from *M. (Megistaspidella)* are difficult to extract from the respective descriptions (Balashova 1976, pp. 91, 97), but at least includes a broader cranium of *M. (Megistaspidella)*, a more pointed, thorn-like posterior projection on the hypostomal margin (projection rounded in *M. (Spinopyge)*), a rounded posterior pygidial margin (posteriorly pointed or with postaxial spine in *M. (Spinopyge)*), and more evenly distributed terrace lines on the pygidial doublure (less dense in the middle part of *M. (Spinopyge)*). The width of the cranium as well as the presence or absence of a postaxial pygidial spine are unreliable characters for subgeneric separation; the importance of the minor hypostomal and doublural differences is uncertain. It is possible, even likely, that the *M. extenuata* species group constitutes a natural unit, which eventually may be separated from the *M. acuticauda* group, but the status and affinities of the younger representatives of *M. (Megistaspidella)* *sensu* Jaanusson (1956a) should be clarified before such a division is formalized. Meanwhile, I prefer to maintain an undivided *Megistaspidella* group (excl. of *M. (Heraspis)* Wandås); the close relationship between *M. (Megistaspidella)* and *M. (Spinopyge)* *sensu* Balashova is proved by the high degree of cephalic similarity.

Whether a taxonomical distinction should be at the genus or lower levels will always rely on judgment; Balashova (1976), unlike the majority of earlier authors, preferred a distinction between the different megistaspid groups at the genus level. As the megistaspid group as a whole is believed to constitute a natural entity, albeit containing several subgroups, it is preferred to maintain *Megistaspis* in the sense of Jaanusson (1956a) (dating back to Angelin 1851), and continue the Scandinavian tradition of separating the megistaspid groups at the subgenus level.

In the present paper the following classification of *Megistaspis* is used:

- M. (Megistaspis)* Jaanusson, 1956
M. (Megistaspidella) Jaanusson, 1956
M. (Ekeraspis) Tjernvik, 1956
M. (Paramegistaspis) Balashova, 1976
M. (Rhinoferus) Balashova, 1976
M. (Heraspis) Wandås, 1984

A couple of species, described in open nomenclature (spp. B, C and cf. *knyrkoi*), possibly together with *M. ringsakerensis* Skjeseth and *M. knyrkoi* Schmidt, may belong to a new, as yet unnamed subgenus of *Megistaspis*.

Megistaspis (Nerudaspis) and *M. (Klabavia)*, defined by Příbyl & Vaněk (1965, 1969), are inadequately known (see also references and figures in Horný & Bastl 1970). It is doubted that they truly belong to *Megistaspis*.

Species limits

The large and spectacular specimens of *Megistaspis* have attracted much attention during the past 150 years or more—a pygidium was figured as early as 1728 by Bromell—but, still, variation ranges, growth, evolution, and the stratigraphical and geographical distributions of most species are surprisingly poorly documented. The established taxa have often been based on very limited materials, in several cases comprising only pygidia or cranidia, and sometimes even only juveniles. As a result the taxonomy is cluttered with poorly defined taxa, and the resulting confusion has inevitably made its way into stratigraphy—a well-known example is the debate focused on the ‘*Limbata Limestone*’ *sensu* Moberg (1890), nourished by the discussion of *M. limbata* and related forms (see Tjernvik 1972, 1980).

The skeletal width of *Megistaspis* appears to have been affected by the environment. Thus the adult pygidial L:W ratio varies around 15–20% in individual palaeoenvironments (Figs. 52–53), but may total about 30% (Fig. 83B), or even more (? 40% in *M. (M.) acuticauda*) for a single species. Likewise, the degree of skeletal convexity, impression of various furrows, development of pygidial border etc. seem to reflect the environment (Table 5, p. 63), and caution is necessary when using these characters for classification. Perhaps the most controversial inference is that the cephalic posterior border furrow of *M. (Megistaspis)* characterizes shallow-water ecophenotypes, and is absent in representatives from intermediate and deeper-water facies, and, accordingly, the furrow is not a salient taxonomical feature. In the same way, the mesial impression in the prelabellar area of *M. (Megistaspis)*, emphasized especially by eastern Baltic authors, seems to be a variable and plesiomorphic feature. It is common for all of these morphologic variations that their biological function largely remains obscure (see section on autecology).

Analogous phenomena are displayed by *M. (Paramegistaspis) planilimbata* and *M. (P.) estonica* (see Tjernvik 1956), of which the former is narrow (typical for shallow-water ecophenotypes) and with a faint to moderately impressed

posterior border furrow on cephalon, whereas the latter is broad (typical for deeper-water–muddy-substrate ecophenotypes) and lacks a posterior border furrow.

In consequence of the different interpretation of megistaspid morphology, the species limits are considerable broader in the present contribution than suggested by Jaanusson (1956a), Balashova (1976), and Tjernvik (1980). Some of the different ecophenotypes may eventually be separated as variants or subspecies.

Discussion of species

Important works dealing with *Megistaspis* have been published by Angelin (1851, 1854, 1878), Brögger (1882, 1886), Schmidt (1898, 1906), Bohlin (1955, 1960), Balashova (1966, 1976), Wandås (1984), and Tjernvik (1956, 1972, 1980). The majority of these contributions was based on museum collections, which limits their stratigraphical use, with Tjernvik (1956, 1972, 1980) as a notable exception.

The collection at hand largely comprises material of *M. (Megistaspis)*, which ranges from the base of the Volkhov Stage and into the lower zone of the Kunda Stage. Contemporaneous subgenera, primarily *M. (Megistaspidella)*, are sparsely represented; the first representatives of *M. (Rhinoferus)* and *M. (Megistaspidella)* appear in the middle of the Volkhov Stage, and the former group dominates in the upper part of the Volkhov Stage, while the latter is dominant in the Kunda Stage. *M. (Heraspis)* (as understood here) is known only from the Kunda Stage. For a discussion of species belonging to the older subgenera *M. (Ekeraspis)* and *M. (Paramegistaspis)*, see Jaanusson (1956a), Tjernvik (1956, 1980) and Balashova (1966, 1976). The species discussed are listed in Fig. 80.

MEGISTASPIS (MEGISTASPIS) LIMBATA (Boeck, 1838) and allied taxa. – *Trilobites limbatus* Boeck, 1838, the type species of *Megalaspis* Angelin, 1851, was described from the Oslo region by Brögger (1882), who distinguished *M. limbata* var. *typica* and an early *M. limbata* var. *minor*. Törnquist (1884) separated *M. limbata* var. *lata*, which Schmidt (1906) synonymized with *M. polyphemus* Brögger, 1882. Schmidt (1906) described *M. limbata* from the eastern Baltic area; a single entire specimen from the Oslo region was separated as *M. limbata* var. *elongata* (redescribed by Balashova 1976). Størmer (1941) selected a specimen, previously figured by Brögger (1882, Pl. 9:2), as lectotype of *M. limbata*. Jaanusson (1956a) regretted the choice of lectotype, which he claimed is different from the Swedish form, traditionally identified with *M. limbata*, and characteristic of the *Limbata Limestone sensu* Moberg (1890). It was Jaanusson’s conviction that the Swedish *M. limbata* exhibits a posterior cephalic border furrow, like the specimens figured by Brögger (1882), Schmidt (1906) and Wiman (1907). According to Jaanusson (1956a) the Swedish species traditionally identified with *M. limbata* may prove within the range of *M. elongata* (Schmidt, 1906), which was ranked as an individual species. Jaanusson

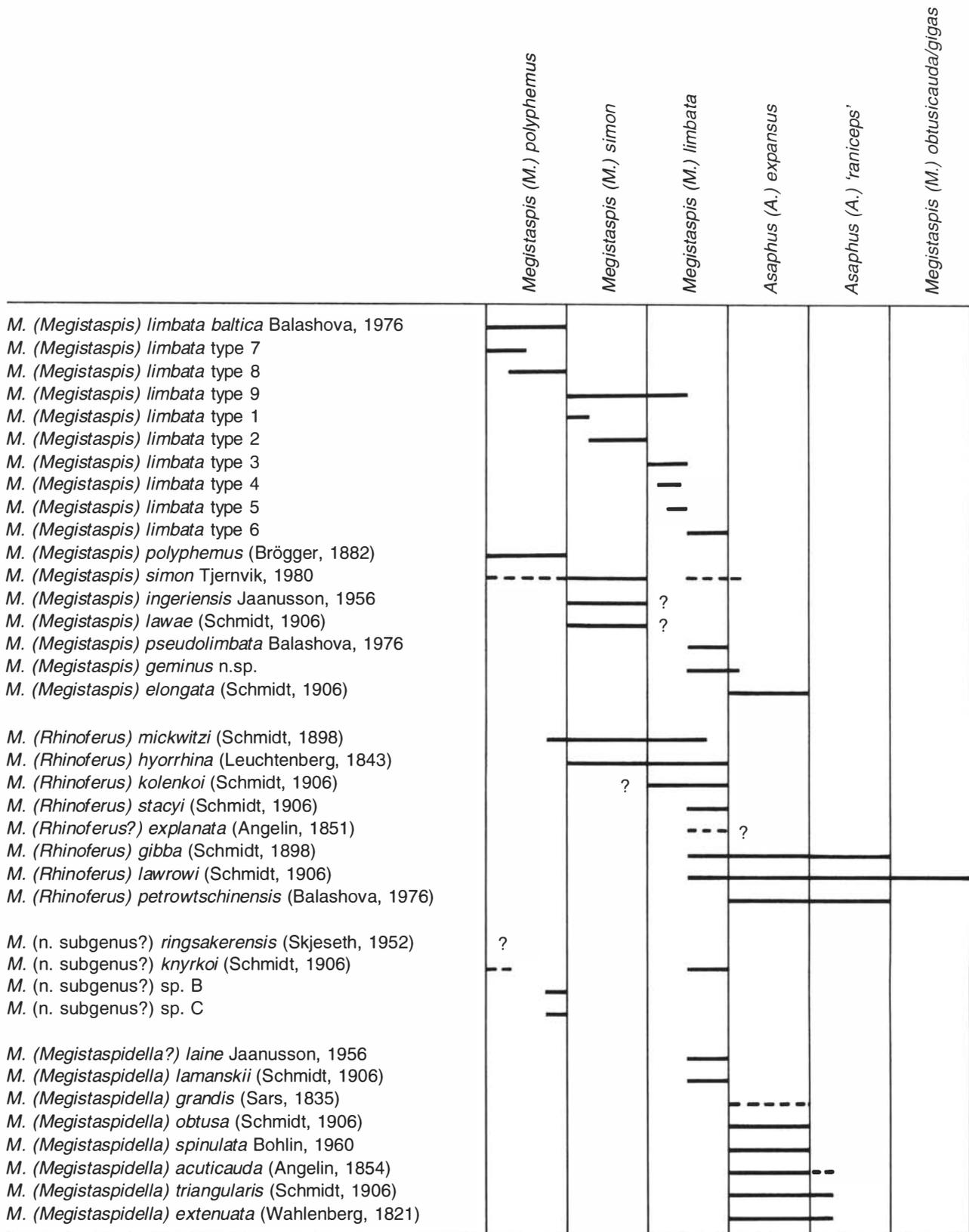


Fig. 80. Stratigraphical distribution of species of *Megistaspis* (*Megistaspis*), *M. (Rhinoferus)* and *M. (?n.subsp.)*. Regarding *M. (Megistaspidella)* only the species referred to in the text are included. (Includes data from Balashova 1976; Bohlin 1960; Schmidt 1906; Jaanusson 1956a; Tjernvik 1980.)

also listed *M. limbata* var. *minor* and the broad form of *M. limbata sensu* Brögger (1882) as individual species. Jaanusson's interpretation of *M. limbata* and *M. elongata* was challenged by Tjernvik (1972, 1980), according to whom the closely related species of *M. (Megistaspis)*, occurring throughout the *Limbata* Limestone [Volkhov Stage] of Sweden, all lack the much emphasized cephalic posterior border furrow, and the few Swedish species showing such a furrow are confined to the succeeding *A. expansus* Zone (Kunda Stage). None of the eastern Baltic *M. limbata* types with a deep posterior border furrow on the cephalon have been encountered in Sweden according to Tjernvik (1972), and *M. limbata* 's.str.' is confined to the upper third of the Volkhov Stage, separated as the *M. limbata* Zone by Tjernvik (1980). A closely related subspecies, treated in open nomenclature, was described from the *M. simon* Zone, and Tjernvik listed *M. (M.) minor* (Brögger) from the *M. limbata* Zone.

Burskij (1970) described *M. limbata* from Paj Choj, northern Urals, which is the only well-documented record of *Megistaspis (Megistaspis)* from outside the Baltoscandian core area. Furthermore, the material actually seems to belong to *M. limbata*.

Balashova (1976) redescribed most of the material studied by Schmidt (1906). *M. limbata sensu* Schmidt was divided among *M. (M.) limbata baltica* Balashova, 1976 and *M. (M.) pseudolimbata* Balashova, 1976. Both of these species were listed from the upper part of BII α , but this is not in accordance with Schmidt (1906, Pl. 1:9; see also text p. 20), who wrote that the cephalon, chosen as holotype of *M. pseudolimbata* by Balashova, is from BII γ .

The present study includes the by far largest material of *M. limbata* yet investigated, and of which the exact stratigraphic provenance is known. It appears that

- 1 During the Volkhovian significant changes of skeletal width occurred, but not in a unidirectional way, and the changes, obviously, reflect environmental oscillations. Hence a separation of broad/narrow or small/large *M. limbata*-like species appears artificial. *M. 'minor'* is here ranked as an informal variant of *M. limbata*, referred to as type 4; no formal distinction should be made, and the name *minor* is best avoided.
- 2 The width across posterior fixigenae apparently increased gradually during the range of *M. limbata*, and this may represent an evolutionary trend (Fig. 82A).
- 3 A cephalic posterior border furrow is normally only faintly indicated or obsolete, but increases in distinctness towards the close of the *M. limbata* Zone; *M. elongata* is confined to the *A. expansus* Zone. This statement concerns only the material at hand and is not valid for the eastern Baltic area.
- 4 The hypostome morphology changes considerably during the range of *M. limbata*; early types show a convex posterior margin while late types show a concave poste-

rior margin. Whether this is valid for all *M. limbata* types within Baltoscandia is unknown, hence it is uncertain whether or not the changes reflect evolution.

These observations indicate that there is no biological basis for the very narrow definition of *M. limbata*, advocated by Jaanusson (1956a), Balashova (1976), and Tjernvik (1980). *M. limbata* is here divided into various ecophenotypes, informally termed types 1 to 9, which grade more or less imperceptibly into each other. It is tempting to refer to these types as subspecies, but with type 6 as a possible exception, such an approach is not workable. The various types intergrade and an unambiguous formal taxonomical distinction appears impossible. In the changed interpretation, *M. limbata* ranges from the base of the Volkhov Stage, i.e. throughout the *Limbata* Limestone *sensu* Moberg (1890). This obviously raises doubt regarding the validity of *M. limbata* 's.str.' [= type 5] as an index fossil of the upper zone of the Volkhov Stage.

The classification of types with a cephalic posterior border furrow is problematic, but some of them are probably conspecific with *M. limbata* and just represent different ecophenotypes; such morphs may conveniently be ranked as subspecies (like *M. limbata baltica* Balashova, 1976). However, *M. elongata* itself is for the time being upheld as a separate species, following established practice. The posterior border furrow is not a unifying character of a monophyletic 'elongata group' (cf. Tjernvik 1972), and this term should be avoided.

M. limbata baltica occurs in the upper part of BII α of the eastern Baltic area. Note that the holotype erroneously was believed to originate from BII γ by Tjernvik (1972, p. 307, Textfig. 2C). The association of the pygidia and the isolated cephalon called *M. pseudolimbata* by Balashova (1976) is questionable, and it is suspected that the described pygidia rather should be included in *M. limbata baltica*, despite differences in border morphology. The two types of pygidia are, apart from the border difference, similar for all practical purposes (cf. Balashova 1976, pp. 81, 83; Pl. 21:7–8 versus Pl. 21:3–5). The stratigraphical provenance of the holotype of *M. pseudolimbata* is, as indicated above, uncertain, but it is presumably from BII γ (see Schmidt 1906, Pl. 1:9). In my opinion the cephalon is within the range of *M. elongata*, or represents a very closely related form.

MEGISTASPIS (M.) POLYPHEMUS (Brögger, 1882). – *M. polyphemus* is based on an exquisite museum specimen of which neither the exact stratigraphical level nor the sampling locality was known (Brögger 1882). There is, however, no doubt that the holotype originates from the basal limestone bed of the Hukodden Limestone, which has a very distinctive lithology (see discussion of *M. polyphemus* for details).

Schmidt (1906) assigned several variants to *M. polyphemus*, viz. var. *Törnquisti*, var. *minor*, var. *Lamanskii*, and var. *Knyrkoi*. *M. polyphemus* var. *Törnquisti* was intentionally erected to accommodate *M. limbata* var. *lata* Törnquist

1884, hence the latter name has priority, but, in accordance with Schmidt's interpretation, *M. polyphemus* (Brögger, 1882) is here regarded a senior synonym of *M. lata* (Törnquist, 1884). The *M. lata* Zone of Jaanusson (1957) must therefore be renamed.

As the remaining *M. polyphemus* variant designations of Schmidt (1906) were applied also to other species of *Megastaspis*, new names were introduced by Jaanusson (1956a): *M. lepikuensis* (pro *M. p.* var. *minor*), *M. ingeriensis* (pro *M. p.* var. *Lamanskiï*), and *M. laine* (pro *M. p.* var. *Knyrkoi*). *M. lepikuensis* comprises a limited, juvenile material (see Schmidt 1906; Balashova 1976) here identified with *M. polyphemus*. *M. ingeriensis* was based on two cranidia from BII α and BII β (Schmidt 1906, p. 28); Balashova (1976, pp. 88–89) described an additional entire specimen from BII α . The cephalon [lectotype] of *M. ingeriensis* from BII β is exceedingly like *M. simon* Tjernvik (cf. Schmidt 1906, Pl. 2:8 vs. Tjernvik 1980, Fig. 9B), and these species are possibly synonymous. The second specimen of *M. 'ingeriensis'* (Schmidt 1906, Pl. 2:7) from BII α seems to have a long glabella, and is otherwise slightly different from the lectotype of *M. ingeriensis*, and is hardly conspecific. The entire specimen of *M. ingeriensis* from BII α , figured by Balashova (1976, Pl. 20:4a–b), shows a very prominent, broad (i.e. 'simon-like') pygidial axis, but the glabella appears relatively long; no additional information is stated in the description (Balashova 1976, pp. 88–89). The specimen is noteworthy, as it may represent an 'extrazonal' *M. simon* type (see below).

M. laine is known from BII γ (see Schmidt 1906, pp. 29–31, Pl. 2:9; Balashova 1976, p. 90), and also occurs in the *Lepidurus* Limestone of northern Öland (unpublished data). *M. laine* is here allocated to *M. (Megistaspidella)* (cf. Jaanusson 1956a). Tjernvik (1980, p. 188) listed a pygidium from the *M. estonica* Zone of Öland, suggested to represent an ancestor to *M. laine*. No further information was given, and the relation, if any, to the coeval, poorly known *M. pogrebowi* is unknown, as is the relation to *M. laine*.

Other species of M. (MEGISTASPIS). – *M. (M.) simon* Tjernvik, 1980 is index species for the middle zone of the Volkhov Stage; it may eventually turn out to be a junior synonym of *M. (M.) ingeriensis* (s.str.) as remarked above. In a stratigraphical context it is relevant that broad-axed 'simon-type' pygidia occasionally are found outside the *M. simon* Zone, although only rarely so (see sections on *M. simon* and *Megistaspis* sp. A for details).

The eastern Baltic *M. lawae*, of which only very sparse material is known, occurs in Zone BII β (Schmidt 1906; Balashova 1976). The species resembles *M. simon* by having an unusually short glabella and no posterior cephalic border furrow, but the pygidial axis is narrow, like in *M. limbata*. The relationship between these species are presently obscure.

Megistaspis (M.) geminus n.sp. characterises the upper part of the *M. limbata* Zone of the Komstad Limestone, but occurs also at the very base of the *A. expansus* Zone. Findings

of a single specimen in the *A. expansus* Zone at Slemmestad indicates that *M. geminus* n.sp. is not confined to the Komstad Limestone, and, albeit purely speculative, it may be the second species of 'elongata-type' from the *A. expansus* Zone of Sweden, referred to by Tjernvik (1972).

Sparse material from Slemmestad and SE Scania, treated in open nomenclature as spp. B and C, is believed to represent a new species (possibly, but not necessarily with two subspecies). Species D and E may be related to *M. ringsakerensis* (Skjeseth, 1952) and *M. knyrkoi* (Schmidt, 1906) [non *M. polyphemus* var. *knyrkoi* Schmidt, 1906 = *M. (M.) laine* Jaanusson, 1956]. As the cephalon of *M. ringsakerensis* and *M. knyrkoi* are unknown, the affinities remain uncertain. Nevertheless, it is possible that these species, or some of them, represent an as yet undefined subgenus of *Megistaspis* with affinity to the *M. (Paramegistaspis)* group, as especially indicated by the cranidial outline of spp. B and C (see section on *Megistaspis* sp. B for details).

M. (M.)? similis was described by Burskij (1970) from Paj Choj (Arctic Russia). The species is characterized by a comparatively broad doublure, and the cephalic outline is closer to *Paramegistaspis* than to *Megistaspis*.

Species of MEGISTASPIS (RHINOFERUS), M. (MEGISTASPIDELLA) and M. (HERASPIS). – *M. (Rhinoferus)* is very sparingly represented in the available material; the subgenus is much more common in the eastern Baltic area. For reviews of the group, see Schmidt (1906, 1907) and Balashova (1976). The poorly known *M. explanata* is here tentatively assigned to this group.

The available material of *M. (Megistaspidella)*, listed in Fig. 80, is also limited, and the reader is referred to Jaanusson (1956a), Bohlin (1960), Balashova (1976), and Wandås (1984) for reviews of the subgenus. It contains at present more than 20 species, but many of them are inadequately known, and several must be considered *nomina dubia*. In view of the strong variability shown by representatives of *M. (Megistaspis)*, it is suspected that the 'narrow' species limits of *Megistaspidella* employed by Bohlin (1955, 1960), Balashova (1976) and Wandås (1984) are artificial, but more material is needed to document this conjecture.

M. (Megistaspidella) grandis (Sars, 1835) is known only from a few poorly preserved Norwegian specimens, re-described by Bohlin (1960); the type material is now believed to originate from the Lysaker Member (Henningsmoen 1971, p. 91). No new material has been found during the present study. Brögger (1882) stated that *M. grandis* appears in the upper part of the *Expansus* Shale, but is more common in the *Orthoceras* Limestone (3cy). Størmer (1953) listed the species from the Transition beds [Killingen Member of the Elnes Formation], but it is not clear what *M. grandis sensu* Størmer covers, as no reference to his material was made by Wandås (1984).

The *M. (Heraspis)* group was discussed by Wandås (1984); *M. lawrowi* is here tentatively allocated to *M. (Rhinoferus)*.

Megistaspis (Megistaspis)

Jaanusson, 1956

pro *Megalaspis* Angelin, 1851; non *Megalaspis* Bleeker, 1851Type species. – (OD) *Trilobites limbatus* Boeck, 1838.*Megistaspis (Megistaspis) limbata*
(Boeck, 1838)

Figs. 81–100

Synonymy. – □v 1882 *Megalaspis limbata*, Boeck, form. *typica* [*partim*] – Brögger, pp. 77–79; Pl. 9:2–4; non Pl. 9:1 [= *M. (M.) elongata*] (description, occurrence, illustrations of cephalon and pygidium). □v 1882 *Meg. limbata*, Boeck, var. *minor* – Brögger, p. 77; Pl. 2:2 (short diagnosis, occurrence, illustration of pygidium). □v 1919 *Megalaspis limbata* Sars & Boeck [*partim*]. – Funkquist, pp. 21, 39 (occurrence). □v 1936 *Megalaspis limbata* Sars & Boeck [*partim*] – C. Poulsen, pp. 48, 50 (listed). □v 1941 *Megalaspis limbata* (Boeck) – Størmer, p. 141 (designation of lectotype). □v 1952 *Megalaspis limbata* (Boeck) [*partim*] – Skjeseth, p. 161; Pl. 1:7; non Pl. 1:3 [*Megistaspis* cf. sp. C] (occurrence, illustration of pygidium). □v 1956a *Megistaspis (Megistaspis) limbata* (Boeck, 1838) – Jaanusson, pp. 60–71; Pl. 1:1–3 (discussion of taxonomy, illustrations of lectotype). □1956a *Megistaspis (Megistaspis)* n.sp. – Jaanusson, p. 70 (listed). □v 1965 *Megistaspis (Megistaspis)* cf. *lata* (Törnquist, 1884) – V. Poulsen, pp. 66–67; Pl. 1:7 (description, occurrence, illustration of pygidium). □1970 *Megistaspis (Megistaspis) limbata* (Boeck) – Burskij, pp. 115–116, Pls. 8:1–2; 9:1, 2, 4, 6; 10:1–3; 16:10 (description, occurrence, illustrations of cranidia and pygidia). □1972 *Megistaspis (Megistaspis) limbata* (Boeck, 1838) – Tjernvik, pp. 303–309; Textfig. 2A (discussion of distribution, drawing of cranidium). □1980 *Megistaspis (Megistaspis) limbata* (Boeck) – Tjernvik, pp. 192, 200; Figs. 7E, 9E–F (short description, occurrence, drawings and illustrations of cephalon, cranidium and pygidia). □? 1980 *Megistaspis minor* (Brögger) – Tjernvik, p. 192 (listed). □1980 *Megistaspis (Megistaspis) limbata* (Boeck) n.subsp. – Tjernvik, pp. 191, 192, 200; Figs. 7D, 9G–H (diagnosis, occurrence, drawings and illustrations of cranidium and pygidium). □1980 *Megistaspis (Megistaspis)* n.sp. no. 1 – Tjernvik, pp. 191, 197–198; Fig. 7B (description, occurrence, drawings of cranidium and pygidium). □? 1980 *Megistaspis (M.)* n.sp. no. 2 – Tjernvik, pp. 191, 199 (short description, occurrence). □v 1980 *Megistaspis (Megistaspis) lata* (Törnquist) [*partim*] – Tjernvik, Fig. 4 (occurrence).

Lectotype. – Complete specimen PMO 1631, figured by Brögger (1882, Pl. 9:2), designated by Størmer (1941). The lectotype specimen is refigured by Jaanusson (1956a, Pl. 1:1–3).

Material. – One complete specimen, 4 cephalon, 120 cranidia, 9 hypostomata, 31 librigenae and 339 pygidia. Sample numbers are listed for individual types.

Occurrence. – *M. (M.) limbata* ranges within the Komstad Limestone from the base of the *M. polyphemus* Zone and to the top of the lower subzone of the *M. limbata* Zone. Within the Slemmestad section the species ranges throughout the *M. simon* and *M. limbata* Zones.

M. limbata is widespread and common in Sweden, and occurs in all zones of the Volkhov Stage. The distribution in the eastern Baltic area is currently unknown, and depends on the interpretation of forms with a cephalic posterior border furrow.

Description. – Medium-sized to large species, largest cranidium 45 mm long, largest pygidium 53 mm long. Cephalic outline triangular (in narrow forms) to parabolic (in broad forms) with L:W ratios varying from about 0.7 to about 0.5 (excl. of genal spines), but the available material is limited. Width of cranidium rather variable, narrow specimens show PW:L values around 0.7, broad specimens around 0.75–0.8, total range 0.60–0.83 (mean 0.73; $N = 76$). The variation is usually only 10% or less for adult material from one horizon. Greatest cranial width is across posterior fixigenae, but also this value is rather variable, showing FW:L ratios varying between 1.12 and 1.48 (mean 1.27; $N = 46$). Early morphotypes generally have short (tr.) posterior fixigenae, while the longest fixigenae are seen in late morphotypes (Fig. 82A, compare also type 7 vs. 9) and this may be an evolutionary trend. Sagittal relief of cranidium moderate, strongest in smaller specimens. Median depression in preglabellar area faint to fairly distinct; lateral part of anterior fixigena gently flexed downwards. Glabella normally subcylindrical, fairly vaulted, stretching (including occipital ring) for 0.67–0.74 of the cranial length (mean 0.71; $N = 75$); it is delimited by fairly impressed dorsal and preglabellar furrows. Larger specimens generally show a less inflated glabella, but the degree of inflation also varies between ecophenotypes. Transverse glabellar furrows, level with palpebral area, faint to fairly impressed on internal moulds; furrows usually elongate, and then directed obliquely inwards-backwards, but some morphotypes show rounded impressions. Occipital furrow fully developed on internal moulds, and is typically of equal depth the whole way; occipital ring fairly prominent, slightly raised above the rear part of glabella. Internal moulds

Table 8. Adult cranidia of *M. limbata*, ranges for variation of PW:L and FW:L ratios in individual morphotypes.

Morph	PW:L range	Mean	N	FW:L range	Mean	N
Type 1	0.68–0.71	0.70	2	–	1.13	1
Type 2	0.69–0.78	0.74	4	–	–	0
Type 3	0.74–0.83	0.79	20	1.26–1.36	1.30	10
Type 4	0.70–0.76	0.73	17	1.18–1.35	1.28	10
Type 5	0.60–0.72	0.68	14	1.12–1.28	1.19	9
Type 6	0.73–0.77	0.76	8	1.32–1.48	1.40	5
Type 7	–	0.72	1	–	1.16	1
Type 9	0.67–0.73	0.70	9	1.26–1.33	1.28	7
Total	0.60–0.83	0.74	75	1.12–1.48	1.27	43

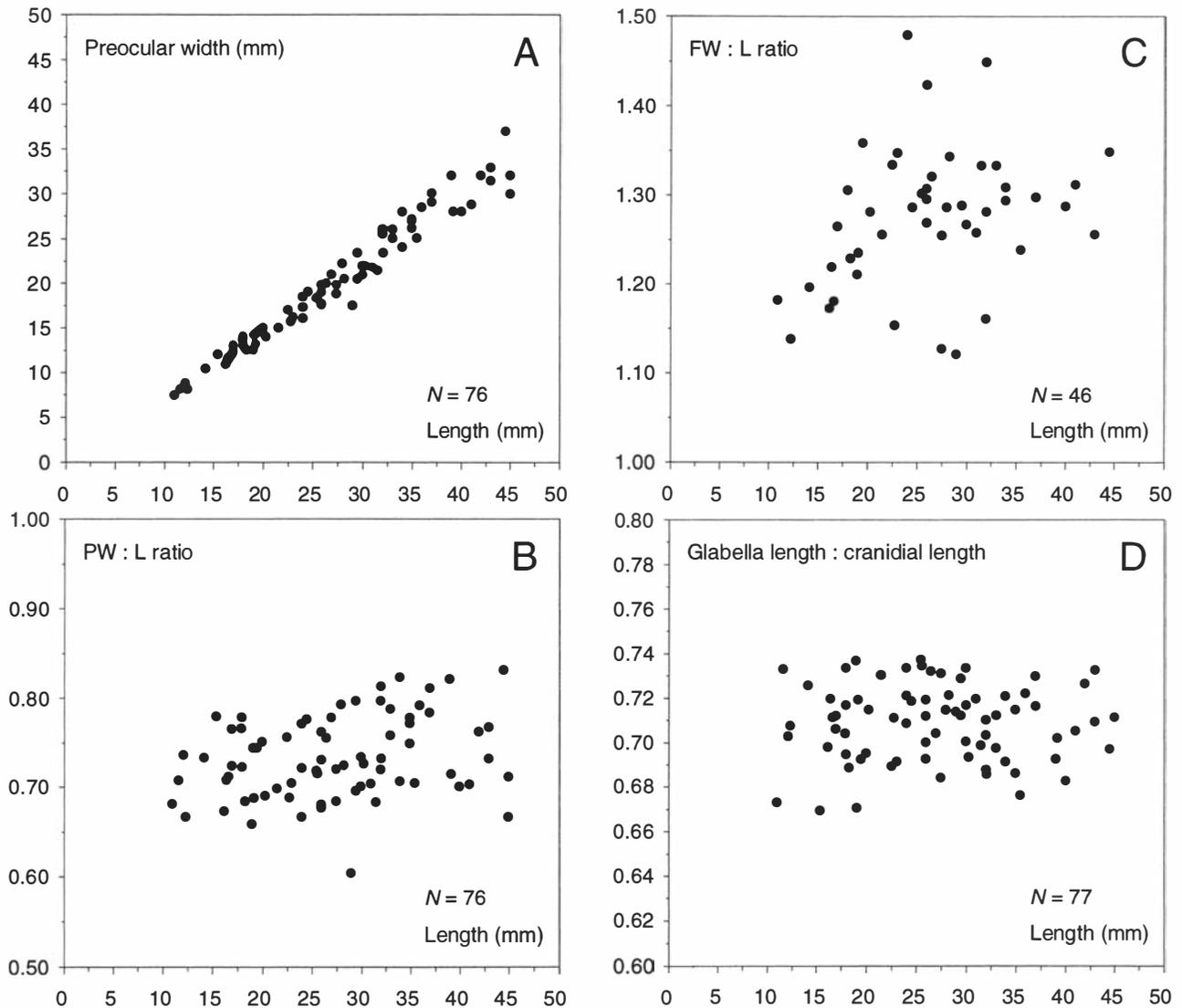


Fig. 81. Crania of *Megistaspis* (*M.*) *limbata* (s.l.). □A. Length (sag.) plotted against preocular width. □B. Ratio between preocular width and sagittal length, plotted against cranial length. □C. Ratio between width across posterior fixigenae and cranial length, plotted against cranial length. □D. Ratio between glabella length and cranial length (sag.), plotted against cranial length.

may show small, indistinct glabellar tubercle immediately in front of occipital furrow, but it is often absent. Baculae indistinct to fairly inflated. Palpebral normally raised a little above glabella in adults; the elevation decreases with size. Lobe length (exsag.) equivalent to about 0.15 of the cranial length; distance to posterior cranial margin corresponds to 1.5 times the lobe length in medium-sized specimens to almost 2 times the lobe length in the largest specimens. The majority of testaceous specimens shows no posterior border furrow, but it is occasionally faintly indicated on internal moulds; type 6 has a shallow border furrow. The anterior branches of facial suture typically diverge in front of the eyes, commonly at an angle of about 10° to sagittal line, then bend inwards, usually converging at an angle of about $120\text{--}125^\circ$ to

sagittal line, to meet in an angulate junction. The outline of facial suture varies, however, between the different eco-phenotypes (total variation $0\text{--}15^\circ$ divergence, $115\text{--}130^\circ$ convergence). Cephalic doublure poorly exposed in the available material.

Librigena steeply ascending to the eye; a narrow lateral border tapers backwards, but enters genal spine. Border best defined in smaller specimens, and relative width decreases with size. Genal spine fairly prominent, directed obliquely backwards-outwards. Furrow at base of eye socle, best seen on internal moulds, variably developed, but is normally rather faint or even effaced. Delicate, short terrace lines occur on the border along margin. The cephalic test surface is otherwise smooth.

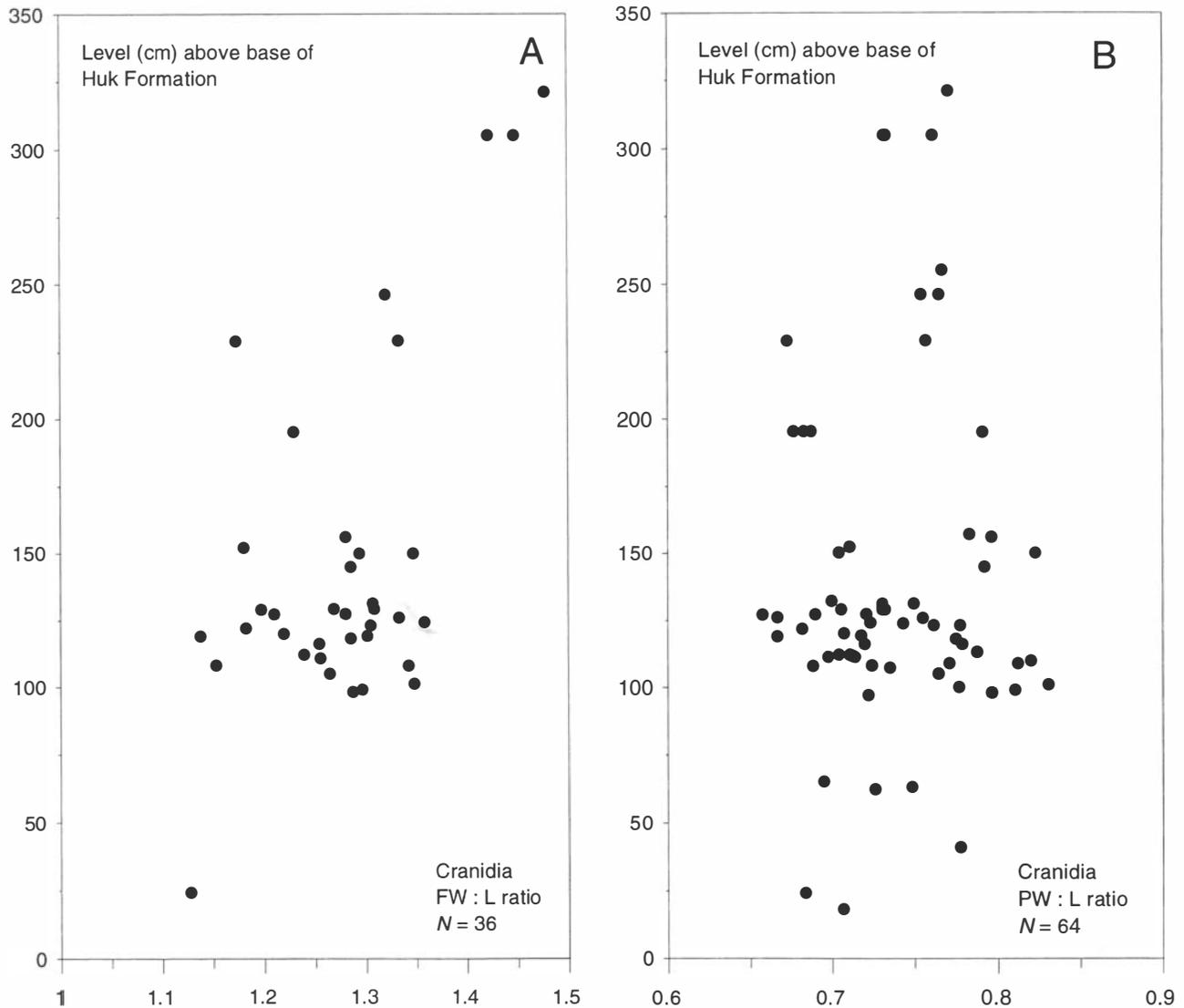


Fig. 82. Cranidia of *Megistaspis (M.) limbata (s.l.)*, Slemmestad section. □A. FW:L ratio plotted against stratigraphic occurrence. □B. PW:L ratio plotted against stratigraphic occurrence.

Largest hypostome 25 mm long. Gross outline quadratic; greatest width is across anterior wings, corresponding to 0.91–1.08 of the hypostome length (sag.) (mean 1.01; $N=6$); width across posterolateral borders equivalent to 0.76–1.04 times the hypostomal length (sag.), (mean 0.88; $N=7$). Median body prominent, oval, strongly inflated, reaching anterior hypostomal margin, or nearly so; median body accounts for 0.89–0.94, (mean 0.91; $N=7$) of the sagittal hypostomal length, and the body W:L ratio is 0.57–0.73, (mean 0.65; $N=7$). A pair of fairly impressed premacular pits is situated close to posterior end of median body; the pits are occasionally united across sagittal line by a very shallow furrow, best defined on internal moulds. The pits divide the median body into a prominent, long anterior lobe, accounting for about 0.9 or more of the median body length, and a short posterior lobe. Anterior margin of hypostome straight

Table 9. Hypostomes of *M. limbata (s.l.)*. I–II. Width (tr.) across anterior (I) and posterior (II) wings (ratio of hypostomal length [sag.]). III. Length of median body (ratio of hypostomal length [sag.]). IV. Median body L:W ratio. V. Distance (exsag.) from anterior margin to lateral border (ratio of hypostomal length [sag.]).

Specimen	Morph	Length (mm)	I	II	III	IV	V
A 22	Type 1	12.4	0.91	0.76	0.94	0.57	0.44
A 752	Type 2	25.0	1.00	0.80	0.94	0.57	0.44
A 963b	Type 4	16.6	1.04	0.83	0.89	0.61	0.40
A 995b	Type 4	ca. 17	—	—	—	—	—
A 78a	Type 4	6.5	0.95	0.76	0.90	0.69	0.45
A 309	Type 6	12.6	1.05	0.98	0.90	0.69	0.33
PMO 64 315	Type 6	15.0	1.08	1.04	0.90	0.67	0.36
IK-P4b	Type 7	ca. 17	0.8*	0.6*	0.9*	0.5*	0.4*
LU 16b	Type 9	15.0	—	0.97	0.89	0.73	0.34
Mean (exclusive of IK-P4b)			1.01	0.88	0.91	0.65	0.39

* Ratio tentative, not included in total mean.

or very slightly curved in main central part, curving backwards distally. Posterior margin convex in early types, concave in late, this is possibly an evolutionary trend. Macular surface smooth, narrow, slanting forwards. Anterior wings very well-developed, ascending strongly in dorsal direction. Main outer anterolateral part of wing is flexed ventrally, defining a narrow anterior border. Wing merges imperceptibly with median body, or a very shallow border furrow may be indicated. Lateral border commences 0.32–0.45 of the hypostomal length (sag.) from anterior margin (mean 0.39; $N = 7$). Border widens backwards to attain maximum width level with premacular pits, continuing without boundary into a posterior border, widest in late types. The border is bounded by a deep border furrow, running backwards from anterior wing, joins premacular pit and continues rearwards into a posterolateral depression and then turns inwards, curving around the posterior lobe of median body. The posterior section of the border furrow is, however, shallow and rather indistinct, and runs immediately adjacent to the posterior margin medially. The entire test surface, except for the main central part of median body, is covered with rather densely spaced terrace ridges, which follow the body contour laterally on median body, cross anterior wings and follow the outer margin on the borders.

Pygidium parabolic to triangular in outline; adult L:W ratios (specimens >15 mm long) vary between 0.60 and 0.86 (Table 10), but within one horizon the variation is usually only about 15% (Figs. 52–53). Larger pygidia tend to be slightly broader than smaller adult specimens (Fig. 83B). Axis narrow or moderately so, and stretches for about 0.85–0.90 of the pygidial length; anterior half tapers gently, posterior half approximately parallel-sided, terminal portion, as seen on internal moulds, may be very slightly expanded. Minimum axial width, which is at axial ring nos. 8–9, equivalent to 0.17–0.23 of the pygidial length (mean 0.21; $N = 205$). Axis delimited by wide, fairly well-impressed axial furrows, shallowing up at the intersection with paradoublural line. Axis and pleural fields of subequal height. Axial segmentation almost effaced on testaceous material; internal moulds show 13 axial segments in addition to the terminal piece and

Table 10. Adult pygidia (>15 mm long) of *M. limbata*, ranges for variation of L:W ratio in individual morphotypes.

Morph	L:W range	Mean	N
Type 1	—	0.75	1
Type 2	0.67–0.81	0.75	8
Type 3	0.63–0.83	0.72	36
Type 4	0.63–0.76	0.70	7
Type 5	0.68–0.86	0.75	33
Type 6	0.60–0.85	0.71	22
Type 7	0.70–0.75	0.72	14
Type 8	0.72–0.74	0.73	4
Type 9	0.64–0.76	0.70	88
Total	0.60–0.86	0.72	213

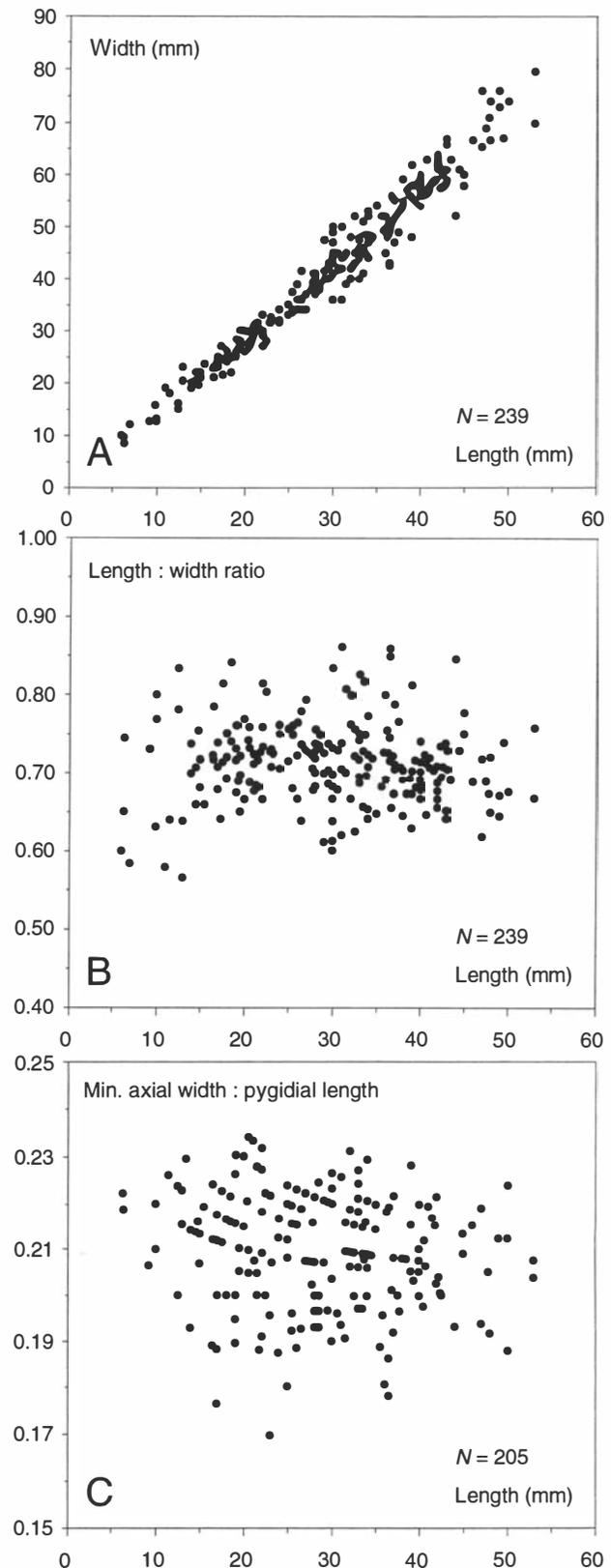


Fig. 83. Pygidia of *Megistaspis* (*M.*) *limbata* (*s.l.*). □A. Maximum width plotted against sagittal length. □B. L:W ratio plotted against pygidial length. □C. Ratio between minimum axial width and pygidial length (sag.) plotted against pygidial length.

anterior half-ring, but only the anterior one to three axial rings, rarely more, are developed as true rings; well-preserved specimens show the axial rings to be double, divided by a shallow transverse furrow. The rear segments are indicated by lateral, paired knobs. Pleural fields evenly convex with 7 pairs of bifurcate low ribs inside paradoublural line, best defined on internal moulds, and to some extent effaced on testaceous material. Articulating facets triangular, concave, slanting forwards, provided with short, irregular low ridges, resembling terrace lines. Pygidial test surface otherwise smooth. Moderately to distinctly concave border present posteriorly; anterolateral margins convex, confluent with pleural fields. Larger as well as broader pygidia have a gently concave, rather narrow border, developed only in the hindmost portion of pygidium, while smaller and in particular narrow pygidia show a much more strongly concave and slightly wider border, upturned postaxially, especially in the latest morphotypes.

Doublure sigmoidal in cross-section with a gently concave, almost horizontal outer half, and a steep, slightly convex inner half; the convexity of the latter increases rearwards, producing a flattened strip along inner margin posteriorly. Outer half of doublure is upturned postaxially. Inner margin shows a small V-shaped axial embayment. Combined width (both sides) of the doublure at anterior margin is equivalent to about 0.2 of the pygidial width. Doublure covered with 15–18 (counted at pygidial midline) moderately spaced, rather coarse terrace lines, most dense along inner margin and in the flexure between inner and outer halves. The exterior lines parallel the outer margin, whereas the lines on the inner half descend from inner margin, run backwards to meet the outer lines discordantly in the flexure. Short interjacent lines are occasionally present on the steep part of the doublure, especially posterolaterally. Lines generally slightly wavy on the steep part. Rearmost lines descending from the inner margin unite across sagittal line, and are therefore V-shaped in dorsal view.

Juveniles. – The degree of glabellar inflation and the depth of lateral glabellar, occipital, dorsal and prelabellar furrows diminish during growth, the sagittal cephalic relief decreases markedly, and the palpebral lobes descend from being significantly raised above glabella to about level with glabella in the largest adults. The lobes are also situated closer to posterior cranial margin in juveniles. It is a general impression that juvenile cranidia are narrower than adult specimens; cranidia 11 to 17 mm long show a W:L ratio across posterior fixigenae of 1.14–1.22 (mean 1.18; $N = 6$), and the preocular width also tends to be slightly smaller, but less distinctly so (Fig. 81B). The lateral cephalic border is more distinctly set off in juveniles.

Pygidia 6–15 mm long are broader than the associated adults, W:L ratios vary between 0.57 and 0.83 (mean 0.68; $N = 20$; Fig. 83B), and show a more strongly inflated axis and better defined segmentation (axis and pleural fields). Juve-

niles up to 10 mm long have a well-defined concave border extending almost to the anterolateral corners, and are overall rather strongly vaulted. Smaller pygidia up to 20 mm long may still have a forward-extending border to about midline across pygidium; the border is best defined on internal moulds.

Affinities. – *M. limbata* is distinguished from *M. simon* by the longer glabella and the narrower pygidial axis; isolated pygidia may, however, occasionally be difficult to assign. In the Komstad Limestone *M. simon* also tends to be broader than the associated *M. limbata* type 9. *M. limbata* is more readily separated from *M. polyphemus*, by being overall narrower, having a comparatively well-inflated, subcylindrical glabella, larger eyes, more prominent genal spines, a more distinct pygidial axial constriction and, in particular in smaller pygidia, an upturned postaxial border.

The differences between *M. limbata* vs. *M. elongata* and *M. geminus* n.sp. are discussed in the respective sections on those species.

Remarks. – The taxonomical status of this species is discussed in the introductory remarks above. It is there concluded that the narrow species concept of *M. limbata* hitherto employed (Jaanusson 1956a; Balashova 1976; Tjernvik 1980) seems unwarranted. Within the present material nine intergrading *limbata* 'morphotypes' are recognized, which are interpreted as ecophenotypes. Which taxonomical distinction (subspecies/variants/no distinction) these should have must be decided by future investigations. In order to stabilize the nomenclature of *Megistaspis*, the present contribution is kept in open nomenclature, awaiting examinations of large, stratigraphically well-documented materials from other areas of the Baltoscandian region. However, a temporary conclusion seems to be that a separation at the subspecies level generally is unworkable, with type 6 as a possible exception.

Megistaspis (Megistaspis) limbata type 1

Figs. 84A–C, 85

Material. – One cephalon, 1 cranidium, 1 hypostome and 1 pygidium.

List of material. – □Cephalon A 17 (pim) [MGUH 22.424]. □Cranidium A 656 (im) [MGUH 22.423]. □Hypostoma A 22 (im). □Pygidium A 653 (im).

Occurrence. – *M. (M.) limbata* type 1 occurs in the lower part of the *M. simon* Zone at Slemmestad, where it has been found in beds M-2 and M-3 of the Hukodden Limestone. Type 1 also seems present near the base of the *M. simon* Zone on northern Öland and in the Finngrundet core, see remarks below.

Description. – Largest cranidium 27.5 mm long (cranial length of cephalon A 17), available pygidium ca. 18 mm long. Cephalic L:W ratio slightly exceeds 0.7. Cranidium narrow

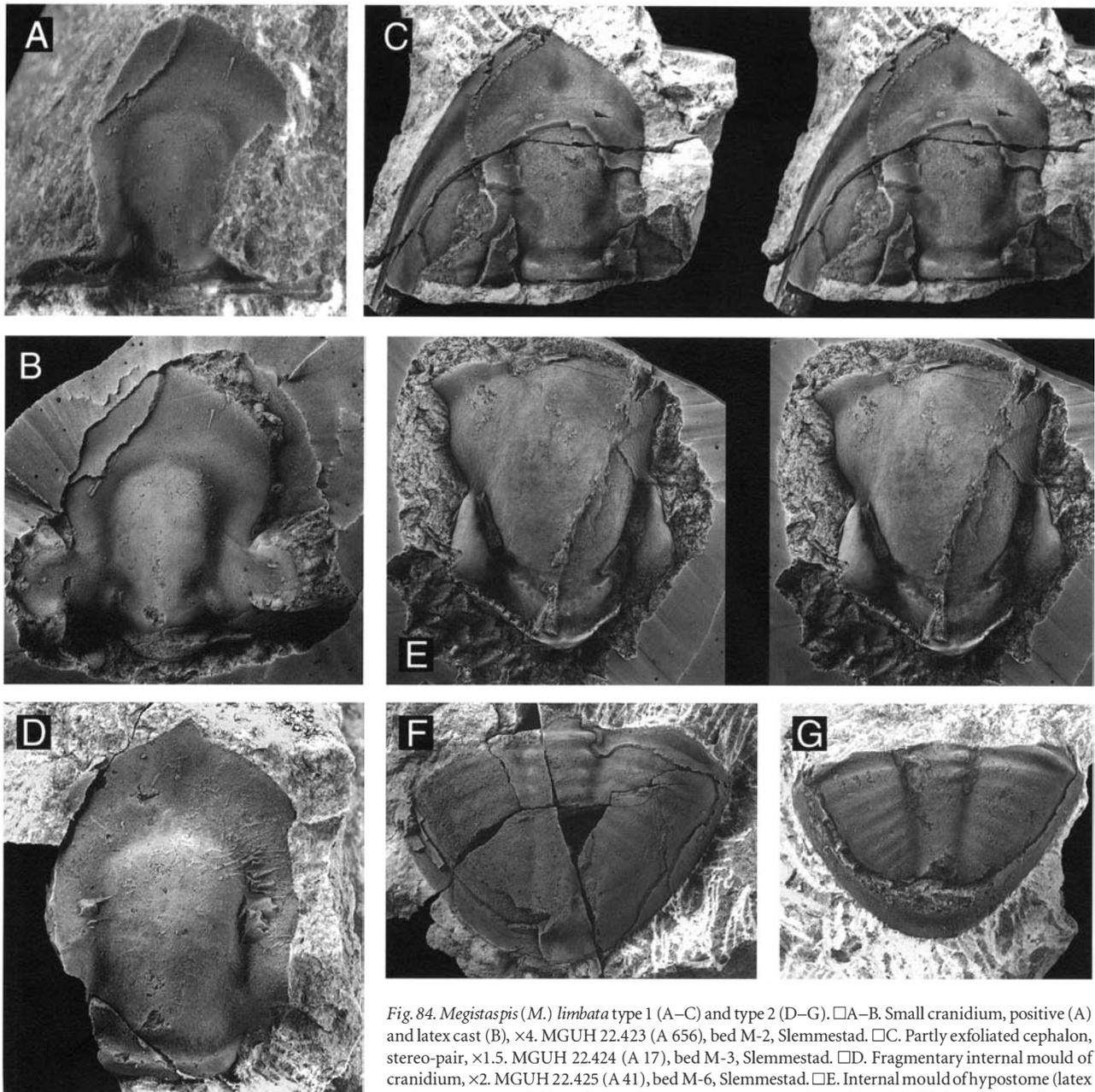


Fig. 84. *Megistaspis* (*M.*) *limbata* type 1 (A–C) and type 2 (D–G). □A–B. Small cranidium, positive (A) and latex cast (B), $\times 4$. MGUH 22.423 (A 656), bed M-2, Slemmestad. □C. Partly exfoliated cephalon, stereo-pair, $\times 1.5$. MGUH 22.424 (A 17), bed M-3, Slemmestad. □D. Fragmentary internal mould of cranidium, $\times 2$. MGUH 22.425 (A 41), bed M-6, Slemmestad. □E. Internal mould of hypostome (latex cast), stereo-pair, $\times 2$. Note the convex posterior margin. MGUH 22.426 (A 752), bed M-6, Slemmestad. □F. Internal mould of pygidium, $\times 1$. MGUH 22.427 (A 782), bed M-6, Slemmestad. □G. Internal mould of small pygidium, $\times 2$. MGUH 22.428 (A 750), bed M-6, Slemmestad.

with moderate sagittal convexity; FW:L ratio unusually low. Median depression in preglabellar area fairly distinct. Glabella of low relief, why glabella is rather poorly set off from preglabellar area, where the test is intact. Elongate transverse glabellar furrows well-impressed on internal moulds, and glabella therefore assumes a faintly pyriform outline. Baculae ill-defined, indicated mainly as posterior shallowings of the axial furrows. Facial sutures diverge at an angle of about 15° to sagittal line in front of eyes, then bend inwards,

converging at an angle of about $120\text{--}125^\circ$ to sagittal line. Genal spine appears prominent, but distal part is damaged.

The hypostome is quite similar to the large hypostome assigned to *M. limbata* type 2, and they are described collectively below. By comparison, the hypostome of type 1 is slightly narrower and with a more slender median body.

Pygidium damaged. It is relatively narrow, L:W ratio ca. 0.75 (Fig. 85); the border is only slightly upturned post-axially.

Remarks. – Tjernvik (1980, pp. 192, 200) briefly described a new subspecies of *M. limbata* from the *M. simon* Zone of Sweden, stated to differ from *M. limbata* (*s.str.*) by having a broader (tr.) cranium, and a pygidium with shorter axis and a correspondingly longer and only slightly upturned postaxial border. Although being roughly contemporaneous, Tjernvik's unnamed subspecies cannot correspond to the relatively narrow *Megistaspis* (*M.*) *limbata* type 1, which is more similar to the later *M. (M.) limbata* '*s.str.*' (here type 5). Compared to *M. (M.) limbata* type 5, the type 1 cranidia have more strongly diverging anterior branches of facial suture (but, still, the preocular width is comparatively small), short (tr.) posterior fixigenae, and a distinctly less vaulted glabella with elongate lateral glabellar furrows (rounded in *M. (M.) limbata* type 5). The degree of upturning of the postaxial border is the only recognized pygidial difference.

Tjernvik (1980, p. 200) mentioned that forms intermediate between the new broad subspecies and *M. (M.) limbata* (*s.str.*) occur at Lanna, and an intermediate specimen was found in the Finngrundet core at 49.61 m (not indicated in the diagram Tjernvik 1980, Fig. 4). This level is, however, within the lower part (!) of the *M. simon* Zone, and the occurrence is equal to the distribution of *M. (M.) limbata* type 1 at Slemmestad. The Finngrundet specimen could not be located in the Tjernvik collection, University of Uppsala.

A cranium collected from the 'Blood Layer' complex (basal Horns Udde Formation *sensu* van Wamel 1974) at Horns Udde, northern Öland, is entirely similar to the limited material of type 1 from Slemmestad. The 'Blood Layer' is generally considered to represent the lower part of the *M. simon* Zone.

It appears that Tjernvik (1980) implicitly assumed that the narrow *M. limbata* '*s.str.*' evolved from the broad *M. limbata* '*n.subsp.*', but such an interpretation is difficult to reconcile with the presence of an 'intermediate' type already at the base of the *M. simon* Zone, i.e. prior to the appearance of broad types. In my opinion the distribution of narrow and broad *M. limbata* types mirrors environment rather than evolution.

Megistaspis (*Megistaspis*) *limbata* type 2

Figs. 84D–G, 85

Synonymy. – □1980 *Megistaspis* (*Megistaspis*) *limbata* (Boeck) *n.subsp.* [*partim?*] – Tjernvik, pp. 191, 192, 200; Figs. 7D, 9G–H (diagnosis, occurrence, drawings and photographs of cranium and pygidium).

Material. – Six cranidia, 1 librigena, 1 hypostoma, and 17 pygidia.

List of material. – □Cranidia A 41 (im) [MGUH 22.425], A 690 (im), A 753a (im), A 753b? (im), A 758 (im), A 787 (pim). □Librigena A 668? (im). □Hypostoma A 752 (im) [MGUH 22.426]. □Pygidia A 21 (im), A 662 (im), A 669 (im), A 671 (im), A 695 (im), A 717 (t), A 720 (im), A 726? (im), A 750 (im) [MGUH 22.428], A 753c (t), A 753d (im), A 771 (im), A 773 (im), A 782 (im) [MGUH 22.427], A 783? (im), A 786 (im), A 788 (pim).

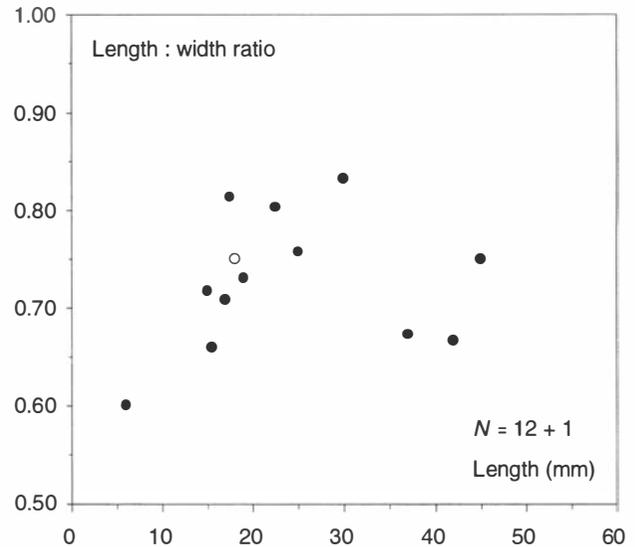


Fig. 85. Pygidia of *Megistaspis* (*M.*) *limbata* types 1 (○) and 2 (●). Ratio between length (sag.) and maximum width plotted against pygidial length.

Occurrence. – *M. (M.) limbata* type 2 is frequent at Slemmestad in bed interval M-4 to M-6, which constitutes the upper part of the *M. simon* Zone. Type 2 also seems to be present in the *M. simon* Zone of Sweden, see discussion below.

Description. – Largest cranium 35 mm long, largest pygidium 45 mm long. Cranium moderately narrow (Table 8); the limited material suggests that cranidia become narrower upwards from bed M-4 to M-6: one cranium from bed M-4 shows a PW:L value of 0.78, whereas three cranidia from bed 6 show 0.69–0.75 (mean 0.72). Sagittal relief of cranidia fairly strong. Median depression in preglabellar area moderately to faintly impressed. Glabella distinctly vaulted; elongate transverse glabellar furrows shallow on internal moulds. Baculae as *M. limbata* type 1. Facial sutures diverge in front of eyes at an angle of about 5–10° to sagittal line, then turn inwards, converging at an angle of 115–125° to sagittal line (115° in the early specimen, 120–125° in the latest).

Hypostome 25 mm long (Fig. 84E); various ratios are listed in Table 9. A 12.4 mm long hypostome from bed M-3, assumed to match *M. limbata* type 1, has a very similar structure. The two specimens differ from later *limbata* hypostomes by showing an evenly convex posterior margin without mesial incurvature, the premacular pits are united across sagittal line by a shallow furrow (the specimens are exfoliated), the anterior wings are comparatively broad, and the lateral border is quite markedly raised (ventral view), hence the adjacent border furrow appears deep; the posterior border is narrow.

Pygidium narrow (Table 10), with axis of variable length, but typically long; length of postaxial border and degree of concavity vary in correspondence to the axial length, so pygidia with a long axis show a short, pronouncedly concave

border. Moderately to distinctly concave border present posteriorly, but is not as upturned as in the later types of *M. (M.) limbata*.

Remarks. – The cranidia referred to as *M. (M.) limbata* type 2 are slightly wider (tr.) than type 1 and has a much more prominent glabella with rather indistinct transverse glabellar furrows, while type 2 cranidia by comparison to type 3 are narrower (tr.), and exhibit a relatively narrower and stronger vaulted glabella. Type 2 is separated from type 5 by showing a wider glabella, generally also a wider cranidium, markedly shallower lateral glabellar furrows and less downflexed anterolateral corners of anterior fixigenae. Type 2 cranidia resemble *M. (M.) simon* with regard to glabellar width, but are characterized by a distinctly longer glabella, the preocular cranial width is usually relatively smaller, and the palpebral lobes are raised slightly higher above glabella, all in specimens of equal size.

The pygidia associated with the type 2 cranidia are more generalized. Smaller pygidia of type 2 show a less upturned postaxial border than smaller pygidia of types 3 and 5, whereas the largest pygidia of these types are indistinguishable.

Megistaspis (M.) limbata type 2 seems to have roughly the same range as the Swedish *M. (M.) limbata* subsp. Tjernvik, 1980, and matches it on several points (compare Tjernvik 1980, p. 200). It is, however, suspected that the material at hand is biased towards the narrower end of variation range; ‘early’ cephalae of type 2 (i.e. from a different palaeoenvironment) are expected to be slightly broader.

The cranidium figured by Tjernvik (1980, Fig. 9G) is certainly a ‘type 2’, as indicated by the fairly strongly arched glabella, preocular width, etc. (the specimen has been examined). Type 2 is therefore taken to be largely identical to *M. limbata* subsp. Tjernvik, but it is suspected that Tjernvik accommodated the broad type 3 in *M. limbata* subsp. as well.

Tjernvik (1980, p. 192) listed a *Megistaspis (M.)* sp. 3 from the *M. simon* Zone. In the absence of a description this species and its occurrence cannot be discussed.

Megistaspis (Megistaspis) limbata type 3

Figs. 86–88

Synonymy. – □cf. 1980 *Megistaspis (Megistaspis) limbata* (Boeck) n.subsp. [*partim?*] – Tjernvik, pp. 191, 192, 200; Figs. 7D, 9G–H (diagnosis, occurrence, drawings and photographs of cranidium and pygidium).

Material. – Two cephalae, 31 cranidia, 8 librigenae, and 70 pygidia.

List of material. – □Cephalae A 42b (t), A 809 (im) with four thoracic segments [MGUH 22.430]. □Cranidia A 92 (c), A 816b (im), A 816c (im), A 816d (pim), A 817 (im), A 828b (im), A 843? (im), A 869? (im), A 891 (im), A 897 (t), A 923 (im), A 937c (im), A 938 (im), A 939 (im), A 948a (im), A 948b (im), A 962 (t) [MGUH 22.429], A 965b (im) [MGUH

22.431], A 975? (im), A 982? (im), A 991? (im), A 1055a (pim), A 1063b (pim), A 1077 (pim). □Juvenile cranidia A 23 (im), A 882 (im), A 933a (pim), A 965f (im), A 966b (im), A 967b (im), A 970a (im). □Librigenae A 37b (im), A 78b? (im), A 121 (im), A 792 (im), A 795 (im), A 847b (im), A 964b (pim) [MGUH 22.432], A 980 (im). □Pygidia A 33a (im) [MGUH 22.435], A 33b (im), A 36b? (im), A 36d (pim), A 37a (im), A 53? (c), A 60 (im), A 61 (pim), A 63? (im), A 68a (pim), A 72 (pim), A 86a (im) [MGUH 22.433], A 98c (c), A 99? (pim), A 102? (im), A 107 (im), A 109 (c), A 128? (im), A 791 (im), A 797 (im), A 813 (im), A 816a (im), A 820 (im), A 824 (im), A 825 (im), A 827 (im), A 828a (im), A 831 (im) [MGUH 22.437], A 845 (im), A 847a (im), A 848 (pim) [MGUH 22.436], A 857a (im), A 858 (im), A 866 (im), A 871 (pim), A 872a (im), A 872b (t), A 879a (im), A 879b (im), A 879d (im), A 884? (im), A 885 (pim), A 889a (im), A 902 (im), A 904 (im), A 908a (pim), A 908b (im), A 908c? (im), A 919 (im), A 924 (im), A 933b (im), A 933c (im), A 933d? (im), A 945? (im), A 954 (im), A 955a (im), A 955b (im), A 961a (im), A 961c (pim), A 962a (im), A 962b (pim) [MGUH 22.434], A 964c (im), A 964d (im), A 989 (im), A 1011? (im), A 1013b (im), A 1025 (im), 1028? (im), A 1056b (im), A 1065a (im/em).

Occurrence. – *M. (M.) limbata* type 3 occurs frequently in bed interval M-7 to M-10 and, sparsely, in bed interval M-11 to A-5 at Slemmestad, i.e. through the lower half of the *M. limbata* Zone.

Cranidia collected from the uppermost part of the Horns Udde Formation (see van Wamel 1974) and the lower part of the *Lepidurus* Limestone of northern Öland are for all practical purposes similar to *M. (M.) limbata* type 3. Both occurrences are within the *M. limbata* Zone.

Description. – Largest cranidium 45 mm long, largest pygidium 53 mm long. Cephalon parabolic in outline, L:W ratio about 0.6 (excl. of genal spines). Cranidium wide (Table 8); the smallest FW:L value is in a cranidium 17 mm long, the lowest adult value is 1.28 (cf. Table 8). Glabella moderately convex, gently forwards-expanding and, therefore, slightly pyriform in outline. Lateral glabellar furrows shallow. Median depression in frontal area fairly distinct on internal moulds. Occipital furrow well-impressed, distinctly deeper laterally, shallower mesially. Palpebral area wide, sloping moderately in adaxial direction. Baculae distinct. Anterior branches of facial suture diverge in front of eyes at an angle of about 15° to sagittal line, then turn inwards and converge at an angle of about 120° to sagittal line.

Librigena has low eye socle with a shallow furrow at the base in the largest specimens. Genal spine comparatively slender.

Pygidium generally broad, especially the larger specimens (Table 10; Fig. 88). The terrace lines on the doublure appear coarse, and a total of only 15–16 lines has been counted at midline across pygidium in a couple of specimens. A large specimen shows more wavy and discontinuous terrace lines on the steep part of the doublure.

Affinities. – The broad *M. limbata* type 3 is superficially somewhat like *M. polyphemus*. By comparison, the cephalon of type 3 is more elongate, has a narrower and slightly more arched glabella, a better impressed occipital furrow, larger eyes, and more stout genal spines. The pygidia of the two species have different axial outlines.

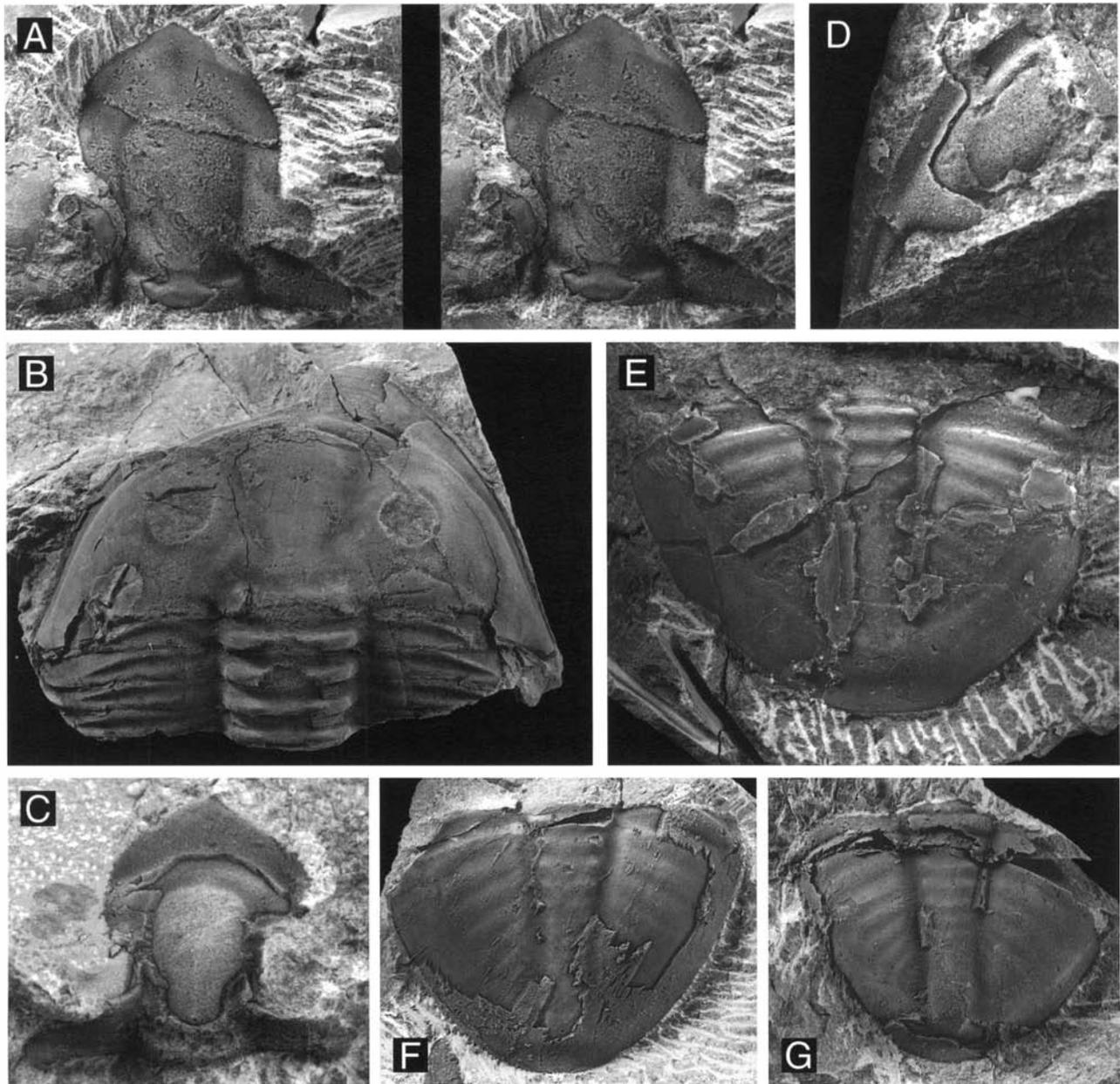


Fig. 86. *Megistaspis* (*M.*) *limbata* type 3. □A. Large, somewhat corroded cranidium, stereo-pair, $\times 1$. MGUH 22.429 (A 962), bed M-9, Slemmestad. □B. Internal mould of damaged cephalothorax, $\times 1.5$. MGUH 22.430 (A 809), bed M-7, Slemmestad. □C. Partly exfoliated small cranidium, $\times 4$. MGUH 22.431 (A 965b), bed M-10, Slemmestad. □D. Partly exfoliated small librigena, $\times 4$. MGUH 22.432 (A 964b), bed M-10, Slemmestad. □E. Internal mould of pygidium, $\times 1.5$. The specimen is from the same sample as Fig. 91B, and illustrates the pygidial W:L range of variation shown by *M.* (*M.*) *limbata*. MGUH 22.433 (A 86a), bed A-3, Slemmestad. □F. Partly exfoliated pygidium, $\times 1$. MGUH 22.434 (A 962b), bed M-9, Slemmestad. □G. Internal mould of pygidium, $\times 1.5$. MGUH 22.435 (A 33a), bed M-9, Slemmestad.

Compared to *M.* (*M.*) *limbata* type 5, type 3 has a markedly wider cranidium with a less inflated and broader, forward-expanding glabella, less raised palpebral lobes (which, however, to some extent may relate to size differences), shallower lateral glabellar furrows and more distinctly inflated baculae. Furthermore, the occipital furrow is typically laterally pinched, whereas type 5 has a well-impressed occipital furrow throughout. *M.* (*M.*) *limbata* type 4 cranidia are intermediate between types 3 and 5.

Remarks. – The distinctions between types 3–4 and 4–5 are tentative and based mainly on cephalic L:W ratios; in most cases the respective pygidia cannot be distinguished. For this reason the pygidia from bed interval M-10 to A-6 are arbitrarily divided into large specimens, assigned to type 3, and smaller specimens, assigned to type 5. The three *limbata* types undoubtedly represent biological variation, and it is stressed that no formal taxonomic distinction should be made.

Fig. 87. Juvenile pygidia of *Megistaspis* (*M.*) *limbata* type 3, both showing a comparatively strongly upturned postaxial border. □A. Internal mould showing axis and forwards stretching concave border, $\times 3$. MGUH 22.436 (A 848), bed M-7, Slemmestad. □B. Internal mould, $\times 2$. MGUH 22.437 (A 831), bed M-7, Slemmestad.

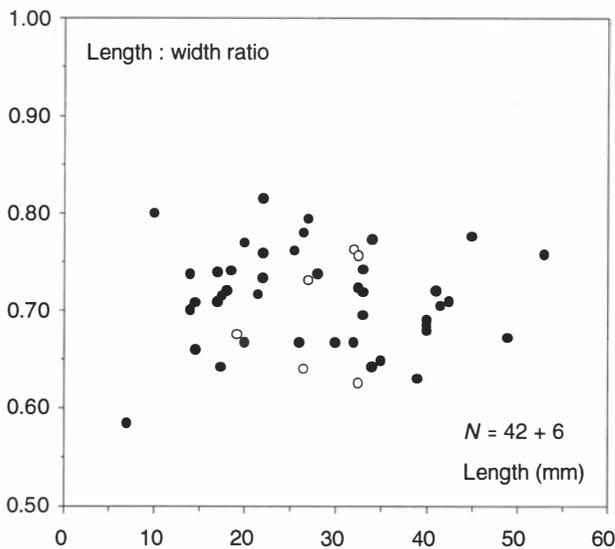
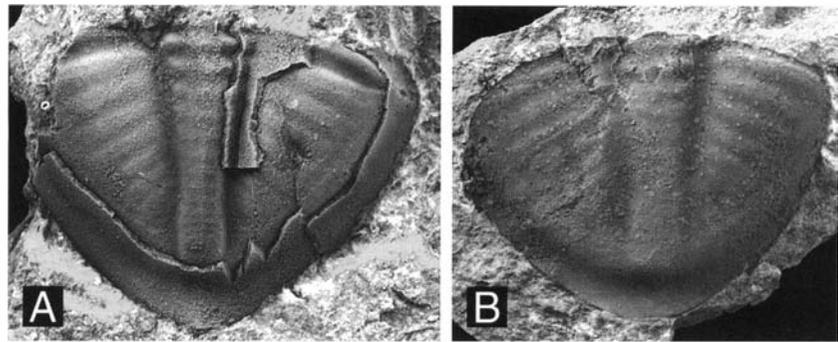


Fig. 88. Pygidia of *Megistaspis* (*M.*) *limbata* types 3 (●) and 4 (○). *M. limbata* type 4 corresponds to 'var. *minor*'. Ratio between length (sag.) and maximum width plotted against pygidial length.

Megistaspis (*M.*) *limbata* type 3 is close to but seems to be slightly broader than *M. (M.) limbata* n.subsp. *sensu* Tjernvik (1980), reported from the *M. simon* Zone and the lower part of the *M. limbata* Zone. It is believed that *M. limbata* subsp. Tjernvik encompasses type 2 as well as type 3 as defined here.

Megistaspis (*Megistaspis*) *limbata* type 4 ('*minor*' Brögger, 1882)

Figs. 88–89

Synonymy. – □v 1882 *Meg. limbata*, Boeck, var. *minor* – Brögger, p. 77; Pl. 2:2 (short diagnosis, occurrence, illustration of pygidium). □non 1906 *Megalaspis polyphemus* var. *minor* m. – Schmidt, pp. 25–27; Pl. 1:5. [= *M. (M.) polyphemus* Brögger, 1882]. □non 1907 *Megalaspis minor*, new species – Weller, p. 563. □? 1980 *Megistaspis minor* (Brögger) – Tjernvik, p. 192 (listed).

Lectotype of *M. MINOR* Brögger, 1882. – Here designated, pygidium figured by Brögger 1882, Pl. 2:2. The specimen is from the Hukodden Limestone (most likely the upper part of the member) of Vestfossen, Oslo area.

Material. – Twenty-eight cranidia, 4 librigenae, 3 hypostomes, and 9 pygidia. The majority of pygidia matching the cranidia, referred to as type 4, cannot be distinguished from *M. (M.) limbata* types 3 and 5, and is described jointly with those.

List of material. – □Cranidia A 39 (im/em), A 40? (im), A 42a (im) [MGUH 22.438], A 899 (im), A 903 (im), A 937a (t), A 950 (im), A 957? (im), A 960a (im) [MGUH 22.440], A 962c (pim), A 962d? (im), A 964a (im), A 967a? (im), A 978 (im), A 1009? (im), A 1012b (im), A 1013g (im), A 1013h? (im), A 1014 (im), A 1033 (im) [MGUH 22.439], A 1038 (im), A 1046b? (im), A 1063c (im). □Juvenilecranidia A 47 (im), A 106? (im), A 837 (im) [MGUH 22.443], A 880? (im). A 1027a (im). □Librigenae A 1013c? (im), A 1013d (im), A 1016b (im), A 1065b (im). □Hypostomata A 78? (im), A 963b (c) [MGUH 22.442], A 995b? (im). □Pygidia A 36a (im) [MGUH 22.444], A 221a? (im), A 896 (c) [MGUH 22.445], A 925? (im), A 935? (pim), A 937b (pim) [MGUH 22.441], A 960b? (im), A 968? (im), A 1078? (pim).

Occurrence. – *M. (M.) limbata* type 4 cranidia occur in bed interval M-9 to M-12 at Slemmestad, which belongs to the lower part of the *M. limbata* Zone. For other occurrences, see remarks below.

Megistaspis '*minor*' pygidia occurs sporadically in bed interval M-9 to M-14; a poorly preserved pygidium from bed A-11 is tentatively assigned.

Description. – Largest cranidium 45 mm long, largest pygidium 33 mm long, but most pygidia are smaller. Cranidia resemble *M. limbata* type 3, but are somewhat narrower (Table 8); cranidia more than 20 mm long show FW:L ratios between 1.25 and 1.35 (mean 1.30; $N = 8$). Glabella is narrower (tr.) than in type 3, and the palpebral lobes are elevated slightly higher above glabella, perhaps owing to the generally smaller average size of the specimens. Facial sutures diverge in front of eyes at an angle of about 5–10° to sagittal line, then turn inwards, converging at an angle of about 125° to sagittal line.

Hypostome A 963 (Fig. 89E), 16.6 mm long, is from bed M-9, and presumably matches the type 4 cranidia; various ratios are listed in Table 9. Posterior margin shows a wide, convex emargination. Premacular pits united across sagittal

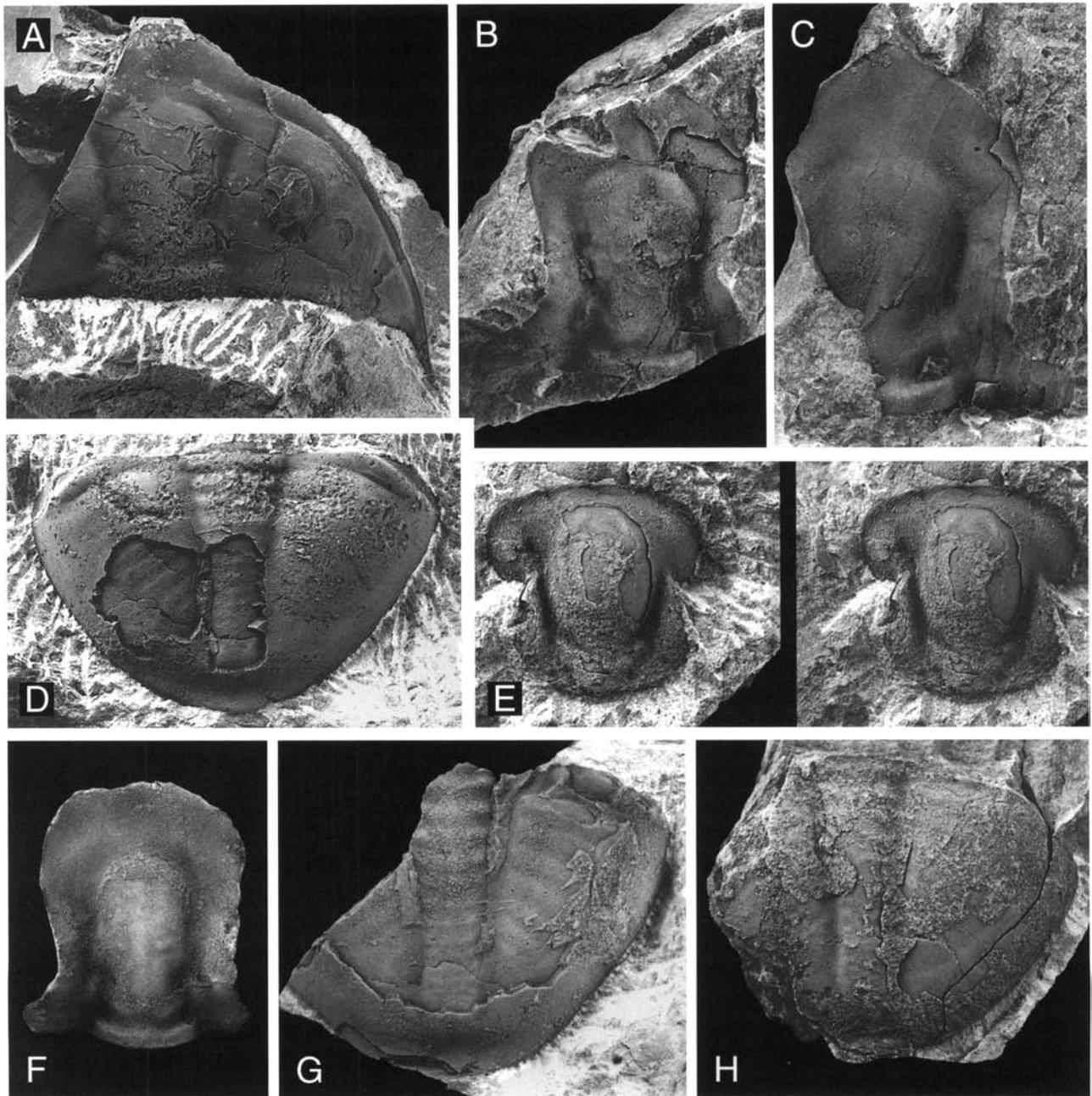


Fig. 89. *Megistaspis (M.) limbata* type 4 ('minor'). □A. Damaged cephalon, $\times 1.5$. MGUH 22.438 (A 42a), bed M-14, Slemmestad. □B. Internal mould of cranium, $\times 1.5$. MGUH 22.439 (A 1033), bed M-11, Slemmestad. □C. Internal mould of cranium, $\times 1.5$. MGUH 22.440 (A 960a), bed M-9, Slemmestad. □D. Comparatively broad pygidium, $\times 1.5$. MGUH 22.441 (A 937b), bed M-9, Slemmestad. □E. Corroded hypostome, stereo-pair, $\times 2$. MGUH 22.442 (A 963b), bed M-9, Slemmestad. □F. Internal mould of small cranium, $\times 3$. MGUH 22.443 (A 837), bed M-7, Slemmestad. □G. Internal mould of pygidium, $\times 1.5$. MGUH 22.444 (A 36a), Bed M-9, Slemmestad. □H. Corroded pygidium, $\times 1.5$. MGUH 22.445 (A 896), bed M-9, Slemmestad.

line by a very shallow furrow, which presumably would be more distinct on an internal mould. A wide, very shallow furrow separates anterior wing from median body. Entire border fairly raised (ventral view), the degree of elevation may be classified as intermediate between the hypostomes of *M. limbata* types 2 and 6. Posterolateral depressions of border furrow less prominent than in type 2.

Hypostome A 995, ca. 17–18 mm long, from bed M-10 is similar to specimen A 963, but the median body is possibly more elongate, and the specimen may belong to *M. limbata* type 5; the apparent elongation may, however, be caused by lateral compression.

Hypostome A 78, 6.5 mm long, from bed A-3 is tentatively assigned to type 4 (Table 9); it looks more like type 6 in many

respects, notably regarding lateral and posterior borders, including mesial incurvature of posterior margin, stretching for about 0.1 of the maximum hypostomal length, but no type 6 cranidia have been found in bed A-3. Some of the differences from the hypostome described above may, though, be size related.

Pygidium broad (Table 10); axis long, tapering comparatively little rearwards, axial constriction indistinct. Posterior border very narrow, present only in hindmost part.

Remarks. – *Megalaspis limbata* var. *minor* Brögger, 1882, ranked as an individual species by Jaanusson (1956a), was listed from the *M. limbata* Zone of Sweden by Tjernvik (1980). The variant was not recognized by Schmidt (1906). *M. minor* was originally distinguished from *M. limbata* 'typica' by its smaller size (pygidial length typically about 26 mm or less), by being relatively wider (pygidial L:W ratio about 2:3), and by almost lacking a pygidial border (Brögger 1882, p. 77); the cranidium was not described. Variant *minor* imperceptibly intergrades with the 'typical' *M. limbata* according to Brögger (1882, p. 161).

The lectotype of *M. minor* (figured by Brögger 1882, Pl. 1:2) has been reexamined. The edge of the pygidium is damaged from the first rib pair and rearwards, so the narrow paradiabular area indicated by Brögger is an artefact, the distinctness of the ribs is also exaggerated in the drawing, and the axial width is slightly smaller in reality. The pygidium is kept together with a cranidium of *M. limbata* type 4.

The few, generally poorly preserved pygidia from Slemmestad described above are similar to the lectotype pygidium; most of them are from beds M-9 and M-10 of the Hukodden Limestone. As stated by Brögger (1882), there is a continuous variation range from *M. minor* to *M. limbata* types 3–5, and *M. minor* definitely cannot be maintained as a separate species, nor as a discrete subspecies. The 'minor' pygidia with an ill-defined concave border and indistinct axial constriction are just slightly atypical *M. limbata* pygidia.

Specimens intermediate between the broad *M. limbata* n. subsp. *sensu* Tjernvik (1980, p. 200) and *M. limbata* 's.str.' was by Tjernvik claimed to occur at Lanna; such specimens may in part or entirely correspond to the type 4 cranidia. The distinction between types 3 and 4 is tentative, and no formal taxonomic distinction should be made. It is unknown what *M. minor sensu* Tjernvik (1980) refers to.

Megistaspis (Megistaspis) limbata type 5

Figs. 90–92

Synonymy. – □v 1882 *Megalaspis limbata*, Boeck, form. *typica* [partim] – Brögger, pp. 77–79; Pl. 9:2 [= lectotype of *M. (M.) limbata*]; non Pl. 9:1 [= *M. (M.) elongata*], non Pl. 9:3–4 [= *M. (M.) limbata* type 6] (description, occurrence, illustration of pygidium). □v 1941 *Megalaspis limbata* (Boeck) – Størmer, p. 141 (designation of lectotype). □v

1956a *Megistaspis (Megistaspis) limbata* (Boeck, 1838) – Jaanusson, pp. 60–71; Pl. 1:1–3 (discussion of taxonomy, illustrations of lectotype). □1972 *Megistaspis (Megistaspis) limbata* (Boeck, 1838) – Tjernvik, pp. 303–309; Textfig. 2A (discussion of stratigraphical distribution, drawing of cranidium). □1980 *Megistaspis (Megistaspis) limbata* (Boeck) – Tjernvik, pp. 192, 200; Figs. 7E, 9E–F (short description, occurrence, drawings and illustrations of cephalon, cranidium and pygidia).

Material. – One complete specimen, 15 cranidia, 2 librigena, and 56 pygidia.

List of material. – □Complete specimen A 1161 (im) [MGUH 22.446]. □Cranidia A 68b (pim), A 97b (em), A 222 (im), A 932 (pim) [MGUH 22.447], A 974 (im), A 990 (pim), A 994a (pim), A 995a (im) [MGUH 22.448], A 1015 (im), A 1016a (im), A 1016d (pim). □Juvenile cranidia A 87 (pim), A 178 (im), A 965d (im), A 1012a (im). □Librigenae A 980b? (im), A 1012c? (im). □Pygidia A 43 (im), A 45 (im), A 48 (im), A 49 (pim), A 51 (im), A 62 (im), A 65 (im), A 67 (im), A 74 (im), A 75 (t), A 77 (im), A 80 (im), A 81 (im) [MGUH 22.450], A 85 (pim), A 86b (pim) [MGUH 22.454], A 88 (im) [MGUH 22.449], A 97a (im), A 98a (pim), A 98b? (im), A 108 (im), A 112 (im) [MGUH 22.451], A 113 (im) [MGUH 22.453], A 134? (im), A 150? (im), A 152 (im), A 965a (im), A 965c (im), A 965g (pim), A 966a (im) [MGUH 22.455], A 966c (im), A 970b? (im), A 971a (im), A 971b (im), A 971c? (im), A 972 (im), A 980c? (im), A 985 (im), A 994b (t), A 1013a (im), A 1013e? (im), A 1013i (im), A 1016c (pim), A 1017 (im), A 1021a (im), A 1021b (im), A 1023a? (im), A 1023b (im), A 1027b (im), A 1037 (im), A 1045a (im), A 1045b (im), A 1046a (im), A 1056a (im), A 1069 (im) [MGUH 22.452], A 1072 (im), A 1076 (pim).

Occurrence. – *Megistaspis (M.) limbata* type 5 occurs in bed interval M-10 to A-3 at Slemmestad; isolated cranidia from beds M-9 and A-11 are also identified with type 5. Bed interval M-9 to A-3 belongs to the lower subzone of the *M. limbata* Zone, while bed A-11 is within the upper subzone of the *M. limbata* Zone. The assignment of pygidia from beds A-4 to A-6 is uncertain as no cranidia are found; they are tentatively assigned to type 5.

M. limbata type 5 corresponds to *limbata* 's.str.' of Tjernvik (1980), the eponymous index fossil of the *M. limbata* Zone of Sweden; see discussion below.

Description. – (See also Tjernvik 1980). Medium-sized, narrow form (Table 8); largest cranidium 30 mm long, largest pygidium 42 mm long, but most pygidia are less than 35 mm long. Cephalon triangular in outline; cephalic L:W ratio about 0.7 (excl. of genal spines). Glabella markedly vaulted with comparatively deep lateral glabellar 'furrows', which appears as rounded impressions (best seen on internal moulds). Glabellar tubercle immediately in front of occipital furrow indistinct, but better defined than in the other types of *M. (M.) limbata*. Mesial depression in frontal area normally indistinct. Bacculae small, but fairly inflated. Palpebral area steeply sloping in adaxial direction. Anterior branches of facial suture approximately parallel in front of eyes, then turn inwards, converging at an angle of about 130° to sagittal line.

Librigena with prominent, rather long genal spine.

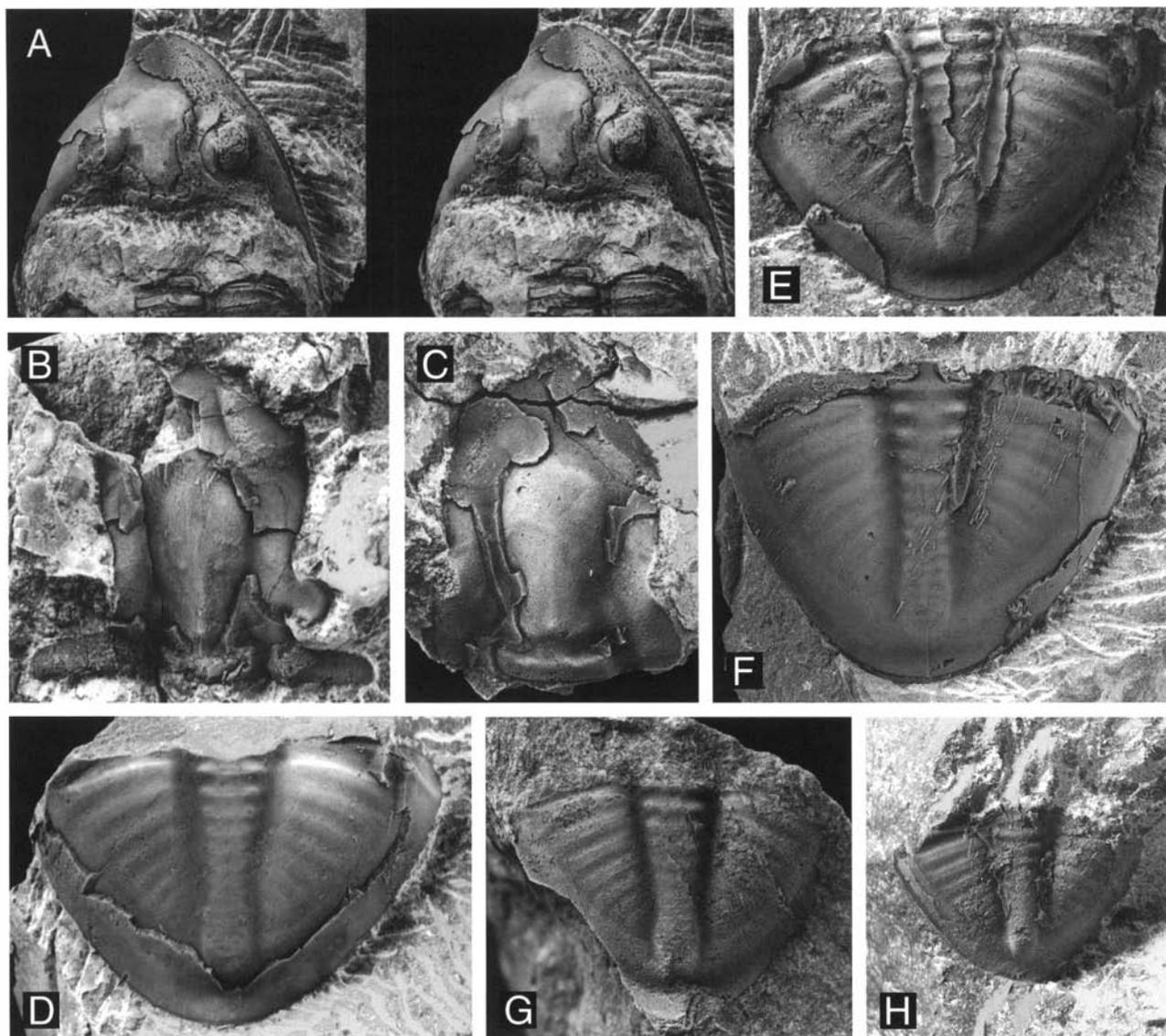


Fig. 90. *Megistaspis* (*M.*) *limbata* type 5. □A. Partly exfoliated cephalothorax of complete specimen, stereo-pair, $\times 1$. MGUH 22.446 (A 1161), Lysaker Member, Slemmestad. □B. Slightly distorted, partly exfoliated cranidium, showing glabellar muscle insertion sites, $\times 2$. MGUH 22.447 (A 932), bed M-9, Slemmestad. □C. Partly exfoliated cranidium, $\times 2$. MGUH 22.448 (A 995a), bed M-10, Slemmestad. □D. Internal mould of pygidium showing axis and upturned posterior border, $\times 2$. MGUH 22.449 (A 88), bed A-3, Slemmestad. □E. Internal mould of small pygidium, $\times 2.5$. MGUH 22.450 (A 81), bed M-9, Slemmestad. □F. Internal mould of pygidium showing axis, $\times 1.5$. MGUH 22.451 (A 112), bed A-4, Slemmestad. □G. Internal mould of juvenile pygidium showing well-developed border, $\times 3$. MGUH 22.452 (A 1069), bed M-14, Slemmestad. □H. Internal mould of juvenile pygidium showing lateral border, $\times 4$. MGUH 22.453 (A 113), bed A-4, Slemmestad.

Pygidium subtriangular in outline, narrow (Fig. 92; Table 10). Border very strongly concave postaxially, somewhat upturned, which is a characteristic feature of type 5. However, large pygidia do not show this 'upturning'. Doublure with 16–18 terrace lines, counted at pygidial midline.

Remarks. – *M. (M.) limbata* type 5 is similar to the lectotype of *M. (M.) limbata*, designated by Størmer (1941), and,

accordingly, corresponds to *M. (M.) limbata* 's.str.' in the sense of Tjernvik (1980). The lectotype specimen probably originates from the lowermost part of the Lysaker Member, but in contradiction to the belief of Brögger (1882), the 'typical' *M. limbata* also occurs in the Hukodden Limestone.

Much confusion has prevailed concerning the identification and taxonomic limits of the 'true' *M. (M.) limbata*, partly because of the general scarcity of cephalic material.

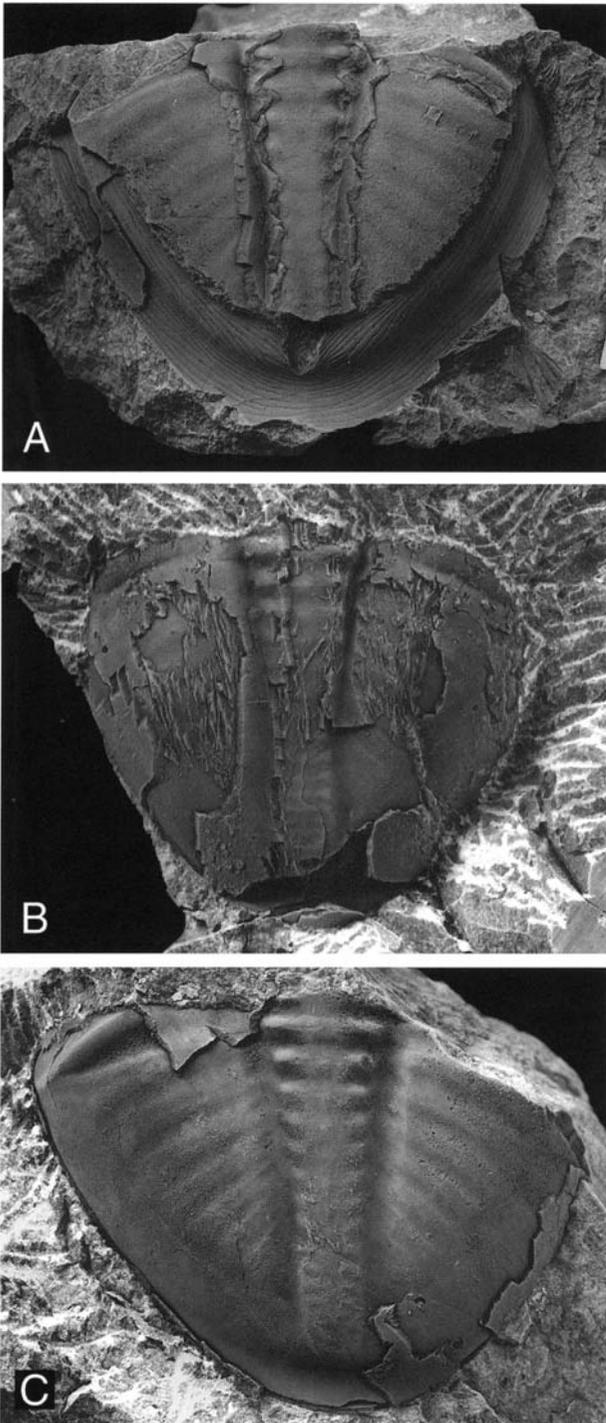


Fig. 91. *Megistaspis (M.) limbata* type 5 ('s.str.'). □A. Internal mould of pygidium showing doubleure, $\times 1.5$. PMO 3178, Lysaker Member, Huk, Bygdøy, Oslo Region. □B. Very narrow pygidium, $\times 1.5$. The specimen is from the same sample as Fig. 86E. MGUH 22.454 (A 86b), bed A-3, Slemmestad. □C. Internal mould of pygidium showing axis and segmentation of pleural fields, $\times 1.5$. MGUH 22.455 (A 966), bed M-10, Slemmestad.

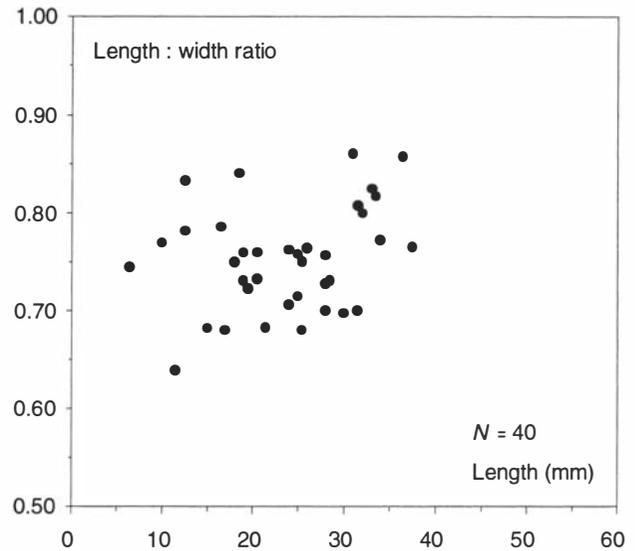


Fig. 92. Pygidia of *Megistaspis (M.) limbata* type 5. Ratio between length (sag.) and maximum width plotted against pygidial length.

Ninety-seven more or less fragmentary cranidia and cephalae from Slemmestad are here identified with *M. limbata (s.l.)*, and it appears that the narrow definition of *M. (M.) limbata*, advocated by Jaanusson (1956a) and Tjernvik (1972, 1980), is unwarranted. The variability of the Norwegian material is highlighted by the distinction of various morphotypes, but the limits of these types are arbitrarily defined, and at least the differentiation of types 1 to 5 is pigeonholing. The same may be said for *limbata* types 7–9 of the Komstad Limestone. A continued recognition of a narrow *M. limbata (s.str.)* seems, accordingly, to be artificial, hence the designation is best avoided. The changed definition of *M. limbata* extends the range outside the *M. limbata* Zone.

The length of the pygidial axis is more variable in the Norwegian material than stated by Tjernvik (1980) (short in *M. limbata* subsp. *long* in *M. limbata* 's.str.'). Tjernvik (1980) emphasized the upturned postaxial border of *M. limbata* pygidia, and it appears that the *M. limbata* types occurring in the *M. limbata* Zone actually tend to show a more upturned postaxial border, compared to the older types, but early, smaller pygidia may possess an equally upturned border which late, large pygidia generally do not have.

M. limbata from the *M. limbata* Zone of Sweden is generally slightly broader than type 5 as here defined, and may be classified as intermediate between types 4 and 5 (unpublished data).

Megistaspis (Megistaspis) limbata type 6

Figs. 93–94

Synonymy. – □v 1882 *Megalaspis limbata*, Boeck, form. *typica* [partim] – Brögger, pp. 77–79; Pl. 9:3–4; non Pl. 9:2 [= *M. (M.) limbata* type 5]; non Pl. 9:1 [= *M. (M.) elongata*] (description, occurrence, illustrations of cephalon and pygidium). □1956a *Megistaspis (Megistaspis)* n.sp. – Jaanusson, p. 70 (listed).

Material. – One cephalon with hypostome, 13 cranidia, 10 librigenae, 1 hypostoma and 41 pygidia.

List of material. – □Cephalon PMO 64315 (fragmentary but with well-preserved hypostome) (t). □Cranidia A 154? (pim), A 185 (pim) [MGUH 22.460], A 188? (im), A 194? (im), A 204 (pim), A 211 (pim), A 221c? (im), A 230? (pim), A 233 (im), A 302b (pim) [MGUH 22.456], A 313 (im), A 322 (pim) [MGUH 22.461], A 335 (pim). □Librigenae A 167b (im), A 186 (im), A 198 (pim), A 220b (pim) [MGUH 22.459], A 241 (pim) [MGUH 22.458], A 271 (im), A 303b (im), A 318a (pim), A 324a (im), A 355 (im). □Hypostoma A 309 (im) [MGUH 22.457]. □Pygidia A 156 (pim), A 167a (im), A 207 (im), A 213 (pim), A 215 (pim), A 220a (t), A 221b (pim), A 228a (im), A 228b (pim), A 231a (im), A 231b (im), A 236 (im), A 243? (im), A 248 (pim), A 249 (im), A 259 (pim), A 266 (im) [MGUH 22.466], A 273 (im), A 276 (im), A 283 (pim), A 284 (pim), A 306 (t), A 308 (t), A 315a (im) [MGUH 22.465], A 315b (im), A 317 (im) [MGUH 22.462], A 318b (pim) [MGUH 22.463], A 318c (im), A 320a (im), A 320b (im), A 320c (im), A 320e (pim), A 321 (im), A 328 (im), A 330 (pim), A 331 (im) [MGUH 22.464], A 332 (im), A 348 (c), A 398 (im), A 1093 (im), A 1096 (im).

Occurrence. – *M. limbata* type 6 has been found in bed interval A-7 to A-28 at Slemmestad, representing the upper part of the *M. limbata* Zone. The identification of pygidia from beds A-5 and A-6 is uncertain, and those specimens are tentatively assigned to type 5. A stratigraphically important pygidium from bed A-28 is a typical, narrow representative of *M. limbata* with upturned postaxial border.

Description. – Large, relatively broad form (Table 8), largest cranidium 43 mm long, largest pygidium 44 mm long. Cephalon almost twice as broad as long (excl. genal spines). Sagittal cranidial relief moderate. Glabella fairly vaulted. Mesial depression in frontal area faint. Lateral glabellar furrows and bacculae as in type 5. Shallow border furrow on posterior fixigena is most distinctly impressed on internal moulds; the feature is unusual for Scandinavian representatives of *M. limbata*. Palpebral lobes comparatively well elevated above glabella. Anterior branches of facial suture diverge from the eyes at an angle of about 10° to sagittal line, then turn inwards, converging at an angle of about 125° to sagittal line.

The most characteristic feature of the librigena is the presence of a fairly deep furrow at the base of the eye socle (best defined on internal moulds). Genal spine slender.

The hypostomes, 12.6 mm and 15.0 mm long, differ somewhat from the remaining hypostomes assigned to *M. limbata* (Table 9). Anterior wings narrow (exsag.), and not separated by shallow furrow from median body; lateral border widens comparatively strongly backwards. A wide mesial

incurvature is present in posterior margin; depth of ‘notch’ equivalent to 0.05–0.11 of the maximum hypostomal length.

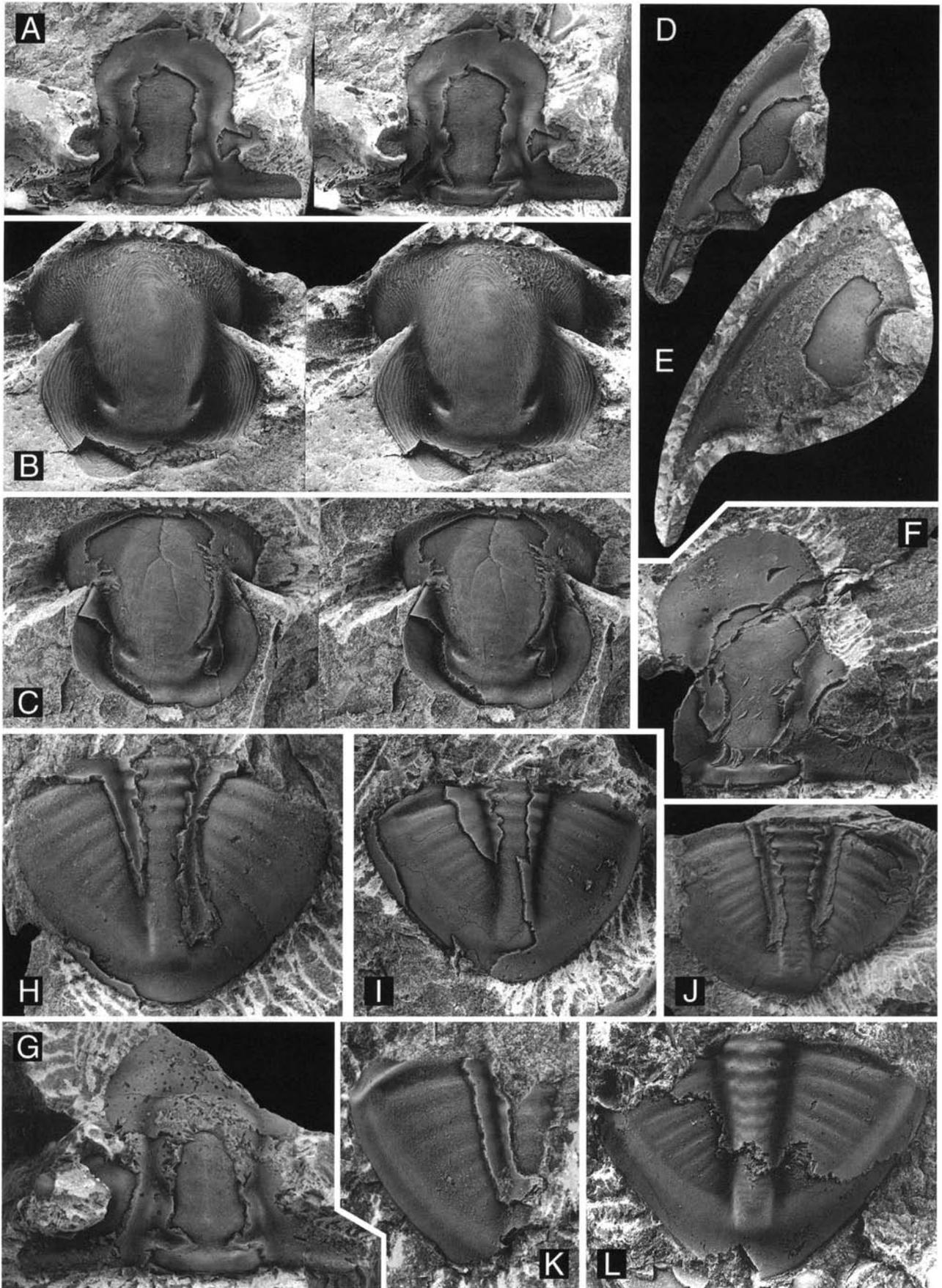
Pygidium typically broadly parabolic in outline with L:W ratios about 0.7, but more narrow, subtriangular pygidia with L:W ratios about 0.8 also occur (Table 10). Internal moulds show up to 5–6 fully developed axial rings. Pleural fields with comparatively well-developed ribs. The postaxial border is evenly concave in broad pygidia, whereas narrower specimens show the characteristic strongly concave, upturned ‘*limbata*-border’. It is inconclusively indicated that the terrace lines on the doublure of type 6 are coarser than in type 5; the total number cannot be verified.

Affinities. – *M. (M.) limbata* type 6 resembles type 5 with regard to the almost parallel course of the facial sutures and the glabellar outline, but type 6 is distinctly broader and normally shows a shallow cephalic posterior border furrow. The pygidia of type 6 are also typically broader, parabolic in outline and with a narrower and less concave border, but some of the narrower specimens are indistinguishable from type 5.

The type 6 hypostome deviates from the remaining Norwegian hypostomes assigned to *M. limbata* by having a more rounded median body, less inflated, flatter lateral and posterior borders, and by showing a shallow mesial incurvature in the posterior margin. Type 6 hypostomes in these respects resemble the fragmentary hypostome assigned to *limbata* type 9.

Remarks. – *M. (M.) limbata* type 6 is identical to Brögger’s (1882) broad *M. limbata forma typica*, which was included in *M. limbata baltica* by Balashova (1976, pp. 80–81). Type 6 differs, however, from the somewhat older *M. limbata baltica* by having, for example, much longer (tr.) posterior fixigenae. The broad form is here interpreted as an eco-phenotype of *M. limbata*, and it may conveniently be ranked

Fig. 93. Megistaspis (M.) limbata type 6. □A. Partly exfoliated cranidium showing faint posterior border furrow, stereo-pair, ×1.1. MGUH 22.456 (A 302b), bed A-19, Slemmestad. □B. Hypostome with well-preserved cuticle showing terrace ridge sculpture, stereo-pair, ×3. PMO 64 315, Lysaker Member, Slemmestad. □C. Largely exfoliated hypostome, stereo-pair, ×3. MGUH 22.457 (A 309), bed A-19, Slemmestad. □D. Partly exfoliated small librigena, ×3. MGUH 22.458 (A 241), bed A-13, Slemmestad. □E. Partly exfoliated librigena, showing well-developed furrow at base of eye socle, ×2. MGUH 22.459 (A 220b), bed A-11, Slemmestad. □F. Fragmentary cranidium, ×1.5. MGUH 22.460 (A 185), bed A-8, Slemmestad. □G. Partly exfoliated cranidium, ×2. MGUH 22.461 (A 322), bed A-19, Slemmestad. □H. Internal mould of pygidium, ×2. MGUH 22.462 (A 317), bed A-19, Slemmestad. □I. Partly exfoliated small pygidium showing fairly strongly upturned border, ×2. MGUH 22.463 (A 318b), bed A-19, Slemmestad. □J. Internal mould of pygidium, ×1. MGUH 22.464 (A 331), bed A-20, Slemmestad. □K. Exfoliated fragment of juvenile pygidium showing well-defined anterolateral concave border, ×4. MGUH 22.465 (A 315a), bed A-19, Slemmestad. □L. Partly exfoliated juvenile pygidium showing well-defined concave border all the way; it is strongly upturned postaxially, ×4. MGUH 22.466 (A 266), bed A-14, Slemmestad.



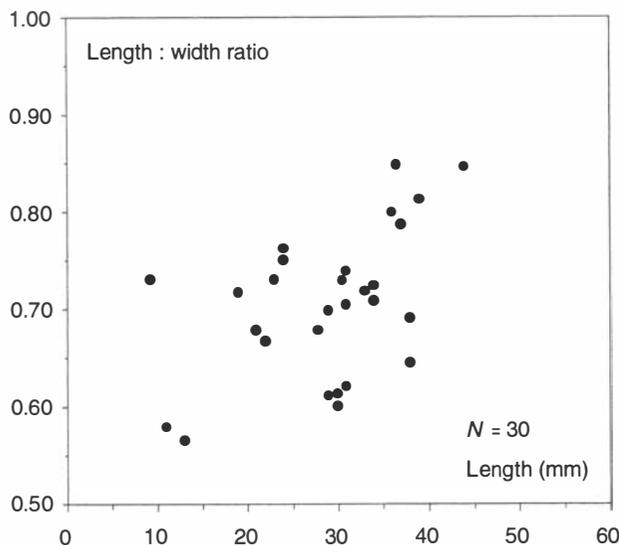


Fig. 94. Pygidia of *Megistaspis (M.) limbata* type 6. Ratio between length (sag.) and maximum width plotted against pygidial length.

as a variant, or, alternatively, as a subspecies, although a formal distinction at the subspecies level probably is unwarranted, as type 6 appears to become gradually rather narrow again in the interval above bed A-20 in the Slemmestad section.

The specimens figured by Brøgger (1882, Pl. 9:3–4) illustrate *M. limbata* type 6 fairly well, although the shown cephalon appears to have a higher sagittal relief than typical for the majority of the available cranidia. It should be noted that the cephalic posterior furrow and the occipital furrow have been accentuated in the drawing, and the lateral cephalic border is not indicated at all. The unusually short genal spines are an artefact, as the original specimen is slightly worn, and appears to have been collected from the beach.

Megistaspis (Megistaspis) limbata type 7

Fig. 95

Synonymy. – □v 1936 *Megalaspis limbata* Sars & Boeck [*partim*] – C. Poulsen, pp. 48, 50 (listed). □v 1952 *Megalaspis limbata* (Boeck) [*partim*] – Skjeseth, p. 161; Pl. 1:7; non Pl. 1:3 [*Megistaspis* cf. sp. C] (occurrence, illustration of pygidium). □v 1965 *Megistaspis (Megistaspis) cf. lata* (Törnquist, 1884) – V. Poulsen, pp. 66–67; Pl. 1:7 (description, occurrence, illustration of pygidium). □1980 *Megistaspis (Megistaspis) n.sp. no. 1* – Tjernvik, pp. 191, 197–198; Fig. 7B (description, occurrence, drawings of cranidium and pygidium). □v 1980 *Megistaspis (Megistaspis) lata* (Törnquist) [*partim*] – Tjernvik, Fig. 4 (occurrence).

Material. – Three cranidia, 1 hypostoma, and 16 pygidia.

List of material. – □Cranidia S 189 (im), S 281 (c), GM 1888.326 (im) [MGUH 22.467]. □Hypostoma IK P-4b (im) [MGUH 22.468]. □Pygidia S 200 (im) [MGUH 22.474], S 205 (im), S 210 (im), S 286 (im) [MGUH 22.471], S 299 (im), S 307 (im) [MGUH 22.470], S 345 (im), S 351 (im), S 1679 (im) [MGUH 22.472], S 1681b? (im), S 1760 (im), GM 1885.42 (im) [MGUH 22.473], GM 1951.41 (pim), GM 1988.21 with two thoracic segments (im), IK P-4a (im) [MGUH 22.469], IK P-19? (im).

Occurrence. – *M. (M.) limbata* type 7 is characteristic of the lower part of the *M. polyphemus* Zone at Skelbro, where it is more abundant than *M. polyphemus* itself; it has been found only in beds –21 and –20. The GM and IK samples most likely originate from these beds as well; the level of hypostome IK P-4b can be fixed to 1.5 cm above the base of bed –20. The well-preserved cranidium GM 1888.326 from Skelbro is from bed –21 or –20, most likely bed –20. Pygidium GM 1885.42 is from 1–4.5 cm below the top of bed –21.

M. limbata type 7 is probably identical to *Megistaspis (M.) sp. 1 sensu* Tjernvik, 1980, characteristic of the lower half of the *M. polyphemus* Zone of Sweden, and type 7 is presumably also present in the lower part of the Stein Limestone at Herramb, southern Norway (see discussion below).

Description. – Largest cranidium (GM 1888.326) 32 mm long, largest pygidium 42 mm long. The description of the cranidium refers to the exfoliated specimen GM 1888.326 (Fig. 95A), if not otherwise stated. Cranidium rather narrow (Table 8), in particular across posterior fixigena, with a fairly high sagittal relief. Mesial depression in frontal area comparatively distinct. Glabella slightly pyriform in outline; lateral glabellar furrows very shallow; occipital furrow deepest laterally and almost effaced mesially. Glabellar tubercle indistinct. Baculae gently inflated, comparatively small, oval. Palpebral lobes pronouncedly elevated above glabella (specimens S 189, S 281), most strongly so in the smallest cranidia. Outer third of posterior fixigena bent somewhat backwards, gently downwards; no posterior border furrow. Anterior branches of facial suture diverge forwards in front of eyes at an angle of 15° to sagittal line, then curve evenly inwards to converge at an angle of about 125° to sagittal line.

The exfoliated hypostome (Fig. 95B) is estimated to have been about 17 mm long; because of its fragmentary state all ratios are estimates (Table 9). Basic outline like the hypostomes of *M. limbata* types 1 and 2, but the specimen is relatively narrower. Median body only moderately inflated (less than in *M. limbata* types 1 and 2, approximately as in *M. geminus* n.sp.), and appears comparatively slender with a W:L ratio in the size order of 1:2. The weakly impressed premacular pits are united across sagittal line by a shallow furrow. A wide, shallow furrow separates median body from anterior wing. Posterior margin as described for *limbata* type 2, but the mesial part appears to be even more emarginate.

Pygidium subtriangular in outline, and very similar to narrow types of *M. limbata* (Table 10). Axis comparatively short; axial constriction most obvious in the smaller pygidia. Doublure of pygidium comparatively wide posteriorly, but poorly exposed in the available material. Compared to *M.*

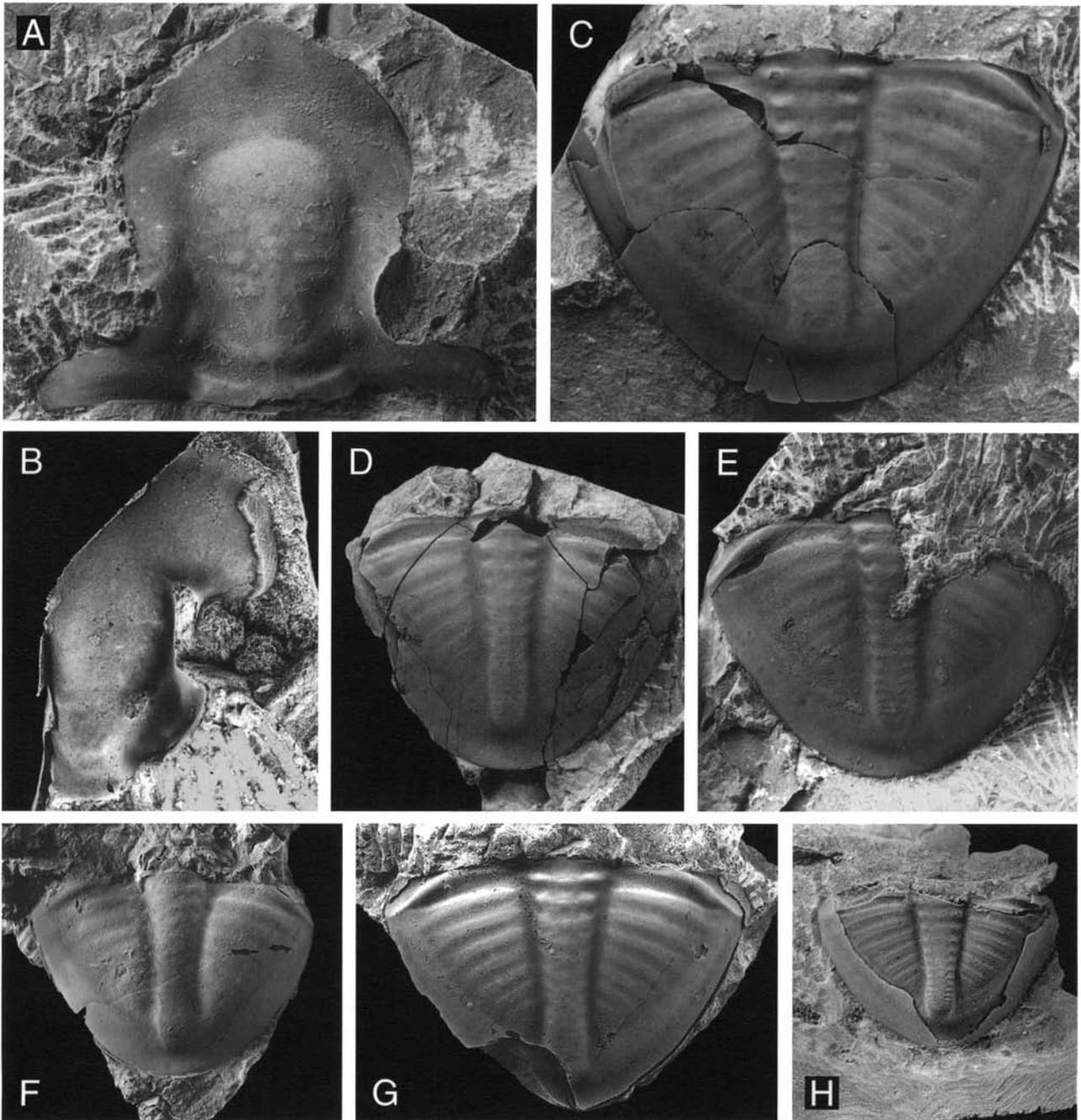


Fig. 95. *Megistaspis (M.) limbata* type 7. □A. Internal mould of cranidium, $\times 2$. MGUH 22.467 (GM 1888.326), Skelbro. □B. Latex cast of fragmentary hypostome, $\times 4$. MGUH 22.468 (IK P-4b), Skelbro. □C. Internal mould of pygidium, $\times 1.5$. MGUH 22.469 (IK P-4a), Skelbro. □D. Internal mould of pygidium, $\times 1$. MGUH 22.470 (S 307), bed -20, Skelbro. □E. Internal mould of pygidium, $\times 1$. MGUH 22.471 (S 286), bed -20, Skelbro. □F. Internal mould of pygidium, $\times 1$. MGUH 22.472 (S 1679), bed -20, Skelbro. □G. Internal mould of small pygidium showing narrow lateral border, $\times 1.5$. MGUH 22.473 (GM 1885.42), Duegård, Bornholm. □H. Partly exfoliated juvenile pygidium showing well-developed anterolateral border, $\times 6$. MGUH 22.474 (S 200), bed -21, Skelbro.

limbata, the inner half of doublure is possibly more convex, so the 'flattened' strip along inner margin appears slightly wider.

The juvenile pygidia S 200 (Fig. 95H) and S 205, 6 and 10 mm long, differ from adult pygidia by the same characters as

described for juveniles of *M. limbata* in general; L:W ratios 0.62–0.64.

Affinities. – The material is exceedingly similar to *M. limbata* (see also remarks by Tjernvik 1980, p. 197), and is considered

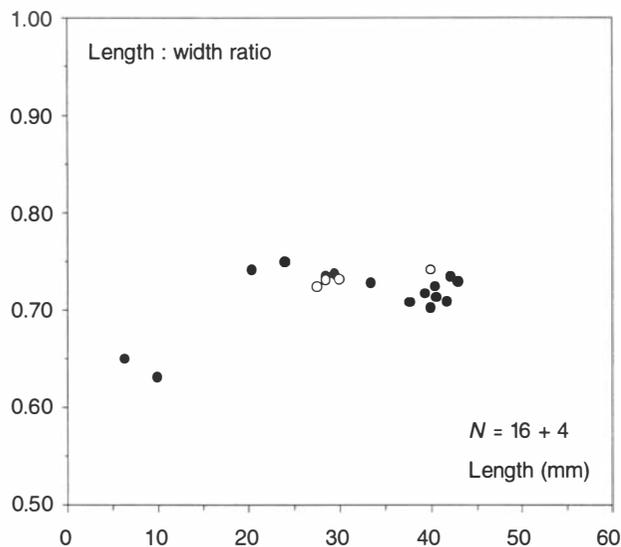


Fig. 96. Pygidia of *Megistaspis (M.) limbata* types 7 (●) and 8 (○). Ratio between length (sag.) and maximum width plotted against pygidial length.

an early ecophenotype of this species. Type 7 resembles type 1, from which it is separated by showing a slightly higher adult cranidial relief, a broader, more pyriform glabella, highly elevated palpebral lobes, a mesially shallower occipital furrow, a narrower hypostome, a shorter pygidial axis and a correspondingly longer postaxial border.

Megistaspis (M.) limbata type 7 very much resembles *Megistaspis (M.)* sp. no. 1 Tjernvik, 1980, and the two forms are believed identical. The cranidia of type 7 and sp. 1 Tjernvik are both narrow (tr.), the anterior fixigenae are laterally bent comparatively strongly downwards, the occipital furrows are deep laterally and rather shallow mesially, the palpebral lobes are raised considerably above the surface of glabella, even in adults, no posterior border furrow is developed and the posterior fixigenae are relatively short (tr.) and directed backwards distally. The pygidia of type 7 generally have a relatively shorter axis than sp. 1 Tjernvik, but this difference is not regarded significant.

Compared to the associated *M. polyphemus*, the pygidia of type 7 differ by being relatively narrower (tr.) and by having a narrower axis (tr.) with a faint constriction. Furthermore, the axis of type 7 is shorter and, consequently, the postaxial border and the posterior part of the doublure are broader. The juvenile pygidia of type 7 differ from juvenile pygidia of *M. polyphemus* by being more triangular in outline, relatively narrower (albeit being quite broad), the axis is shorter and with a distinct constriction, and the postaxial border is broader.

Remarks. – The pygidium identified with *M. limbata* by Skjeseth (1952) may represent *M. limbata* type 7. According to the label, the specimen is from the basal part of the Stein Limestone ('3cα'). The associated small cranidium (Fig.

126), also assigned to *M. limbata* by Skjeseth (1952), has a distinct preglabellar furrow, a gently inflated paradoublural crest in front of glabella, a shallow posterior border furrow, and the posterior margin of fixigenae is raised. These characters, which cannot be explained as due to the small size of the specimen, suggest an affinity to *Megistaspis* spp. B and C (see remarks on *M. sp. C*).

A pygidium from level 56.4 m in the Finngrundet core, assigned to *M. lata* by Tjernvik (1980), rather belongs to *M. limbata* type 7 [sp. 1 *sensu* Tjernvik] (the specimen has been examined).

Megistaspis (Megistaspis) limbata type 8

Figs. 96–97

Synonymy. – □? 1980 *Megistaspis (M.)* n.sp. no. 2 – Tjernvik, pp. 191, 199 (short description, occurrence).

Material. – Five pygidia.

List of material. – □ Pygidia S 302 (im) [MGUH 22.476], S 704 (c), S 771 (im) [MGUH 22.475], S 772a (c), S 776b (im).

Occurrence. – *Megistaspis (M.) limbata* type 8 occurs in bed interval –20 to –13 at Skelbro, Zone of *M. polyphemus*; four of the five pygidia are from bed interval –16 to –13. Type 8 is perhaps identical to *M. (Megistaspis) sp. 2* Tjernvik, 1980, which occurs in the upper half of the *M. polyphemus* Zone of Sweden.

Description. – Largest specimen 40 mm long. Pygidium triangular in outline and rather narrow (tr.) (Table 10). Axis appears narrow, short, terminal part gently, but clearly expanded, so axis has a well-defined constriction; minimum axial width equivalent to 0.20–0.21 of the pygidial length as typical for *M. limbata*. It is characteristic that the middle one third of the axis is below the level of adjacent pleural fields, which are more vaulted than usual for *M. limbata*. Doublure comparatively wide, but not exposed in the material. Internal moulds show indistinct paradoublural furrow.

Affinities. – Compared to *M. limbata* type 7, the pygidia called type 8 differ by showing a more pronounced axial constriction, and the middle axial portion is below the level of the more vaulted pleural fields. It also looks as if the axis is tapering for a longer distance, and hence appears slightly narrower in type 8, but the ratio axial width:pygidial length is, however, of usual size order.

Compared to pygidia of the coeval *M. (M.) polyphemus*, *Megistaspis limbata* type 8 is narrower (tr.), with a more triangular outline, and a shorter and narrower, distinctly constricted axis, and the posterior border is correspondingly longer.

Remarks. – Tjernvik (1980, p. 199) briefly described a *Megistaspis* n. sp. 2, stated to be characteristic of the upper part of the *M. polyphemus* Zone at Lanna, central Sweden. The

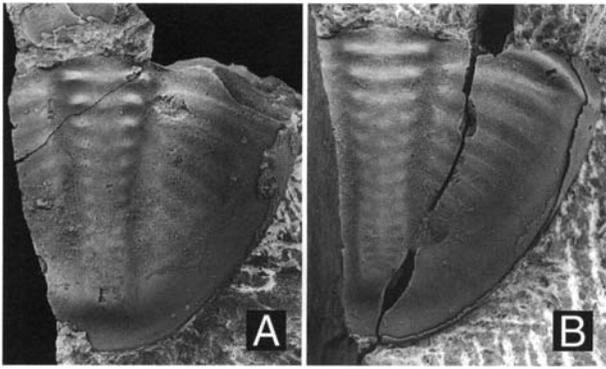


Fig. 97. *Megistaspis (M.) limbata* type 8. □A. Fragmentary internal mould of pygidium, $\times 1$. MGUH 22.475 (S 771), bed -13, Skelbro. □B. Fragmentary internal mould of pygidium, $\times 1$. MGUH 22.476 (S 302), bed -20, Skelbro.

pygidium of sp. 2 was separated from sp. 1 *sensu* Tjernvik by having a short and low pygidial axis and a correspondingly longer postaxial border, and it is therefore possible that *Megistaspis* sp. 2 corresponds to *M. limbata* type 8. The unusually low axis of type 8 seems, however, to be even more subsided than described for sp. 2.

The two pygidia from the middle part of the *M. polyphemus* Zone of the Finngrundet core, referred to as '*Megistaspis (M.) n.sp.*' by Tjernvik (1980, Fig. 4), have been examined, and they presumably belong to *M. polyphemus*.

Crania collected from the top of the Bruddesta Formation on northern Öland most likely represent *Megistaspis* sp. 2 Tjernvik; the material is from the upper part of the *M. polyphemus* Zone. The specimens are narrow, with PW:L ratio about 0.75, and FW:L ratio about 1.13. Glabella moderately vaulted, narrow; front truncate; mesial impression in frontal area fairly distinct; baculae indistinct. Occipital furrow narrow (sag.), entire, even on testaceous specimens. Palpebral lobes well raised above glabella (adults). Extreme distal part of fixigenae flexed backwards, less so than in *M. limbata* type 7. The cranidia are rather similar to those of *M. limbata* type 1, but are slightly broader, show shallower lateral glabellar furrows, a slightly more arched glabella, shorter occipital furrow (sag.), and a slightly truncate glabellar front. These cranidia, which most likely represent *Megistaspis* sp. 2 Tjernvik, definitely belong to *M. limbata*.

Megistaspis (Megistaspis) limbata type 9

Figs. 98–100

Synonymy. – □v 1919 *Megalaspis limbata* Sars & Boeck [*partim*] – Funkquist, pp. 21, 39 (occurrence). □v 1936 *Megalaspis limbata* Sars & Boeck [*partim*] – C. Poulsen, pp. 48, 50 (listed).

Material. – Twenty-four cranidia, 6 librigenae, 1 hypostoma and 124 pygidia.

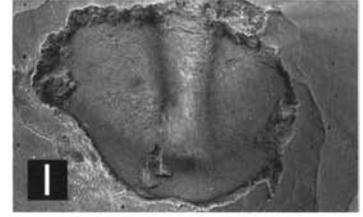
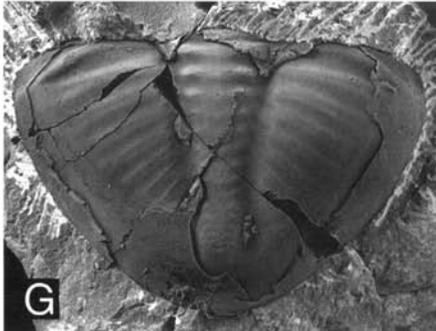
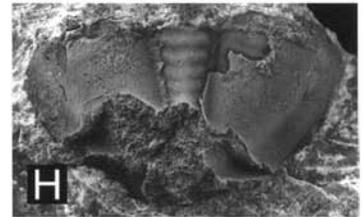
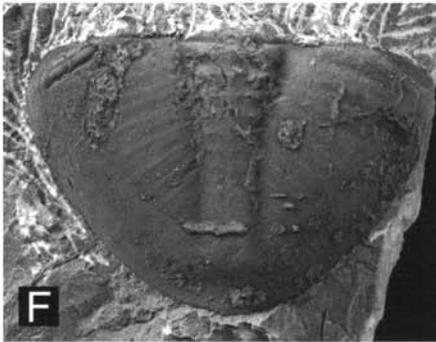
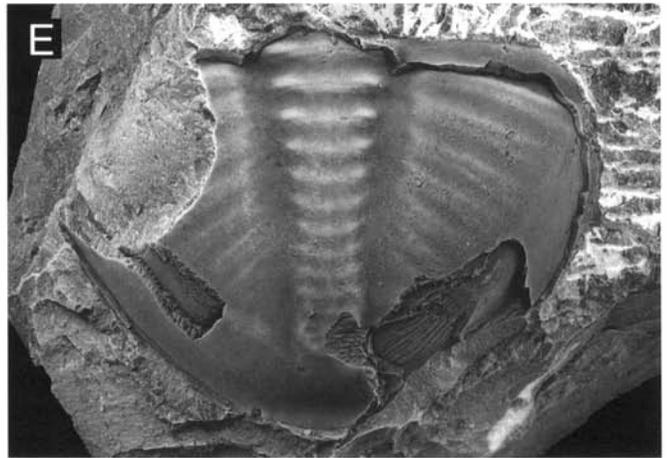
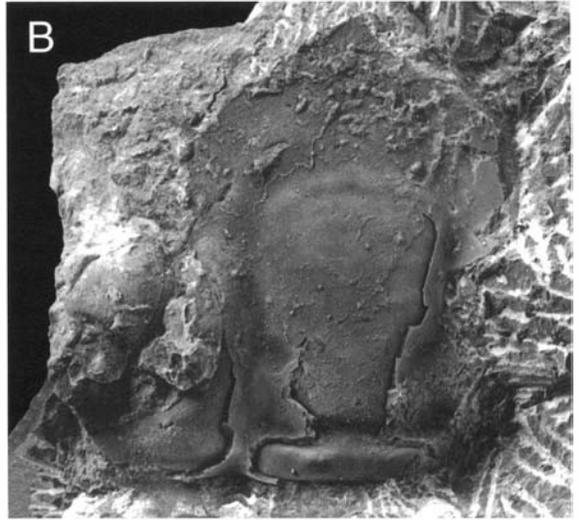
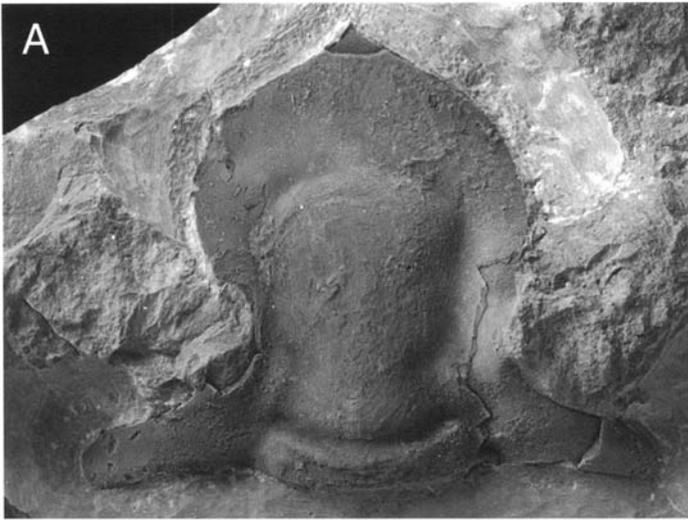
List of material. – □Crania S 1765a (im), S 1765b? (im), S 1765c (em), K 44 (t), 75 (t), K 90 (t) [MGUH 22.479], K 189 (im), K 208 (c), K 609b (im), K 617b (c), K 619 (t), K 665 (im), K 678 (pim) [MGUH 22.478], K 714 (c), K 727a (pim), K 727b (c), K 773 (pim), GM 1984.1803 (pim) [MGUH 22.477], LU 18c (im), LU 23b (im), LU 27 (im/em), LU 47 (c), LU 92b (em), LU 156d? (t). □Librigenae K 506 (c) [MGUH 22.480], K 668 (im), K 697a (im), K 697b? (im), LU 18 (im), LU 97 (c). □Hypostoma LU 16b (im) [LO 7071]. □Pygidia S 860? (im), S 865? (c), S 876? (c), S 880 (pim), S 888? (im), S 908 (pim), S 933 (im), S 968? (c), S 1070 (c), S 1077 (t), S 1081 (c), S 1083 (t) [MGUH 22.482], S 1084 (pim) [MGUH 22.483], S 1085 (t), S 1086 (im), S 1088 (pim), S 1089 (im), S 1155 (im), S 1168 (em), S 1213 (im), S 1218? (c), S 1226 (im), S 1308? (c), S 1337 (im), S 1348 (pim) [MGUH 22.488], S 1656? (c), S 1658 (c), S 1766 (c), K 14 (im), K 30 (c), K 31 (c), K 38 (c), K 51 (t), K 64 (c), K 81 (c), K 93? (c), K 111 (c), K 117 (pim), K 140? (c), K 166b (c), K 172 (c), K 213? (c), K 217 (c), K 233 (pim), K 384 (t), K 385 (pim), K 406 (c), K 407 (c), K 408 (c), K 410 (c), K 413 (c), K 433 (im), K 470 (im), K 505 (c), K 507 (c), K 509 (im), K 510 (c), K 535 (c), K 609a? (c), K 617a (t) with one thoracic segment, K 618 (c), K 629 (c), K 630 (im/c), K 643 (c) [MGUH 22.486], K 655 (c), K 657 (c), K 671 (c), K 677 (pim), K 687 (c), K 694 (im), K 698 (em+pim) [MGUH 22.485], K 710 (c), K 715a (c), K 715b (c), K 715c? (c), K 718 (c), K 722 (pim) [MGUH 22.484], K 728b (c), K 741 (c), K 742 (im), K 743a (c), K 743b (pim), K 745 (pim), K 747 (c), K 763 (c), K 765 (c), K 770 (c), K 774 (c), K 1343 (c), F 299 (im) [MGUH 22.487], DGU 4 (im) [MGUH 22.481], IK P-6 (im), IK P-7 (c), LU 9 (im), LU 16a (c), LU 16c (pim), LU 18d (im), LU 22 (im), LU 23a (im) [LO 7078], LU 23c (im), LU 32c (im), LU 32d (c), LU 32e (im), LU 32f? (im), LU 32g? (im), LU 34 (im), LU 43a (c), LU 45 (t), LU 48a (c), LU 48c? (c), LU 48d? (c), LU 49a? (im), LU 50a (t), LU 50b? (c), LU 51c? (c), LU 52b (im), LU 53a? (im), LU 53b (im), LU 55 (im), LU 76 (c), LU 79 (im), LU 92a (c), LU 156a? (im), LU 156b? (im).

Occurrence. – *Megistaspis (M.) limbata* type 9 is the most frequent megistaspid in the Komstad Limestone of SE Scania and Bornholm, where it occurs in the *M. simon* Zone and in the lower subzone of the *M. limbata* Zone. Type 9 has been found in bed interval -6 to +7 at Skelbro; a poorly preserved pygidium from bed -7 is tentatively assigned. Pygidium IK P-6 from Skelbro most likely comes from bed -4, judging from the lithology as well as the adjoining fossils (*Rhombampyx* sp. and *Nileus orbiculatoides*). Pygidium IK P-7, also from Skelbro, derives from bed interval +1 to +7. Pygidium DGU-4 (from Skelbro) is from bed interval -4 to -7. No cranidia have been found *in situ* at Skelbro, but sample S 1765 contains three specimens, and a fourth specimen (GM 1984.1803) is kept at the Geological Museum, Copenhagen. All four cranidia originate from bed interval 0 to +7, as shown by the lithology.

M. limbata type 9 has been found in SE Scania at Gårdlösa-1 (beds N-M), Gårdlösa-4a (beds 2 to 12), and Killeröd (beds -7 to +7). A large collection in the University of Lund comes from Komstad, Tommarp, Smedstorp and Andrarum. Most of the samples cannot be assigned to precise level; the bulk of the material from Komstad originates from an interval equivalent to beds -2 to -9 at Killeröd.

A single pygidium was found at Fågelsång in bed 1, which is within the *M. limbata* Zone (lower subzone).

Description. – Largest cranidium 45 mm long, largest pygidium 52.5 mm long. Cranidium appears broad, but PW:L ratios are not high (Table 8). The available material does not indicate any stratigraphically controlled variation of the PW:L ratio (see remarks below). Sagittal relief of cranidium



moderate, strongest in smaller specimens. Glabella moderately to fairly vaulted. Mesial impression in frontal area faint. Elongate lateral glabellar furrows weakly impressed. Two pairs of rather indistinct, lateral, comma-shaped glabellar muscle insertion sites are occasionally seen in front of the lateral furrows on internal moulds. Mesial glabellar tubercle mostly absent. Occipital furrow deepest laterally. Bacculae indistinct. Anterior branches of facial suture diverge in front of eyes at an angle of 10 to 15° to sagittal line, then gently turn inwards, converging at an angle of about 125–130° to sagittal line.

All librigenae poorly preserved. Internal moulds show a shallow furrow at the base of eye socle. A fragmentary hypostome (Fig. 99A) is quite similar to *M. (M.) limbata* type 6, but is more elongate (Table 9).

Pygidia from the upper part of the *M. simon* Zone are narrower than pygidia from the *M. limbata* Zone, showing, respectively, L:W ratios of 0.68–0.75 (mean 0.71; $N=16$) and 0.64–0.72 (mean 0.68; $N=24$) (see also Table 10). Pleural ribs usually defined also on testaceous specimens, but by comparison to types 1–6 from Slemmestad this may relate to preservational differences. Concave border postaxial border is not turned upwards, except in small pygidia. Most specimens have 18 lines across the doublure at pygidial midline, a few specimens show only 16–17 lines.

Affinities.—By comparison to the material of *M. (M.) limbata* from Slemmestad, the cranidia of type 9 are quite similar to type 4, although they mostly are but slightly narrower (tr.); the border of smaller type 9 pygidia is less distinctly upturned than seen in types 3 and 5. It is stressed that type 9 should be treated only as an ecophenotype of *M. (M.) limbata*, there is no basis for a formal separation.

The pygidia of *M. limbata* type 9 are distinguished from *M. (M.) simon* by having a narrower axis, but within the Komstad Limestone the *M. limbata* pygidia from the *M. simon* Zone are also markedly narrower than the associated pygidia of *M. simon*. The type 9 cranidia have a longer and more prominent glabella, a significantly smaller preocular width

Fig. 98 (opposite page). *Megistaspis (M.) limbata* type 9. □A. Cranidium, $\times 1.5$. MGUH 22.477 (GM 1984.1803), Skelbro. □B. Slightly damaged, partly exfoliated cranidium, $\times 1.5$. MGUH 22.478 (K 678), bed 8, Gårdlösa-4a. □C. Smaller cranidium, $\times 2$. MGUH 22.479 (K 90), bed -5, Killeröd. □D. Flattened internal mould of large librigena, $\times 1.5$. MGUH 22.480 (K 506), bed 2, Gårdlösa-4a. □E. Internal mould of comparatively narrow pygidium showing axis and segmentation of pleural fields, $\times 1.5$. MGUH 22.481 (DGU 4), Skelbro. □F. Pygidium with intact test showing segmentation of pleural fields, $\times 1$. MGUH 22.482 (S 1083), bed 0, Skelbro. □G. Internal mould of comparatively broad pygidium, $\times 1$. MGUH 22.483 (S 1084), bed 0, Skelbro. □H. Fragmentary juvenile pygidium showing lateral border, $\times 4$. MGUH 22.484 (K 722), bed 9, Gårdlösa-4a. □I. Latex cast of juvenile pygidium showing well-developed border, $\times 4$. MGUH 22.485 (K 698), bed 9, Gårdlösa-4a. □J. Small pygidium showing strongly upturned postaxial border, $\times 2$. MGUH 22.486 (K 643), bed 7, Gårdlösa-4a.

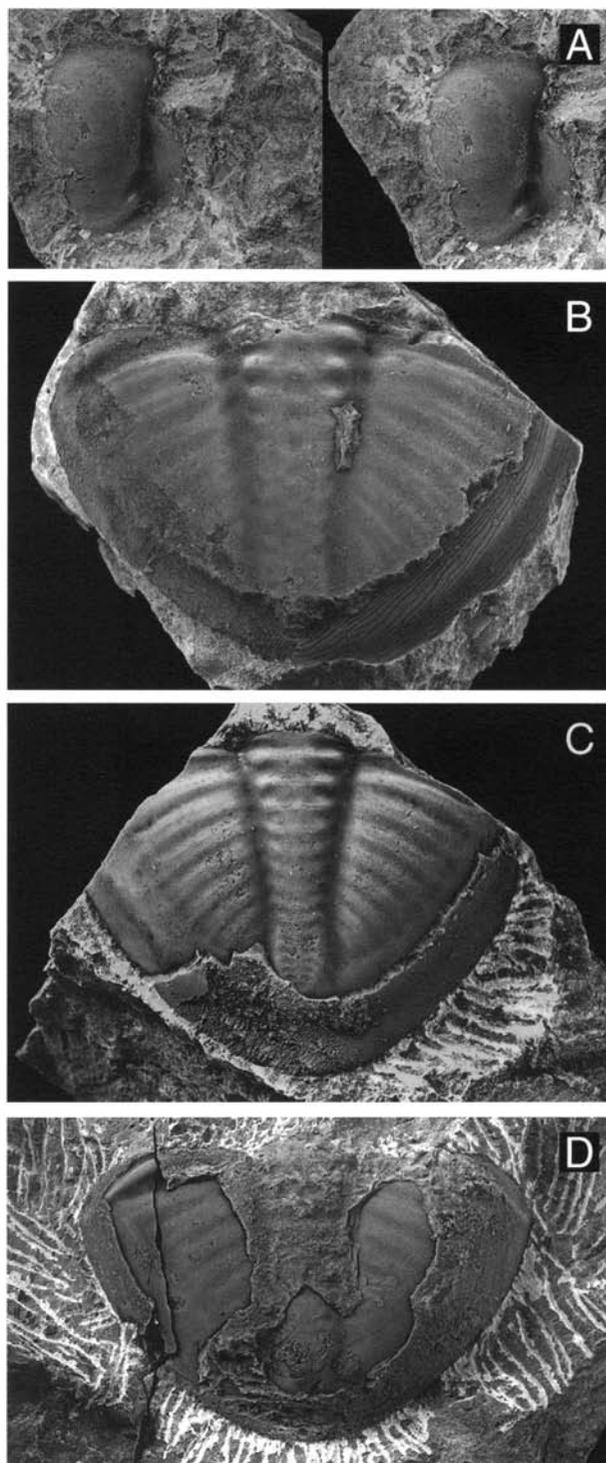


Fig. 99. *Megistaspis (M.) limbata* type 9. □A. Fragmentary internal mould of hypostome, stereo-pair, $\times 2$. LO 7071 (LU 16b), Andrarum. □B. Internal mould of pygidium showing doublure, $\times 1.5$. LO 7078 (LU 23), Andrarum. □C. Internal mould of small pygidium showing axis, $\times 2$. MGUH 22.487 (F 299), bed 1, Fågelsång. □D. Partly exfoliated, comparatively broad pygidium, $\times 1$. MGUH 22.488 (S 1348), bed +7, Skelbro.

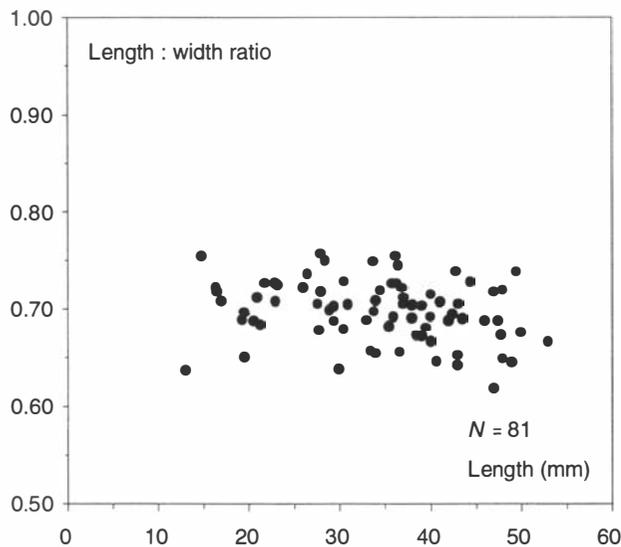


Fig. 100. Pygidia of *Megistaspis (M.) limbata* type 9. Ratio between length (sag.) and maximum width plotted against pygidial length.

and larger eyes, compared to the material of *M. simon* from Slemmestad.

Remarks. – Pygidia of type 9 from inferred shallow-water facies are relatively narrower than pygidia from deep-water intervals of the Komstad Limestone (Fig. 52). A matching systematic variation cannot be demonstrated for the sparse material of cranidia at hand, but it should be noted that the majority of cranidia assigned to type 9 and sampled *in situ* originates from the upper part of the *M. simon* Zone. A variation of librigenae width cannot be demonstrated either, as the few librigenae found *in situ* also are from the *M. simon* Zone.

The bulk of the material, assigned to *Megalaspis limbata* by Funkquist (1919), belongs to *M. limbata* type 9, as do some of the pygidia listed as *M. limbata* by C. Poulsen (1936).

Megistaspis (Megistaspis) elongata (Schmidt, 1906)

Figs. 101–103

Synonymy. – □v 1882 *Megalaspis limbata*, Boeck, form. *typica* [*partim*] – Brøgger, pp. 77–79; Pl. 9:1a–b; *non* Pl. 9:2 [= *M. (M.) limbata* type 5] and Pl. 9:3 [= *M. (M.) limbata* type 6] (description, occurrence, illustrations of enrolled specimen). □v 1886 *Megalaspis limbata*, Boeck. [*partim*] – Brøgger, p. 42, Pl. 2:22 (brief description and illustration of hypostome). □cf. 1890 *Megalaspis limbata* var. *elongata* m. – Pompecki, pp. 83–84; Pl. 4:15 (brief diagnosis, illustration of pygidium). □1906 *Megalaspis limbata* var. *elongata* m. – Schmidt, pp. 18–19; Pl. 1:12a–b (short description, illustrations of entire specimen). □cf. 1906 *Megalaspis limbata*

Boeck [*partim*] – Schmidt, pp. 18–19; Pl. 1:9 (description, illustration of cephalon [holotype of *M. pseudolimbata* Balashova, 1976]). □v 1907 *Megalaspis limbata* S. et B. – Wiman, pp. 91–92; Pl. 5:11–12 (occurrence, illustrations of cranidium, pygidium). □v 1907 *Megalaspis limbata* v. *elongata* Fr. Schmidt – Wiman, p. 91; Pl. 5:1–2 (occurrence, illustrations of enrolled specimen). □v 1956a *Megistaspis (Megistaspis)* cf. *elongata* (Schmidt, 1906) [*partim*] – Jaanusson, pp. 69–71; Textfig. 1A; *non* 1B [= *M. (M.) geminus* n.sp.] (discussion of *Megistaspis*, drawing of cephalon). □1972 *Megistaspis (Megistaspis) elongata* (Fr. Schmidt, 1906) [*partim*] – Tjernvik, pp. 307–309; Figs. 2B, 4C; *non* Fig. 3A [= *M. (M.) geminus* n.sp.] (discussion of *Megistaspis* distribution, drawings of cranidia). □1976 *Megistaspis (Megistaspis) elongata* (F. Schmidt, 1906) – Balashova, pp. 84–85; Pls. 20:7; 29:5; 33:4 (description of holotype; frontal and side view of cephalon, close up of librigena, illustration of pygidium). □cf. 1976 *Megistaspis (Megistaspis) pseudolimbata* sp.n. [*partim*] – Balashova, pp. 82–84; Pls. 20:8; 30:2; ?*non* Pl. 21:3–5 [? = *M. limbata baltica* Balashova] (description; illustrations of cephalon and hypostome).

Holotype. – By monotypy, complete specimen 255/42-18425 from the Lysaker Member of the Oslo region, probably from the *A. expansus* Zone. The specimen is figured and described by Schmidt (1901) and Balashova (1976).

Material. – Seven complete specimens, 4 cephalae, 1 hypostoma, 1 cranidium (badly preserved), and 10 pygidia.

List of material. – □Complete specimens A 468 (pim), A 482 (pim) [MGUH 22.491], A 1162 (im) [MGUH 22.489], GM 1909.101 (pim) [MGUH 22.490], PMO 143.512 (pim), PMO 2448 (im), PMO H 2615 (pim) [= Brøgger 1882, Pl. 9:1]. □Cephalae A 454 (pim, fragmentary), PMO 2244 with hypostome (pim), PMO 2262 (im), PMO 2277 (t). □Cranidium A 405c (c). □Pygidia K 1252 (im), A 405a? (im), A 409a (im) [MGUH 22.492], A 409b (t), A 418 (im), A 431? (im), A 462? (im), A 463 (im), A 566 (im), A 1101 (pim) [MGUH 22.493].

Occurrence. – *M. (M.) elongata* occurs in bed interval A-29 to A-40 at Slemmestad, representing the lower part of the *A. expansus* Zone. Complete specimen A 1162 and the material listed from the Paleontological Museum, Oslo, are from the Lysaker Member, but cannot be assigned to exact level. A single pygidium is from bed 11 at Killeröd site b, i.e. uppermost part of the *A. expansus* Zone. An additional megistaspid pygidium (*Megistaspis* sp.) is from bed 20 at Killeröd site b and possibly belongs to *M. elongata*, but the very poor preservation prevents an assignment to species.

Description. – (See also Balashova 1976). *M. elongata* is rather similar to *M. limbata*, and the description focuses primarily on the differences. Medium-sized species, largest measurable cranidium 30.5 mm long, largest pygidium 40 mm long; largest complete specimen is ca. 115–120 mm long. Cranidium A 405c is fragmentary, but may have had an original length of about 40 mm. Cephalon pronouncedly triangular in outline, L:W ratio varies between 2:3 and 3:4. Cranidium narrow, PW:L ratio 0.58–0.61 (mean 0.59; *N* =

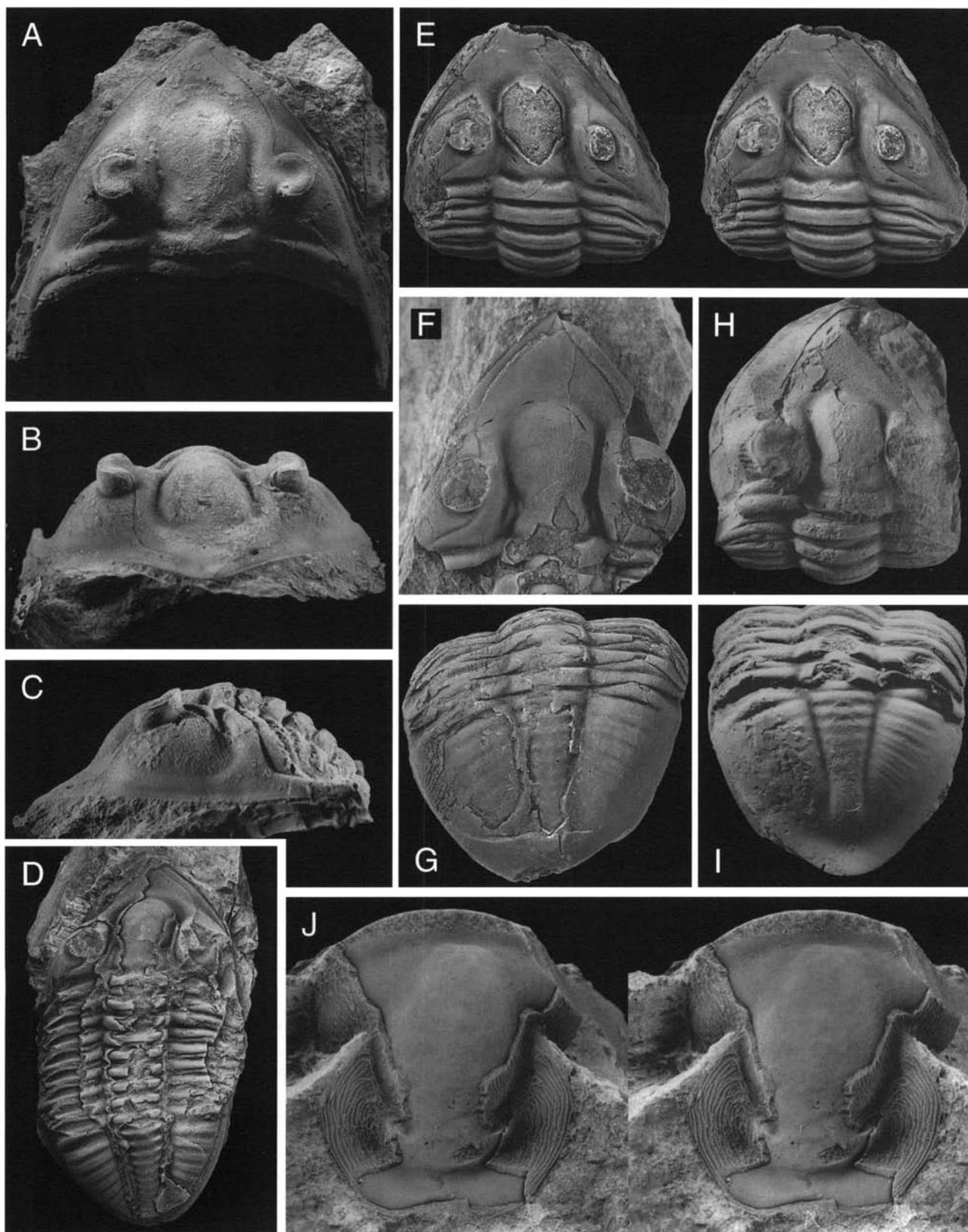


Fig. 101. *Megistaspis (M.) elongata* (Schmidt, 1906). □A–C. Cephalothorax, dorsal, frontal and side views, $\times 1.5$. B 113, Trästa, Häfverö, Baltic Sea. Previously figured by Wiman (1907, Pl. 5:11) and Jaanusson (1956a, Textfig. 1A). □D. Largely exfoliated complete specimen, $\times 1$. MGUH 22.489 (A 1162), Lysaker Member, Slemmestad. □E, G. Cephalon (stereo-pair) and pygidium of partly exfoliated complete specimen, $\times 1$. PMO H2615, Lysaker Member, Tøyen, Oslo. Previously figured by Brögger (1882, Pl. 9:1). □F. Cephalon, $\times 1.5$. PMO 2277, Lysaker Member, Håkavik, Asker, Oslo region. □H–I. Small complete specimen, $\times 2$. The well-developed pygidial border reflects the small size of the specimen. B 105, Trästa, Häfverö, Baltic Sea. Previously figured by Wiman (1907, Pl. 5:1–2). □J. Partly exfoliated hypostome, stereo-pair, $\times 4$. Cephalon PMO 2244, Lysaker Member, Gjeitungholmen, Slemmestad.

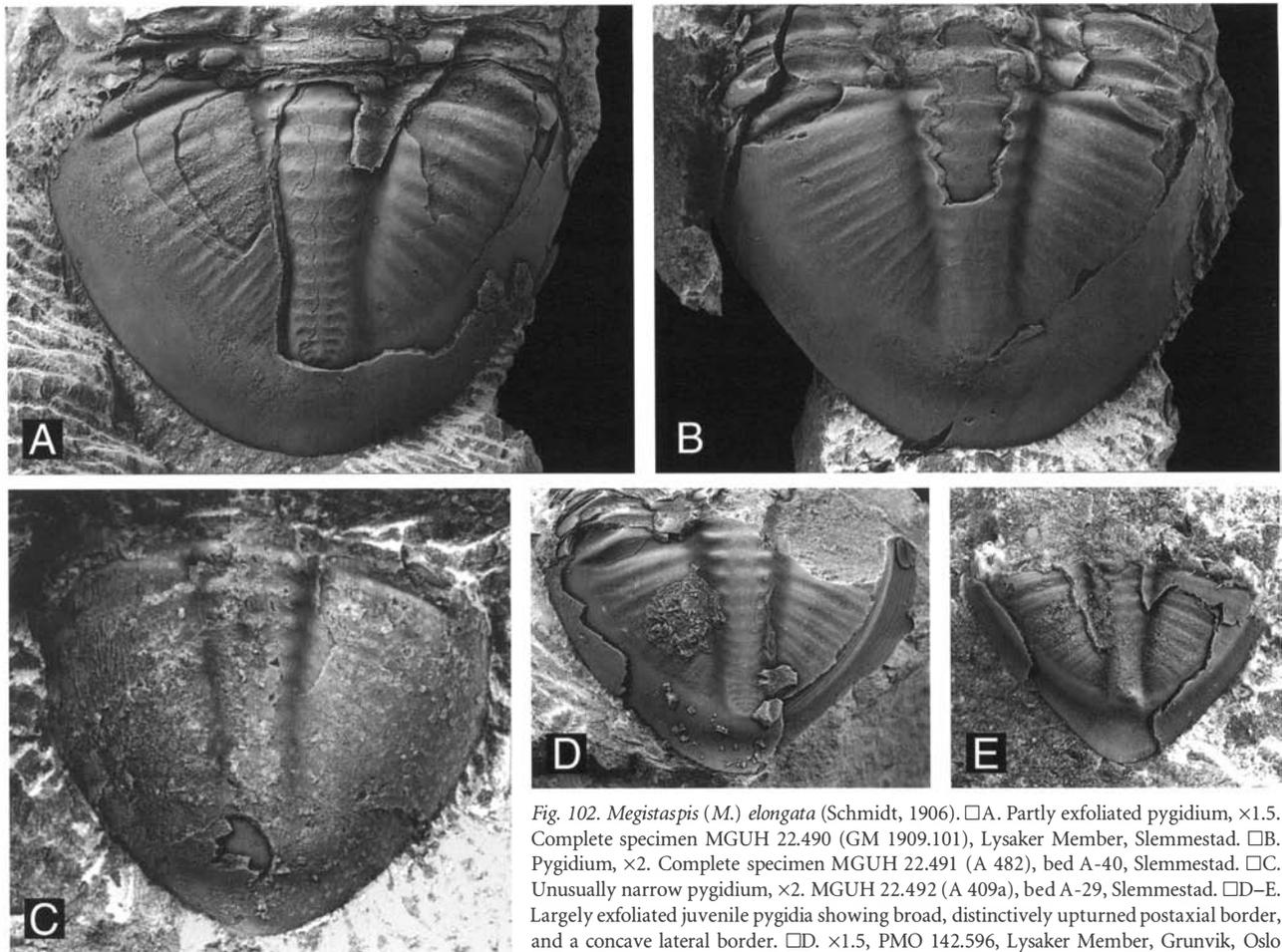


Fig. 102. *Megistaspis* (*M.*) *elongata* (Schmidt, 1906). □A. Partly exfoliated pygidium, $\times 1.5$. Complete specimen MGUH 22.490 (GM 1909.101), Lysaker Member, Slemmestad. □B. Pygidium, $\times 2$. Complete specimen MGUH 22.491 (A 482), bed A-40, Slemmestad. □C. Unusually narrow pygidium, $\times 2$. MGUH 22.492 (A 409a), bed A-29, Slemmestad. □D–E. Largely exfoliated juvenile pygidia showing broad, distinctly upturned postaxial border, and a concave lateral border. □D. $\times 1.5$, PMO 142.596, Lysaker Member, Grunvik, Oslo Region. □E. $\times 4$, MGUH 22.493 (A 1101), bed A-32, Slemmestad.

6); FW:L ratio is usually between 1.13 and 1.18 ($N = 4$), but a single specimen shows a ratio of 1.07. Sagittal cephalic relief fairly strong. Glabella comparatively strongly arched; it is delimited by shallow, wide furrows, which though are augmented by the change of slope. Glabella appears long, prominent, but is, nevertheless, relatively short, stretching for only 0.62–0.70 of the cranidial length (mean 0.66; $N = 6$), which is due to the course of the facial suture. Mesial impression in frontal area vestigial or absent. Lateral glabellar furrows weakly to moderately impressed. Occipital furrow rather shallow, deepest laterally, but augmented by the inflated occipital ring. Bacculae indistinct, almost effaced, only a single cephalon shows fairly defined bacculae. Posterior fixigena with wide, deep border furrow. Palpebral area of fixigenae sloping quite strongly in adaxial direction. Palpebral lobes appear large, but the material is fragmentary; palpebral length (exsag.) presumably equivalent to about 0.2 or slightly less of the cranidial length and the distance to posterior margin is about 1.2 to 1.5 times the lobe length (tentative measurements, $N = 4$). Anterior branches of facial suture subparallel in front of eyes, diverging only slightly forwards,

then, level with glabellar front, turn inwards, converging at an angle of about $135\text{--}140^\circ$ to sagittal line, to bend forwards close to sagittal line, meeting at a very pointed angle. The anterior snout extends the cranidium, hence the prominent glabella becomes relatively short. When exfoliated the librigena shows a fairly deep furrow at base of eye socle. It is probably characteristic that well-preserved internal moulds show a 'punctate' pattern, fine so on glabella and librigenae, more coarse on frontal area (see discussion below).

Cephalic doublure narrow, strongly concave, provided with fine, continuous terrace lines, laterally running subparallel to outer margin; level with eye was counted 19 lines ($N = 2$). The line pattern is interrupted by the median suture, and large, round panderian openings are present near genal angles. Terrace lines irregular below genal angle; no lines on doublure below genal spine. Inner margin of doublure curves gently upwards medially, forming a socket for the hypostome.

Hypostome largely similar to *M.* (*M.*) *limbata* type 6, but differs by having a less inflated median body, and posterolateral borders are narrower (tr.) and with a slightly different

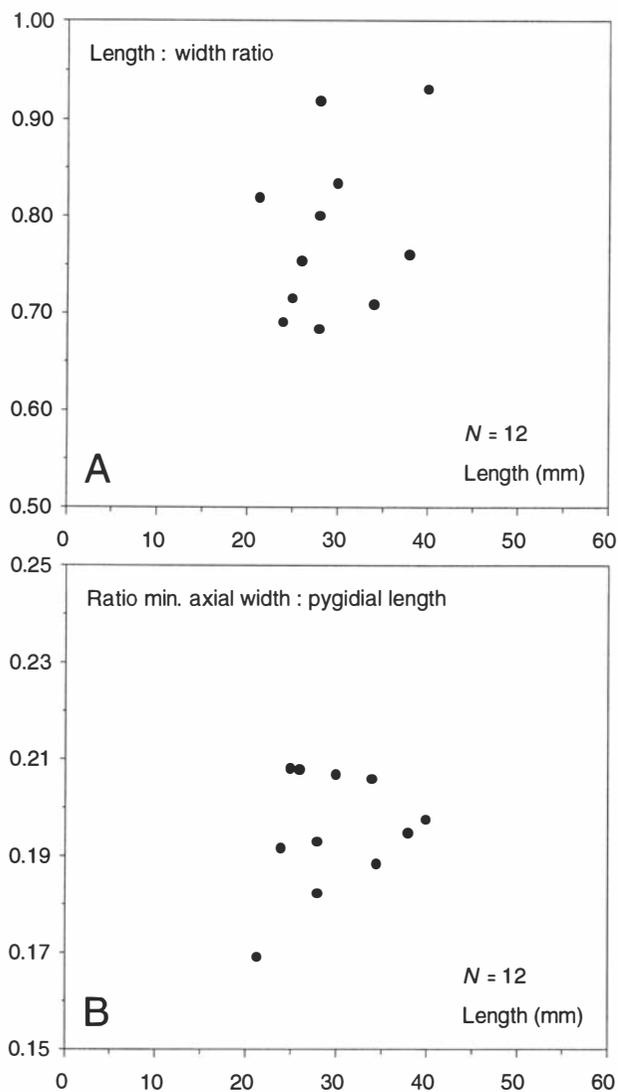


Fig. 103. Pygidia of *Megistaspis (M.) elongata*. □A. Ratio between length (sag.) and maximum width plotted against pygidial length. □B. Ratio between minimum axial width and pygidial length, plotted against length of pygidium.

outline, attaining maximum width level with beginning of premacular pits, whereas *M. limbata* type 6 have posterolateral borders, widening backwards for a longer stretch, attaining maximum width (tr.) level with base of maculae. Available hypostome 12.9 mm long, sagittal length 12.3 mm. Width across anterior wings equal to sagittal length, width across posterolateral borders 0.88 of maximum length. Median body stretches for 0.80 of maximum length, body W:L ratio 2:3. Distance (exsag.) from anterior margin to lateral border 0.34 of maximum hypostomal length.

Pygidium narrow parabolic in outline, adult L:W ratio rather variable, showing values between 0.71 and 0.93 (mean 0.78; $N = 12$, see Fig. 103A). Even if limited, the material shows a clear trend from very narrow pygidia in bed A-29

(L:W ratios 0.92–0.93) to broader pygidia in the succeeding beds, with a minimum pygidial L:W ratio of 0.76 in bed A-40 (Fig. 53). Axis narrow, minimum axial width at constriction equivalent to 0.17–0.21 of the pygidial length (mean 0.19; $N = 15$; Fig. 103B). Axis exceeds level of pleural fields all the way, but especially so anteriorly (see Balashova 1976). Axial segmentation comparatively distinct except posteriorly and visible also when the test is intact; number of segments as in *M. limbata*. Pleural fields show eight pairs of bifurcate ribs, of which the posterior pair is very faint, and some pygidia only show seven pairs. Concave border wide postaxially and stretches forwards in some specimens, so only the anterolateral portions of the pygidium are convex, while other specimens show a border only posteriorly. Because of the long postaxial border, the axis appears short.

Pygidial doublure as described for *M. limbata*, but the lines are slightly coarser; 13–15 lines were counted across the doublure at pygidial midlength.

A juvenile pygidium, 6.8 mm long (Fig. 102E), is distinctly triangular in outline, and shows a L:W ratio of 0.68. Axis pronouncedly arched and well raised above pleural fields; pygidial segmentation distinct. Concave border is very wide and slightly upturned postaxially, and then stretches forwards, so a narrow, well-defined border is present also anterolaterally. A couple of pygidia, 21–25 mm long, are still rather triangular in outline and with a slightly upturned postaxial border, but otherwise resemble the larger adult specimens. Note that the holotype has a pygidium ca. 20 mm long (see Schmidt 1906; Balashova 1976).

Affinities. – *M. (M.) elongata* is distinguished from *M. (M.) limbata* type 5 by usually being more elongate, so the cranial PW:L and FW:L ratios are smaller, the posterior fixigenae show well-impressed border furrows, the palpebral lobes are slightly larger, the pygidial border has a different outline, and the pygidial segmentation (axis and pleural fields) is more distinct. The relative length of glabella is affected by the different course of the facial suture, producing a short anterior snout in *M. elongata*. As the differences overall are rather minimal, a separation at the subspecies level appears more appropriate, and I am most inclined to regard *M. elongata* merely as a shallow-water ecophenotype of *M. limbata*. Nevertheless, pending investigations of larger collections, including East Baltic material, a separation at the species level is maintained, following established practice. That *M. elongata* actually was affected by environment is shown by the pygidial width, which changes markedly in the interval from bed A-29 to A-40, during which the pygidial length:width ratio decreases from about 0.92–0.93 to 0.76. This trend, although admittedly based on limited material, almost certainly mirrors environmental changes (inferred deepening).

The relations to *M. (M.) pseudolimbata* Balashova, 1976 are discussed below.

Remarks. – It has been overlooked that the name *M. limbata* var. *elongata* was preoccupied by *M. limbata* var. *elongata* Pompecki, 1890 (see Pompecki 1890, pp. 83–84; Pl. 4:15). Var. *elongata* Pompecki may, incidentally, very well turn out to be identical to var. *elongata sensu* Schmidt, but the original description and figuring is inadequate for a confident identification. Considering that the name *M. limbata* var. *elongata* Pompecki is a *nomen dubium*, based on ‘geschiebe’ material of unknown provenance, and that the whereabouts of the type material is unknown, while *M. elongata* (Schmidt) is a well-defined taxon, there is little point in changing the concept of *M. elongata*. Besides, var. *elongata* Pompecki never has been referred to by any other authors. It is therefore suggested to suppress the name *M. limbata* var. *elongata* Pompecki, 1890, and, accordingly, all references to *M. elongata* in the present work apply to *M. (M.) elongata* (Schmidt, 1906).

Jaanusson (1956a, p. 71) considered it quite likely that the traditional *M. limbata* of Sweden may prove within the limits of *M. elongata*, rather than within the range of *M. limbata* as fixed by Störmer’s designation of a lectotype in 1941. Jaanusson’s conception was based on the belief that the *M. limbata*, characterizing the Swedish ‘*Limbata* Limestone’, possesses a cephalic posterior border furrow, like the eastern Baltic material identified with *M. limbata* by Schmidt (1906), and like the specimens identified with *M. limbata* by Brögger (1882) and Wiman (1907), but unlike the lectotype of *M. limbata*, which lacks such a furrow. Jaanusson’s interpretation was refuted by Tjernvik (1972), who emphasized that the representatives of *Megistaspis* (*Megistaspis*) in the Volkhov Stage of Sweden lack a posterior border furrow, and that types possessing such a furrow are confined to the *A. expansus* Zone (Kunda Stage). The available new material of *M. limbata* and *M. elongata* is basically in accordance with Tjernvik’s statements of 1972.

Megistaspis (*Megistaspis*) species showing a well-defined cephalic posterior border furrow occur already in the BII α Zone of the East Baltic area (cf. Schmidt 1906; Balashova 1976), and also the earlier species of the *Paramegistaspis* group show variable development of the much-debated feature (compare *M. (P.) planilimbata* vs. *M. (P.) estonica*). It is inferred that the outline of the border furrow was governed by the environment; in a general way the presence appears associated with shallow-water habitats (see section on autecology). It follows that the misleading term *M. elongata* ‘group’, used for representatives of *M. (Megistaspis)* with a cephalic posterior border furrow, should be avoided.

Tjernvik (1972, pp. 307–308) mentioned that two species of ‘*elongata*-type’ occur in the *A. expansus* Zone at Lanna, of which one is similar to *M. l.* var. *elongata* as figured by Schmidt (1906) and Wiman (1907), whereas the other type was said to be similar to *M. limbata sensu* Wiman (1907) (= the cephalon of *M. (M.) cf. elongata* drawn by Jaanusson 1956a, Textfig. 1A). Wiman’s material has been examined

(see Fig. 101A–C, H–I), and it appears that *M. limbata* as well as *M. l.* var. *elongata sensu* Wiman belong to *M. (M.) elongata*. There are no important differences between the figured specimens, except for the size; the pygidium (Pl. 5:2 in Wiman 1907) is only ca. 17 mm long, and shows a relatively wide, rather upturned postaxial border (Fig. 101I). It is therefore uncertain what Tjernvik aimed at; the entire specimen N 921, referred to by Tjernvik (1972, p. 308), could not be located in the collections of the University of Uppsala.

The cranidium of *M. limbata sensu* Schmidt (1906, Pl. 1:10, later redrawn by Tjernvik (1972, Fig. 2C)) is from BII α , and not from BII γ , as indicated by Tjernvik (1972), while another cranidium, very similar to that of *M. elongata*, is from BII γ according to Schmidt (1906, Pl. 1:9). The latter cephalon is the holotype of *M. (M.) pseudolimbata* Balashova, 1976; material from the upper part of BII α was suggested to represent the matching pygidium (Balashova 1976), but this is hardly so if the pygidia are from BII γ and the cephalon from BII α . *M. elongata* is, according to Balashova (1976, p. 85), separated from *M. pseudolimbata* by having a more elongate cephalon, a wider occipital furrow, a strongly forwards bent occipital ring, more posteriorly situated eyes, and the librigena slopes down immediately from the eye. The holotype of *M. pseudolimbata* is damaged, so the relative proportions are uncertain, but it appears that glabella occupies about 2/3 of the cranidial length (cf. Schmidt 1906, Pl. 1:9), so the difference in elongation indicated by Balashova (1976, pp. 82, 85), stating the length of the frontal area in *M. pseudolimbata* to be only about 0.27–0.29 of the cranidial length, is not convincing. The eyes are situated 1.6 times the palpebral lobe length (exsag.) from posterior margin in *M. pseudolimbata*, which is slightly more advanced than apparent from the available material of *M. elongata*, but the range for variation remains to be documented by better material, and the difference is not considered significant (compare growth related changes in *M. limbata*). The librigena does not slope down immediately from the eye in *M. elongata*, this is a distortion of the holotype (cf. Balashova 1976, Pl. 20:7a). The hypostome of *M. pseudolimbata* (see Balashova 1976, p. 83; Pl. 30:2) is very similar to that of *M. elongata*. It is therefore the impression that *M. pseudolimbata* either is very closely related to or identical with *M. elongata*.

Balashova (1976, p. 82) included the narrow variety of *M. limbata forma typica sensu* Brögger (1882) in the list of synonyms for *M. pseudolimbata*. The narrow variety of *M. limbata*, figured by Brögger (1882, Pl. 9:1), clearly belongs to *M. (M.) elongata*, as shown, e.g., by the presence of distinct cephalic posterior border furrows; the specimen is included in the present study (Fig. 101E). The frontal area is slightly longer in reality than evident from the drawing published by Brögger. Furthermore, the inferred genal spines are drawn too slender and short, as indicated by available additional material (see also Schmidt 1906, Pl. 1:12a; Balashova 1976, p. 84).

Megistaspis (Megistaspis) geminus n.sp.

Figs. 104–107

Synonymy. – □v 1851 *Megalaspis limbata*. S-s & B-k. [*partim*] – Angelin, p. 18, Pl. 16:3 (occurrence, illustration of pygidium). □v 1886 *Megalaspis limbata*, Boeck [*partim*] – Brögger, p. 42; Pl. 2:23 (brief description of hypostome, illustration of hypostome [the same specimen is later refigured by Lindström (1901), Jaanusson (1956a) and Tjernvik (1972)]. □v 1901 *Megalaspis limbata* Boeck – Lindström, p. 61; Pl. 5:7 (illustration of hypostome). □v 1936 *Megalaspis limbata* Sars & Boeck [*partim*] – C. Poulsen, p. 48 (listed). □v 1937 *Megalaspis limbata* Sars and Boeck [*partim*] – Ekström, pp. 15 (not line 1!), 42, 49 (not line 37!); Textfig. 8 (occurrence, illustration of pygidium [not seen]). □v 1956a *Megistaspis (Megistaspis) elongata* (Schmidt, 1906) [*partim*] – Jaanusson, Textfig. 1B (drawing of hypostome). □v 1972 *Megistaspis (Megistaspis) elongata* (Fr. Schmidt, 1906) [*partim*] – Tjernvik, Fig. 3A (drawing of hypostome).

Derivation of name. – Latin *geminus* = twin, alluding to the circumstance that the species previously was mixed with *M. (M.) elongata*.

Holotype. – Cranidium MGUH 22.498 (S 1702) (Fig. 105A) from the uppermost part of bed +13 at Skelbro, basal *A. expansus* Zone.

Paratypes. – Cranidium MGUH 22.495 (S 1710) (Fig. 104D), horizon and locality like the holotype; pygidium Ar 24126 (Fig. 106D) from Fågelsång, which most likely is from the upper part of the *M. limbata* Zone. The paratype pygidium is surmised to be the original of Angelin (1851, Pl. 16:3).

Additional material. – Three cranidia, 5 librigenae, 4 hypostomata, and 79 pygidia, plus 2 complete specimens, tentatively assigned to the species.

List of additional material. – □ Complete specimens [referred to as *M. (M.) cf. geminus* n.sp.] A 429 (pim) [MGUH 22.497], PMO S 1614 (im). □ Cranidia S 1713 (im), F 42 (im) [MGUH 22.496], GM 1869.873 (im) [MGUH 22.494]. □ Librigenae F 196 (im) [MGUH 22.499], LU 1 (em), LU 26a (im) [LO 7084], LU 61 (pim) [LO 7088], LU 63b (pim). □ Hypostomata S 1587 (im), S 1593 (im) [MGUH 22.500], LU 72b (im), Ar 24113 (im). □ Pygidia S 1365? (c), S 1427 (im), S 1442 (im), S 1491 (im), S 1494 (im), S 1503 (im), S 1515 (im), S 1519 (im), S 1529? (im), S 1591 (im), S 1620 (im), S 1621 (im), S 1683 (im), S 1684 (im), S 1695 (pim), S 1769 (im), K 249 (c), K 261? (c), K 289 (c), K 396? (im), K 916 (c), K 941? (im), K 963? (c), K 984 (c), K 990 (c), K 991? (c), K 992 (c), K 1001? (c), F 28 (im), F 36? (c), F 44 (im), F 46 (im), F 50 (im), F 51 (im), F 52 (im), F 57 (im), F 58 (pim) [MGUH 22.501], F 59 (im), F 60 (im), F 61 (c), F 293 (im), GM 1881.1820 (im), GM 1888.301 (im), GM 1984.1802 (im) [MGUH 22.502], GM 1934.242 (im), LU 3 (im) [LO 7062], LU 25? (c), LU 26b (im) [LO 7085], LU 26c (im), LU 29b? (c), LU 30a (im) [LO 7088], LU 30b (im), LU 30c (im), LU 31a (im), LU 40 (im), LU 46 (im), LU 52a (im), LU 56 (im), LU 58b (im), LU 58c? (c), LU 59a (c), LU 59b? (c), LU 59c (c), LU 59c? (pim), LU 60 (c), LU 63a (im), LU 66a? (im), LU 66b? (im), LU 71 (im) [LO 7103], LU 72a (c), LU 72c (c), LU 72d (im), LU 74a (c), LU 74b (c), LU 74c? (im), LU 74d (im), LU 85 (em), LU 130? (c), LU 156c? (im).

Occurrence. – *M. (M.) geminus* n.sp. characterises the upper subzone of the *M. limbata* Zone in the Komstad Limestone,

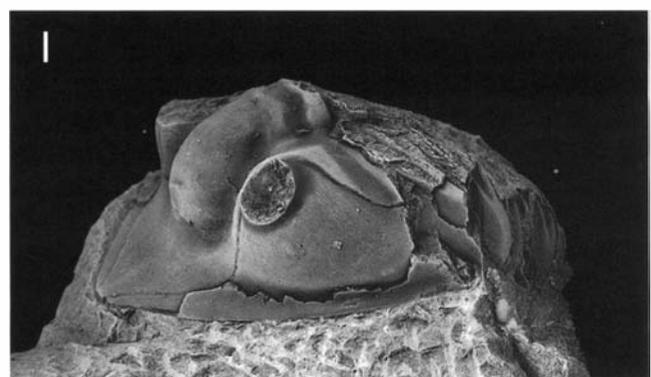
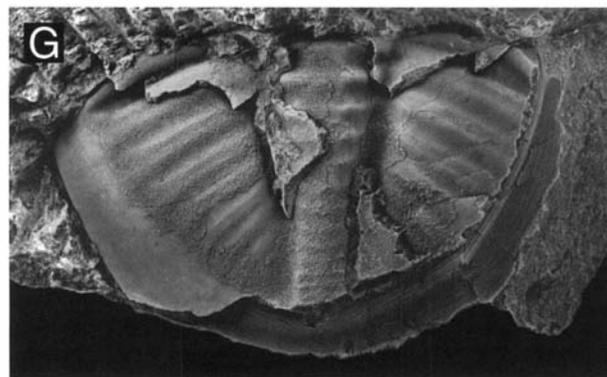
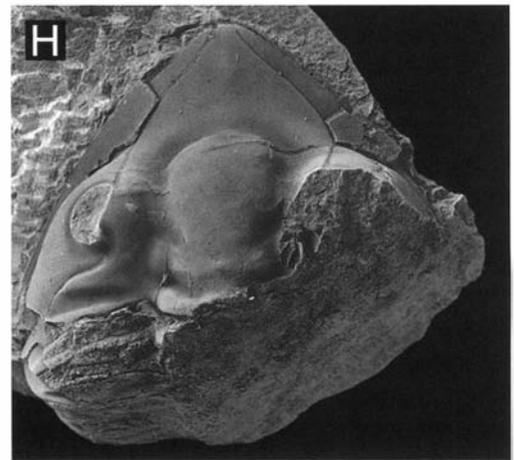
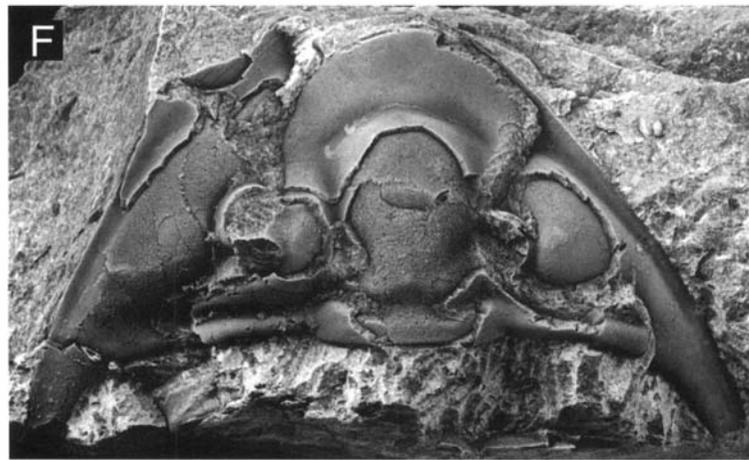
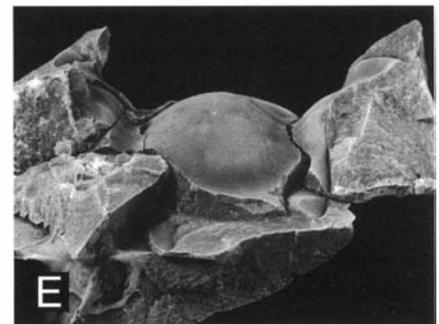
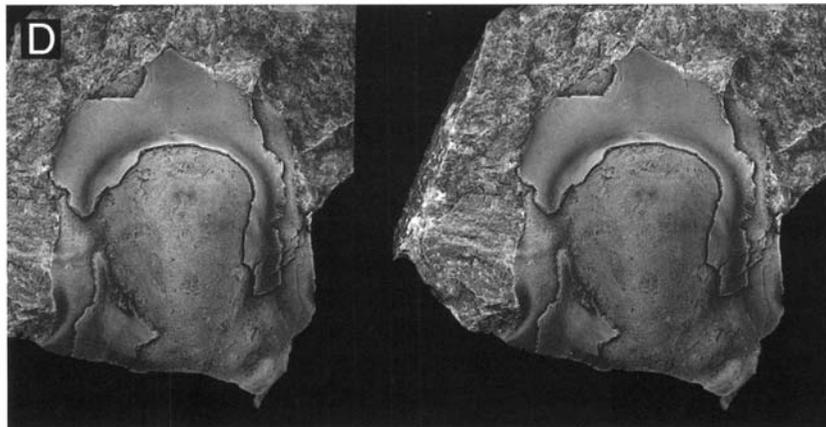
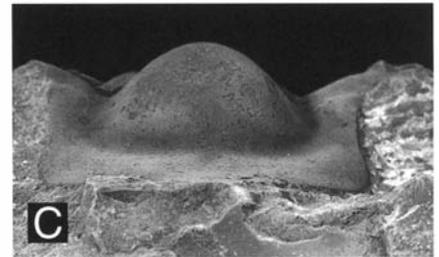
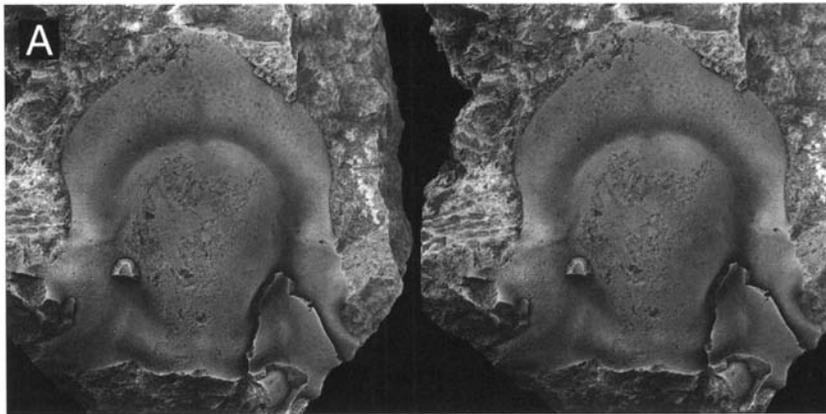
but ranges into the very basal part of the *A. expansus* Zone. It has been found in bed interval +9 to +14 at Skelbro, bed interval +9 to +18 (+19?) at Killeröd, and in beds 7, 8, 9 and 20 at Fågelsång.

Pygidia GM 1984.1802 and GM 1881.1820 from Skelbro and Duegård, Bornholm, are from the upper 6 cm of bed +13 (base of the *A. expansus* Zone), while GM 1888.301 comes from bed interval +9 to +12 of Skelbro, most likely bed +9 or the basal part of bed +10. Material collected by Funkquist and Ekström at Fågelsång (Univ. of Lund coll.) derives from bed interval 5 to 9 (= beds g–m of Ekström 1937, p. 15); additional LU material is from bed interval 2–10, (exact beds unknown; *M. limbata* Zone) and bed interval 18–22 (base of the *A. expansus* Zone); cranidium GM 1869.873 is also from beds 18–22 (most likely 18–20). Pygidium LU 46 (coll. Funkquist) from the upper part of the limestone at Tommarp is probably from the *A. expansus* Zone (the sample contains a juvenile cranidium identified with *Nileus cf. armadillo*). A couple of poorly preserved pygidia, also from Tommarp, are from a slightly lower level, presumably the upper part of the *M. limbata* Zone. Pygidium LU 40, sampled at Andrarum, is from a loose boulder; the sample possibly represents the *A. expansus* Zone.

An impaired entire specimen is from bed A-31 (A 429) at Slemmestad, i.e. basal part of the *A. expansus* Zone. An additional entire specimen (PMO S 1614) is from an unknown level within the Lysaker Member of Slemmestad; both Norwegian specimens are referred to as *M. (M.) cf. geminus* n.sp.

Diagnosis. – Glabella strongly inflated, slightly pyriform, comparatively long in adults, well set off from unusually flat frontal area; posterior fixigenae long (tr.) and with deep border furrow; eyes large. Segmentation of pygidium distinct, showing 8 pairs of ribs and 15 axial rings; no concave border; pygidial doublure covered with comparatively fine and dense terrace lines.

Description. – Fairly large species, largest cranidium ca. 46 mm long, largest pygidium 60 mm long. Cranidium appears broad, but the PW:L ratio is only about 0.70; FW:L ratio is 1.5 in one specimen (ca. 43 mm long), the two Norwegian specimens (22 and 23.5 mm long) show 1.27–1.34; this variation is presumably size-related (cf. Fig. 81C). Sagittal cranidial relief very strong. Glabella unusually prominent, strongly inflated, slightly pyriform, delimited by shallow dorsal and preglabellar furrows, but the indistinct furrows are augmented by the pronounced change of slope. Glabella comparatively long, stretching for 0.72–0.77 of the cranidial length; the limited material indicates that it is perhaps relatively shorter in smaller specimens, as glabella accounts for only 0.66 of the sagittal length in the smallest Norwegian specimen, ca. 22 mm long (Fig. 104H–I), and for 0.74 in the other Norwegian specimen, 24 mm long (Fig. 104F). Lateral margins of anterior fixigenae bent insignificantly downwards in large cranidia, slightly more so in smaller speci-



mens. As a whole, anterior fixigenae and frontal area are unusually flat and well set off from the steeply rising glabella. Mesial impression in frontal area nebulous. Lateral glabellar furrows moderately impressed, most so in small cranidia. It seems to be characteristic that internal moulds have a wide, rounded, very shallow mesial impression on the upper part of the glabellar front. Occipital furrow shallow, deepest laterally, more strongly impressed in smaller cranidia, but the relatively indistinct occipital furrow is accentuated by the raised, prominent occipital ring. Characteristically, the occipital ring is expanded mesially, bulging forwards. Bacculae very indistinct, almost effaced. Posterior border furrow wide, deep. Palpebral area of fixigenae convex, sloping adaxially, distinctly stronger so in smaller cranidia (less than 25 mm long); palpebral lobes are positioned below the level of glabellar crest in large cranidia (Fig. 104C), and distinctly raised above in the smallest cranidium (Fig. 104E). Lobes appear to be comparatively large (material fragmentary), exsagittal length corresponds to more than 0.2 of the cranidial length in the smallest specimen, while a larger cranidium seems to have lobes with an exsagittal length equivalent to slightly less than 0.2 of the cranidial length. Distance from lobe to posterior margin approximately equal to the lobe length (exsag.). Anterior branches of facial suture subparallel in front of eyes, diverging very gently forwards, then, level with glabellar front, turn inwards and converge at an angle of about 120–125° to sagittal line to meet in an angulate junction.

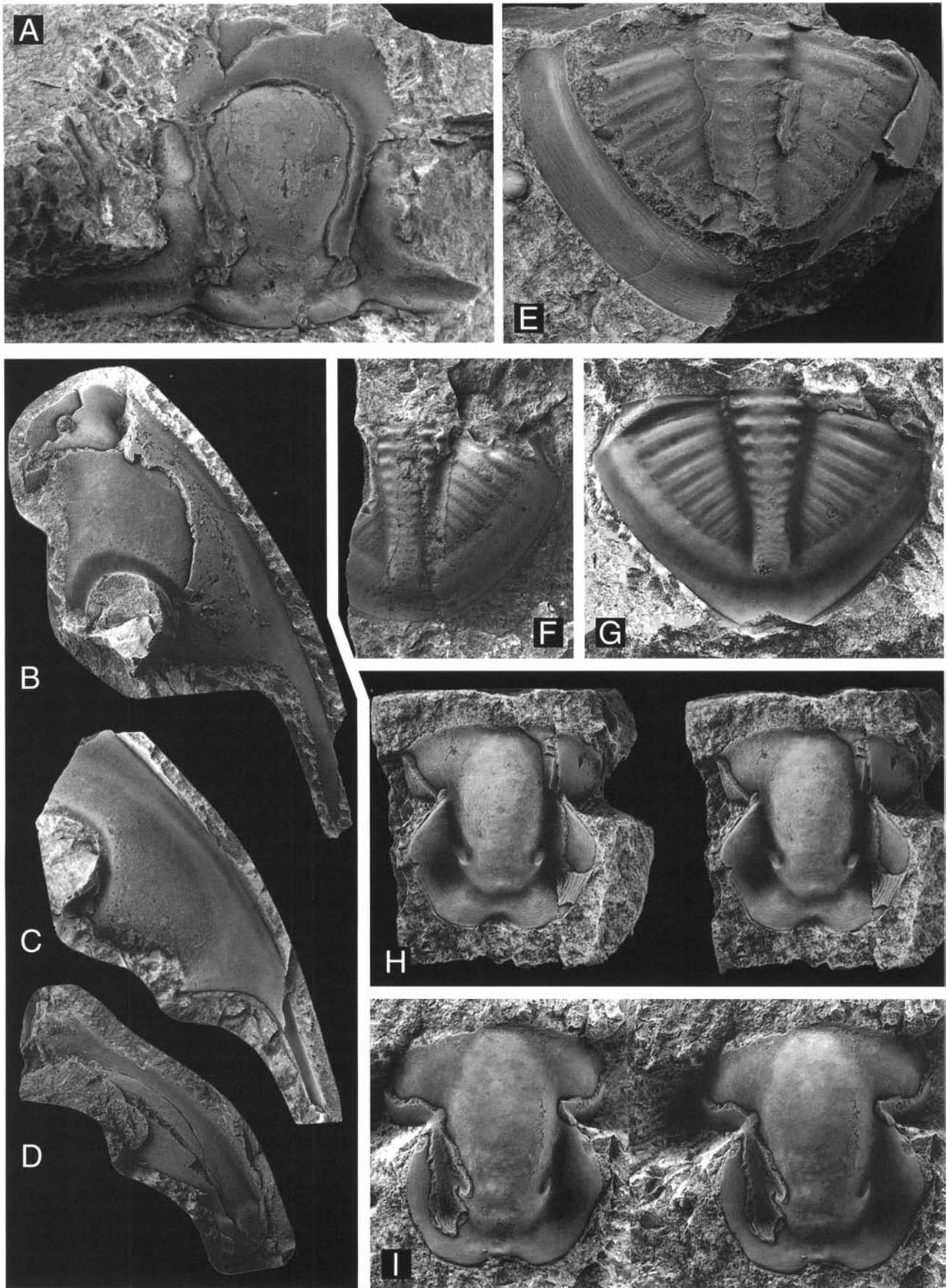
Librigena strongly vaulted; internal moulds show a deep furrow at the base of eye socle and a wide, shallow paradoublure furrow; anterior continuation of librigena flat and of equal width all the way, in posterior direction continuing into a narrow lateral border which narrows rearwards, but almost reaches genal angle. Posterior border furrow just enters the librigena and then shallows up. Genal spines fairly long. Doublure narrow, very steep, almost vertical laterally; inner margin descends markedly in front of eye level, forming a socket to the hypostome.

Hypostome fairly large-sized, largest specimen ca. 24 mm long (posterior border damaged); gross outline roughly rectangular, W:L ratio across posterior borders varies between

0.8 and 0.9 (mean 0.84; $N = 3$). Greatest width, which is across anterior wings, equivalent to 0.92–0.97 of the hypostomal length (sag.) (mean 0.94; $N = 3$). Central part of anterior margin almost straight, distal parts curve backwards. Median body oval, fairly vaulted, but distinctly less so than in *M. limbata*, reaching hypostomal margin anteriorly. A pair of weakly impressed premacular pits present close to posterior end of median body, indistinctly dividing the median body into a long, prominent anterior lobe and a short posterior lobe. W:L ratio of median body 0.58–0.62 (mean 0.59; $N = 4$); the body occupies 0.81–0.84 of the hypostomal maximum length (mean 0.82; $N = 3$), corresponding to 0.83–0.88 of the sagittal length. Maculae very narrow, elongate, with smooth surfaces; they are most distinct in smaller specimens and almost indistinct in larger hypostomes. Anterior wings ascend strongly in dorsal direction; anterolateral corner bent in ventral direction, defining a short (both ways) anterior border. Anterior wing goes all the way to furrow delimiting the median body. Lateral border starts 0.34–0.38 of the hypostomal maximum length from anterior margin (mean 0.36; $N = 3$). Border widens to attain maximum width level with maculae; lateral border confluent with posterior border. Posterior mesial notch wide, so posterior border is slightly bilobate; depth of notch equivalent to 0.03–0.06 of maximum hypostomal length (mean 0.05; $N = 3$). Entire lateral and posterior border rather flat, and slopes towards the border furrow. Median body separated by a wide border furrow, running rearwards from anterior wing, joining the indistinct premacular pit, thence continues into a wide, fairly deep posterolateral depression. Here the posterolateral border is steepest, sloping rather strongly towards the depression. Border furrow continues from the depression inwards-backwards around posterior end of median body. The four hypostomes at hand are exfoliated, but patches of intact test and impressions on the mould surfaces show that terrace ridges are crowded on the posterolateral border, laterally on median body, and less dense across anterior wing. The border furrow, at least, lacks terrace ridges, but it is unknown if the central part of the median body also is smooth.

Pygidium may approach a triangular outline, but is generally parabolic, or even subsemicircular in outline. L:W ratio varies between 0.66 and 0.74 in specimens more than 15 mm long (mean 0.70; $N = 40$; Fig. 107A). In gross outline the pygidium of the new species is similar to *M. limbata*, but *M. geminus* n.sp. has a slightly narrower axis, a more distinct segmentation of axis and pleural fields with a higher number of segments, and adult pygidia lack a border. Minimum axial width (tr.) at constriction corresponds to 0.18–0.22 of the pygidial length (mean 0.19; $N = 24$). There are 15 axial rings in addition to the terminal piece and anterior half-ring; eight pairs of bifurcate pleural ribs are defined in most specimens, but the posterior very short ribs may be effaced when the test is intact. Nine pairs can, actually, be counted on a few internal moulds, but the posterior pair is then very indistinct. Internal moulds show a longitudinal mesial keel on axis,

Fig. 104. □A–E. *Megistaspis (M.) geminus* n.sp. □A–C. Internal mould of medium-sized cranidium, showing proportionally short glabella. A stereo-pair, $\times 1.5$, B side view, $\times 1.5$, and C, frontal view, $\times 2$, the latter showing that the palpebral lobes level with glabella. MGUH 22.494 (GM 1869.873), Fågelsång. □D. Paratype. Partly exfoliated fragmentary cranidium, stereo-pair, $\times 1$. MGUH 22.495 (S 1710), bed +13, Skelbro. □E. Small cranidium, frontal view, $\times 2$. The palpebral lobes are highly elevated above glabella (cf. C). MGUH 22.496 (F 42), bed 9, Fågelsång. □F–I. *Megistaspis (M.) cf. geminus* n.sp. □F–G. Largely exfoliated complete specimen; pygidium showing part of the doublure, $\times 2$. MGUH 22.497 (A 429), bed A-31, Slemmestad. □H–I. Cephalothorax of small specimen showing proportionally short glabella, dorsal and oblique side views, $\times 2$. The specimen is slightly distorted by compaction. PMO S1614, Lysaker Member, Gjeitungholmen, Slemmestad.



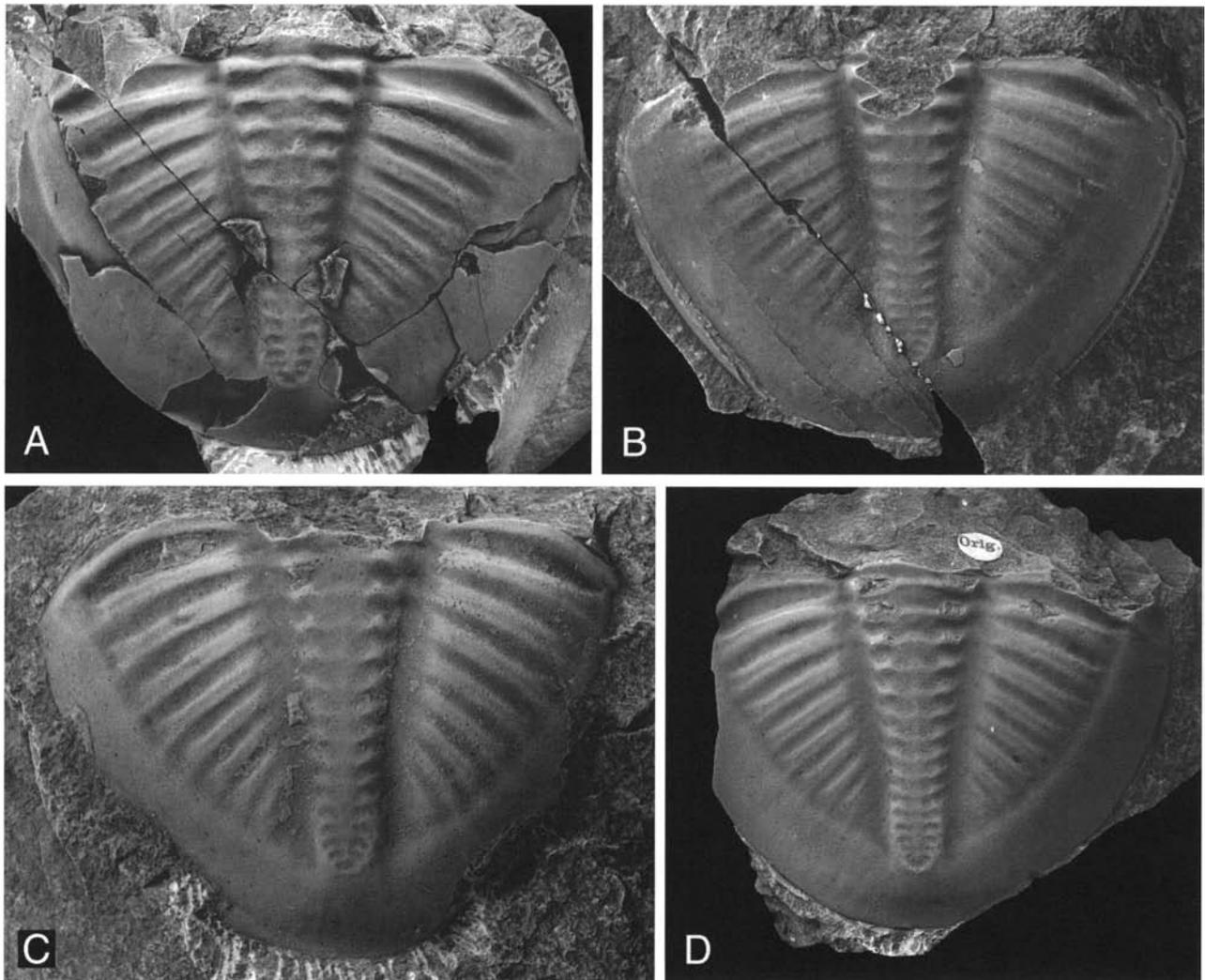


Fig. 106. *Megistaspis (M.) geminus* n.sp. □A–D. Internal moulds of pygidia showing distinct segmentation of axis and pleural fields. Note the absence of a concave border. □A. $\times 1$. MGUH 22.501 (F 58), bed 9, Fågelsång. □B. $\times 1.5$. LO 7103 (LU 71), Fågelsång area. □C. $\times 1.5$. MGUH 22.502 (GM 1984.1802), Skelbro. □D. Paratype, $\times 1$. Ar 24 126, Fågelsång. Probably the original of Angelin (1851, Pl. 16:3).

Fig. 105. *Megistaspis (M.) geminus* n.sp. □A. Holotype. Largely exfoliated cranium, $\times 1.5$. MGUH 22.498 (S 1702), bed +13, Skelbro. □B. Partly exfoliated librigena showing comparatively deep furrow at base of eye socle, $\times 2$. LO 7088 (LU 61), Fågelsång area. □C. Internal mould of librigena, $\times 2$. LO 7084 (LU 26a), Fågelsång area. □D. Internal mould of librigena showing doublure, $\times 1$. MGUH 22.499 (F 196), bed 20, Fågelsång. □E. Internal mould of pygidium showing doublure, $\times 1.5$. LO 7088 (LU 30a), Fågelsång. □F. Internal mould of small pygidium showing well-developed border, $\times 2$. LO 7062 (LU 3), Fågelsång area. □G. Internal mould of juvenile pygidium showing well-developed border all the way, and which is upturned postaxially, $\times 6$. LO 7085 (LU 26b), Fågelsång. □H. Internal mould of hypostome, stereo-pair, $\times 2.5$. Ar 24113, Fågelsång. Previously figured by Brögger (1886, Pl. 2:23), Lindström (1901, Pl. 5:7) and Jaanusson (1956a, Textfig. 1B). □I. Internal mould of large hypostome, stereo-pair, 2.5. MGUH 22.500 (S 1593), bed +13, Skelbro.

connecting all posterior axial rings from ring no. 4 and rearwards. No border, although the margin may have a steep, very slight concavity postaxially, seen primarily on internal moulds. A very narrow flattened strip is defined postaxially in a few, smaller pygidia. A juvenile pygidium, 8.5 mm long, is moderately broad, with a L:W ratio slightly below 2:3; the axis is highly convex, raised above pleural fields, and a concave border extends all the way to articulating facets (Fig. 105G). A concave border is still seen in pygidia up to 20 mm long, and specimens 20–30 mm long occasionally show a moderately steep border postaxially. Doublure similar to *M. limbata*, but the terrace lines are finer and there are 17–20 lines at midline across pygidium; furthermore, the axial embayment is smaller and affects the postaxial terrace lines less, so these lines are openly U-shaped, not sharply V-shaped in dorsal view.

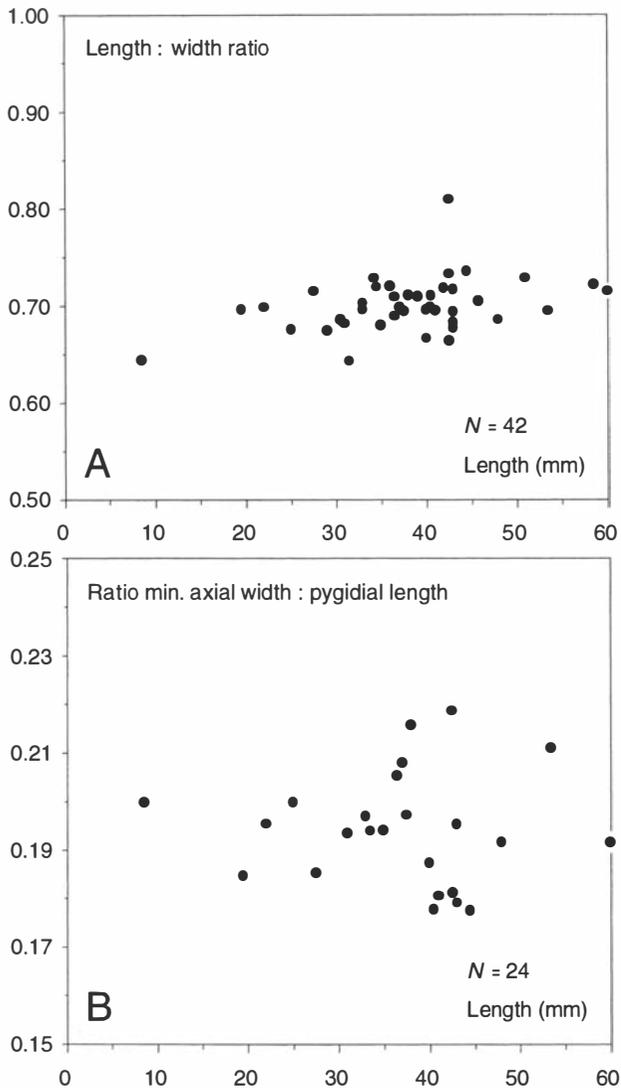


Fig. 107. Pygidia of *Megistaspis* (*M.*) *geminus* n.sp. □A. Ratio between length (sag.) and maximum width plotted against pygidial length. □B. Ratio between minimum axial width and pygidial length, plotted against pygidial length.

Affinities. – The relations to the other species of *M.* (*Megistaspis*) are obscure. *M.* (*M.*) *geminus* n.sp. is separated from *M.* (*M.*) *limbata* by the much more inflated and prominent glabella, by the flat, almost horizontal frontal area, by the well-developed cephalic posterior border furrows, and by the elongate hypostome, showing a less inflated, usually more elongate median body, less raised [ventral view] lateral and posterior borders, and a more distinct notch in the posterior margin. Pygidial differences are mentioned above.

Compared to *M.* (*M.*) *elongata*, *M.* (*M.*) *geminus* n.sp. has a more convex and prominent glabella, the sagittal cranial relief is stronger, with an almost flat frontal area and a steeply rising glabellar front; the glabellar outline is more pyriform, and the lateral glabellar furrows and the occipital furrow are better impressed. The hypostome has a less arched, more elongate median body.

M. (*R.*) *gibba* (Schmidt, 1898) also shows a distinctly inflated glabella, but is otherwise quite different from *M.* *geminus* n.sp., as its facial sutures diverge strongly in front of the eyes, the frontal area is rather short, the lateral glabellar furrows are quite deep, the posterior fixigenae are short (tr.) and the pygidium has a wide, concave border.

Remarks. – Specimen A 429 (Fig. 104F–G) from the *A. expansus* Zone at Slemmestad shows a similar prominent glabella, an unusually flat frontal area, and a pygidial doubleure with fine terrace lines and a minimal axial incision, and the specimen either belongs to *M.* *geminus* n.sp. or a very close subspecies. However, a small patch of intact border attests to the presence of a concave border, and a well-developed postaxial border may be assumed. Another Norwegian specimen (Fig. 104H–I) also resembles *M.* (*M.*) *geminus* n.sp. by showing a flat frontal area and a steeply rising glabella; the glabella is unusually short, but this may size-related. Also this specimen shows a well-developed pygidial border. Both Norwegian specimens probably belong to *M.* (*M.*) *geminus* n.sp., and the presence of a pygidial border is surmised to relate to environment. Future studies may ascertain whether different ecophenotypes of *M.* (*M.*) *geminus* n.sp. can be distinguished.

Three fragmentary pygidia (A 324b, A 379, A 401) from the upper part of the *M. limbata* Zone at Slemmestad (beds A-20 to A-28) probably represent *M.* cf. *geminus* n.sp., but the poor preservation hinders a confident identification, and the material is treated as indeterminate.

Hypostome Ar 24113 from Fågelsång (Fig. 105H), firstly described by Brögger (1886) and later refigured by Lindström (1901), Jaanusson (1956a), and Tjernvik (1972), has lately been identified with *M.* *elongata* (Jaanusson 1956a and Tjernvik 1972). However, by comparison to *M.* (*M.*) *geminus* n.sp. the hypostome of *M.* *elongata* has a less elongate, more inflated median body, the maculae are more distinct, the posterior mesial incision is slightly shallower, and the maximum width across posterolateral borders is attained relatively more forwards (compare Fig. 101J). The repeatedly figured specimen is 15 mm long, so the maculae are more distinct than in larger specimens.

Megistaspis (*Megistaspis*) *polyphemus* (Brögger, 1882)

Figs. 108–110

Synonymy. – □v 1882 *Megalaspis polyphemus*, n.sp. – Brögger, pp. 73–75; Textfigs. 2–3 (description, illustrations of complete holotype specimen [refigured by Skjeseth 1952]). □1884 *Megalaspis limbata* Boeck forma *lata* – Törnquist, pp. 93, 97; Pl. 3:12 (description, occurrence, illustration of cranidium [refigured by Tjernvik 1980]). □1906 *Megalaspis polyphemus* var. *Törnquisti* m. – Schmidt, pp. 23–25; Textfig. 6; Pl. 2:6 [refigured by Balashova 1976, Pl. 21:10] (descrip-

tion, occurrence, illustrations of cephalon and pygidium). □1906 *Megalaspis polyphemus* var. *minor* m. – Schmidt, pp. 25–27; Textfig. 7; Pl. 1:5–7 (description of juvenile specimens, occurrence, illustrations of complete specimen, cephalon and thorax with pygidium). □v 1936 *Megalaspis limbata* Sars & Boeck [*partim*] – C. Poulsen, pp. 48, 50 (listed). □v 1952 *Megalaspis polyphemus* Brögger, 1882 [*partim*] – Skjeseth, pp. 162–164; Pl. 1:2, 5, 6; non Pl. 1:1, 11 [*indet.*] (description, occurrence, illustrations of holotype). □v non 1956 *Megistaspis limbata lata* [*partim*] – Tjernvik, p. 155 (pygidium listed from the Böda Hamn core). □1956a *Megistaspis* (*Megistaspis*) *lepikuensis* n. nom. – Jaanusson, pp. 69–70 (change of name, *M. minor* preoccupied). □v 1965 *Megistaspis* (*Megistaspis*) sp. no. 2 – V. Poulsen, p. 68; Pl. 2:1 (description, occurrence, illustration of pygidium). □1976 *Megistaspis* (*Megistaspis*) *lata* (Törnquist, 1884) – Balashova, p. 82; Pl. 21:9 (description of pygidium, occurrence, illustration of pygidium). □1976 *Megistaspis* (*Megistaspinus*) *polyphemus* (Brögger) *törnquisti* (F. Schmidt, 1906) emend. – Balashova, pp. 85–87; Pls. 20:2–3; 21:10 (description, occurrence, illustrations of pygidia, side-view of cephalon). □1976 *Megistaspis* (*Megistaspinus*) *lepikuensis* (Jaanusson, 1956) – Balashova, pp. 87–88; Pls. 31:8; 32:3; 33:7 (redescription of original material, occurrence, illustrations of cephalic, thoracic and pygidial doublure). □v 1980 *Megistaspis* (*Megistaspis*) *lata* (Törnquist) [*partim*] – Tjernvik, pp. 188, 189, 191, 197; Figs. 7A, 8J–L, 9A (description, occurrence, illustrations of complete specimen, cephalon, cranidium, pygidia).

Holotype. – By monotypy, complete specimen PMO 66 398. Figured by Brögger (1882, Textfigs. 2–3) and Skjeseth (1952, Pl. 1:2, 5, 6); herein refigured on Fig. 108A–B.

Material. – Four complete specimens including the holotype, 4 fragmentary cranidia and 38 pygidia.

List of material. – □Complete specimens PMO 66398 (im) [holotype], PMO 94538 (c), Ar 16169 (t), GM 1883.802 (c) [MGUH 22.503]. □Cranidia PMO 604 (t), S 129 (im), S 1678 (im), S 297 (im) [MGUH 22.505]. □Pygidia S 60 (im) [MGUH 22.507], S 70 (im) [MGUH 22.511], S 295 (t) [MGUH 22.506], S 388 (im), S 554 (c), S 600 (im), S 641 (c), S 657 (c), S 665 (c), S 666 (c), S 667 (c), S 681? (c), S 688 (c), S 693 (im), S 694 (pim), S 696 (c), S 701? (c), S 708 (c), S 709 (c), S 710 (c), S 715 (c) [MGUH 22.509], S 722 (c) [MGUH 22.508], S 756 (c), S 758 (c), S 764? (im/em), S 770? (c), S 776 (c), S 1673a (im), S 1673b (im), S 1680 (c), S 1681a (im) [MGUH 22.504], S 1773 (im) [MGUH 22.510], GM 1871.1003 (im) [MGUH 22.512], GM 1874.32 (im), GM 1875.1484 (c), GM 1889.220 (im), MGUH 9425 (im), IK P-3 (c).

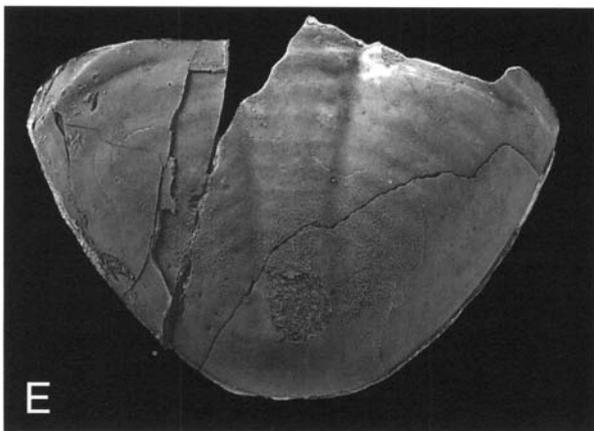
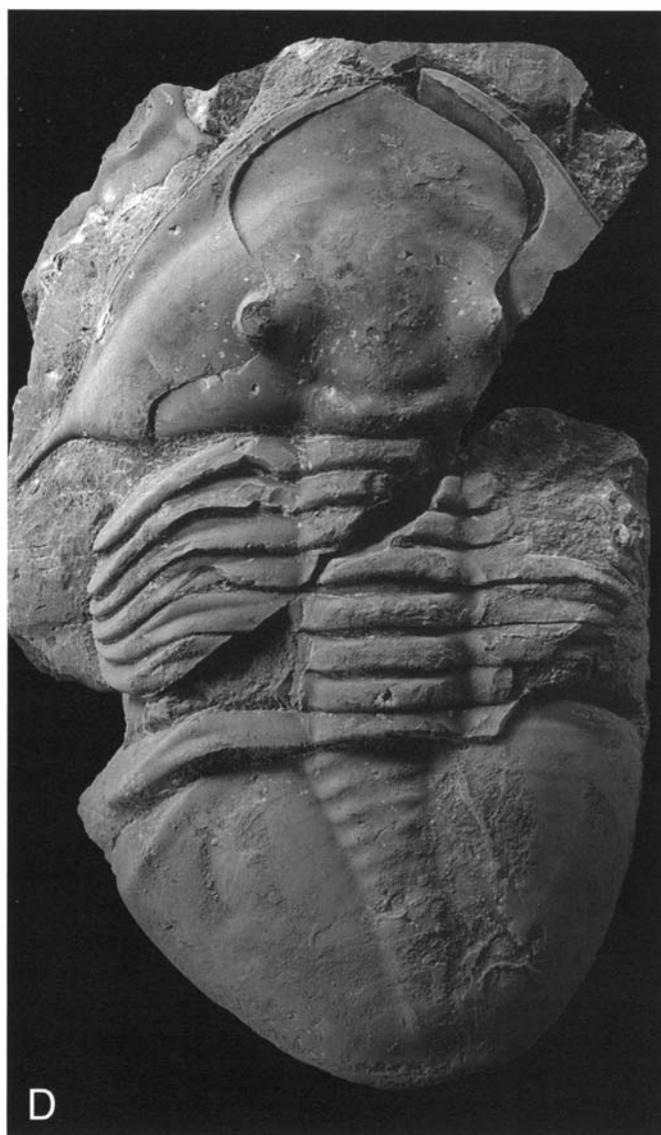
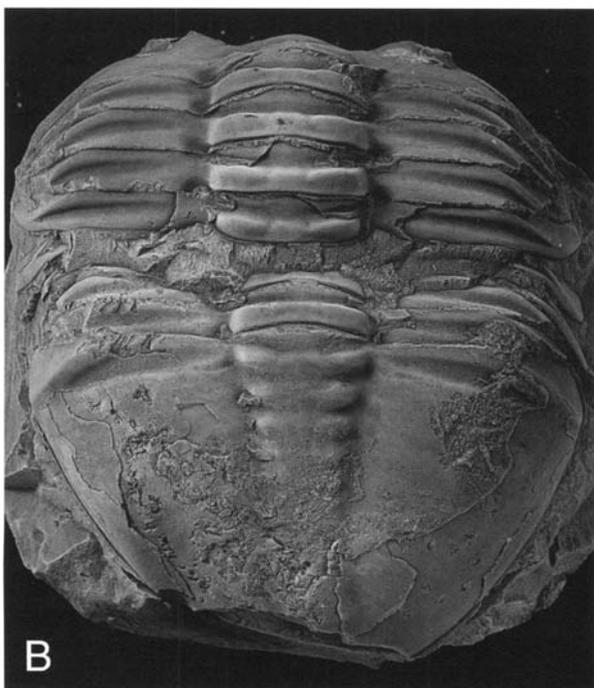
Occurrence. – *M. polyphemus* is quite frequent in beds –21 to –13 (lower part) at Skelbro; the range defines the *M. polyphemus* Zone. The listed GM and IK samples are from bed interval –19 to –14 of Bornholm, except for pygidium GM 1874.32, which is from bed –20; complete specimen GM 1883.802 most likely derives from bed interval –17 to –14. A poor pygidium, possibly representing *M. polyphemus*, was found in the basal limestone bed at Gislövshammar (not numbered).

PMO 94538 was collected from the uppermost limestone nodule level of the Tøyen Shale, 3–5 cm below the Hukodden Limestone in the ‘Graptolite Valley’ at Slemmestad (Bruton coll.). Cranidium PMO 604 is from the basal bed of the Hukodden Limestone at Bjerkåsholmen, 3–5 cm above the base (Tjernvik coll.). The holotype, PMO 66398, is from an unknown locality of the Oslo Region (Brögger 1882); the very characteristic lithology of the sizeable sample leaves no doubt that the specimen is from 4 to 9 cm above the base of bed M-1, most likely from a locality in the central Oslo-Asker area.

Complete specimen Ar 16169 is from Östergötland, central Sweden.

M. polyphemus is characteristic of the *M. polyphemus* Zone of Sweden (cf. Tjernvik 1980), and it most likely occurs also in Zone BIII α of the eastern Baltic area (cf. Balashova 1976).

Description. – See also Brögger (1882), Törnquist (1884), Schmidt (1906), and Tjernvik (1980). Very large, broad species, outstretched length of holotype ca. 200–210 mm; original length of largest isolated cranidium about 45 mm (holotype ca. 62 mm), length of largest isolated pygidium 66 mm (holotype damaged, but pygidium was about 70–72 mm long). Cephalon broadly parabolic in outline, L:W ratio slightly below 0.6. Cranidium pronouncedly wide (tr.), PW:L ratio about 0.8–0.85 in a specimen from the Komstad Limestone and in complete specimen Ar 16169, 0.9–0.95 in the Norwegian specimens; FW:L ratio estimated at about 1.4 in a fragmentary cranidium from the Komstad Limestone, 1.34 in the Swedish specimen and 1.45 in the holotype. Sagittal cranidial relief moderate to low. Glabella broad, usually somewhat forward-expanding and, consequently, slightly pyriform in outline, most pronouncedly so in the Bornholm–Norwegian material; glabellar front gently rounded, separated from frontal area by a fairly defined preglabellar furrow. Glabella comparatively little inflated, and stretches (including occipital ring) for about 0.7 of the cranidial length. Lateral parts of anterior fixigenae gently depressed; mesial impression in frontal area distinct. Lateral glabellar furrows very shallow, even on internal moulds; occipital furrow deepest laterally; occipital ring wide (sag.), rather prominent, raised above rear part of glabella. Bacculae slightly to moderately inflated, best defined on internal moulds. No border furrow on posterior fixigena. Length of palpebral lobes (exsag.) estimated to equal about 0.15 of the cranidial length in the Bornholm–Norwegian material, slightly less in the Swedish specimen; the lobes are barely elevated above glabella. Distance from posterior cranidial margin to hind corner of palpebral lobe seems to be from about 1.2 times the lobe length in smaller cranidia (about 40 mm long) to 1.8 in the holotype; the Swedish specimen has very small lobes, so the distance to posterior margin is almost 2 times the lobe length. Anterior branches of facial suture diverge in front of eyes at an angle of about 30° to sagittal line, then converge at an angle of about 120° to sagittal line, to meet angularly. Posterior branches of facial suture curve



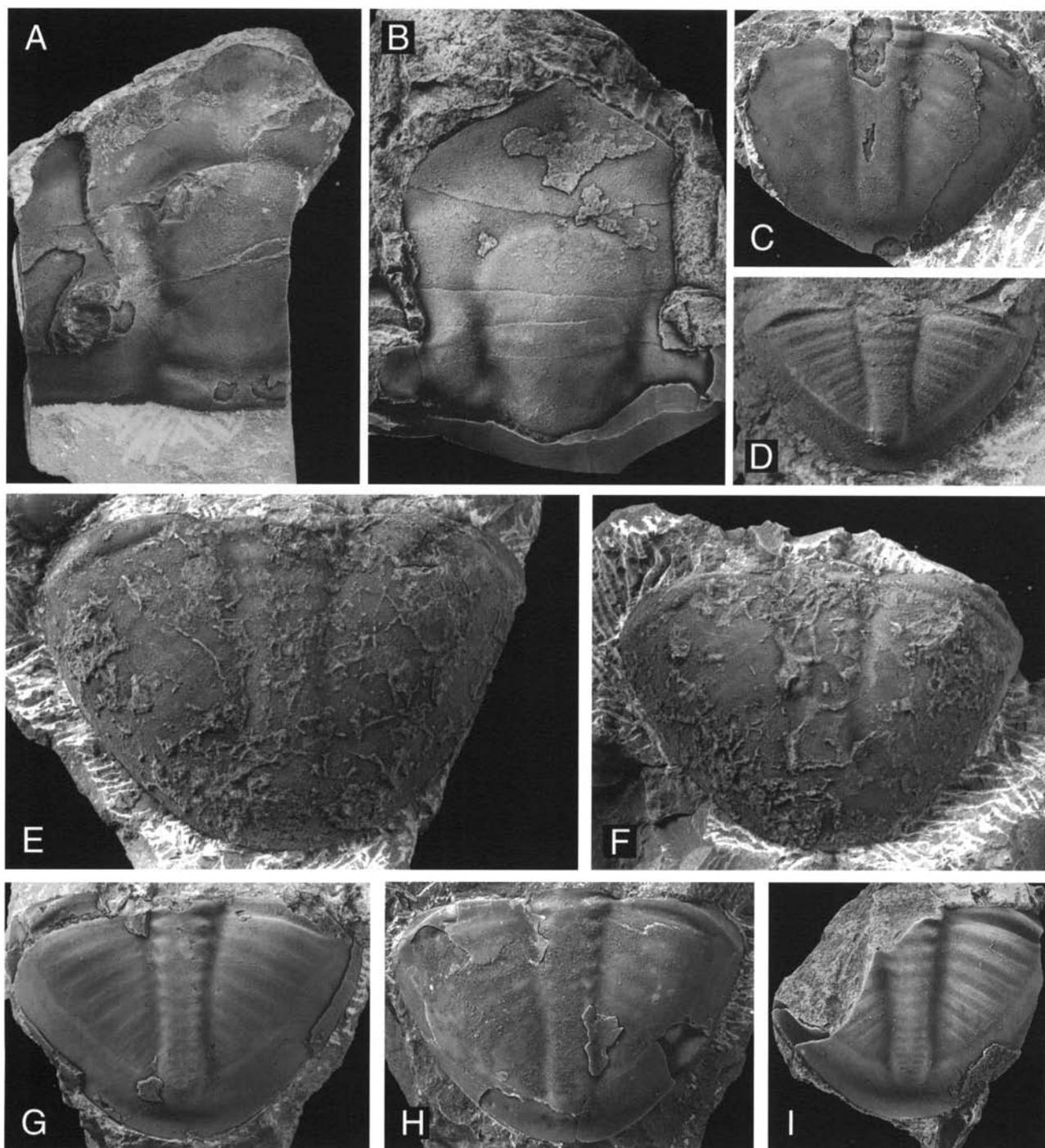


Fig. 109. *Megistaspis (M.) polyphemus* Brögger, 1882. □A. Fragmentary cephalon, $\times 1.5$. PMO 604, bed M-1, Bjerkåsholmen, Slemmestad (coll. T. Tjernvik). □B. Latex cast of fragmentary cranidium, $\times 1.5$. MGUH 22.505 (S 297), bed -20, Skelbro. □C. Small pygidium showing lateral border, $\times 1.5$. MGUH 22.506 (S 295), bed -20, Skelbro. □D. Internal mould of juvenile pygidium showing well-defined lateral border, $\times 6$. MGUH 22.507 (S 60), bed -21, Skelbro. □E-F. Pygidia attacked by bio-erosion, $\times 1$. MGUH 22.508 (S 722 [E]), MGUH 22.509 (S 715 [F]), bed -15, Skelbro. □G. Internal mould of pygidium, $\times 1$. MGUH 22.510 (S 1773), bed -21, Skelbro. □H. Internal mould of pygidium, $\times 1$. MGUH 22.511 (S 70), bed -21, Skelbro. □I. Internal mould of small pygidium showing posterolateral border, $\times 2.5$. MGUH 22.512 (GM 1871.1003), bed 21, Skelbro.

Fig. 108 (opposite page). *Megistaspis (M.) polyphemus* Brögger, 1882. □A-B. Holotype, complete specimen, cephalon $\times 1$, pygidium $\times 0.75$. PMO 66 398, bed M-1, unknown locality, Oslo area. Previously figured by Brögger (1882, Textfigs. 2-3) and Skjeseth (1952, Pl. 1:2, 5, 6). □C. Complete specimen, $\times 0.75$. MGUH 22.503 (GM 1883.802), locality unknown, Bornholm. □D. Complete specimen, $\times 1$. Ar 16169, Berg, Östergötland. Previously figured by Tjernvik & Johansson (1980, Fig. 8L). □E. Internal mould of pygidium, $\times 1$. MGUH 22.504 (S 1681a), bed -21, Skelbro.

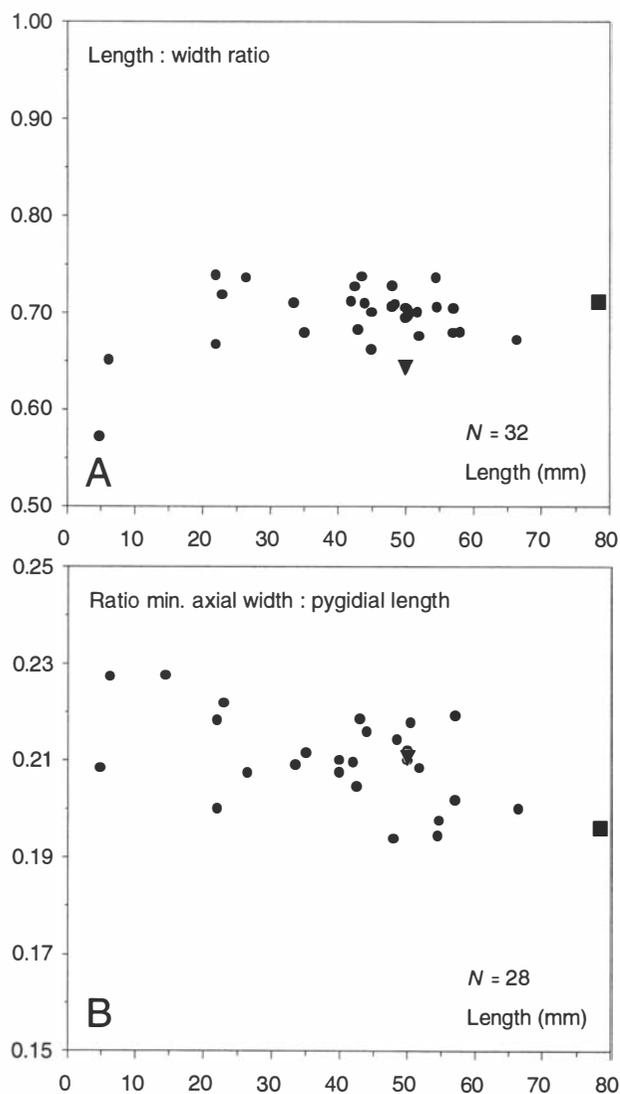


Fig. 110. Pygidia of *Megistaspis (M.) polyphemus*. ■ = holotype, ▼ = Ar 16169 from Östergötland. □A. Ratio between length (sag.) and maximum width plotted against pygidial length. □B. Ratio between minimum axial width and pygidial length, plotted against pygidial length.

outwards from palpebral lobe, run almost straight outwards-backwards at an angle of ca. 110° to sagittal line, then bend sharply backwards and intersect posterior margin.

Librigena broad, sloping rather gently outwards; eye socle well-developed. Lateral border narrow, tapers rearwards, but almost reaches genal angle. Genal angle continues into a comparatively gracile, short spine, directed obliquely backwards-outwards (Fig. 108D).

Pygidium parabolic in outline, L:W ratio varies between 0.66 and 0.74 for pygidia more than 20 mm long (mean 0.70; $N = 29$, see Fig. 110A). Axis delimited by deeply impressed axial furrows; anterior half tapers gently in posterior direction, posterior half approximately parallel-sided, but the terminal portion may be very slightly expanded; because of

the comparatively inconspicuous axial constriction, the axis appears broad, but minimum axial width varies between 0.19 and 0.23 of the pygidial length (mean 0.21; $N = 27$) like in *M. limbata*. The ratio is slightly growth related (Fig. 110B). Axial segmentation indicated by paired low lateral swellings, the sagittal axial area is smooth, even on internal moulds; only the anterior one or two axial rings are fully developed. Number of axial and pleural segments and outline of pleural fields as described for *M. limbata*. Border outline variable (see description of juveniles below); large pygidia typically show a rather narrow concave border only postaxially, whereas lateral parts of pygidium are confluent with pleural fields. Doublure poorly exposed in the available material.

Juveniles. – Two tiny juvenile pygidia (S 60 and S 388), 4.7 and 5.7 mm long, differ from the adult pygidia by being more strongly vaulted and relatively broader, L:W ratios are 0.57–0.59 (Fig. 110A), axis is more prominent and significantly raised above pleural fields, axial and pleural segmentation is more distinct, and a well-defined concave border extends all the way to articulating facets (Fig. 109D); anterolateral part of border is, however, rather steep. A 14.5 mm long pygidium shows a L:W ratio of 0.66; axis is still fairly vaulted, and the pleural segmentation is slightly better marked than in adult specimens (Fig. 109I). Anterolateral corners damaged, but a concave border extends forwards to the limit of the preserved parts, but rather likely extended further forwards. Three out of four pygidia, 22–26.5 mm long, have a narrow, rather steep concave border extending forwards to about midlength of pygidium (Fig. 109C).

Affinities. – The large-sized *M. polyphemus* is separated from other species of *M. (Megistaspis)* by its size, comparatively pronounced broadness, little inflated glabella, small eyes, lack of posterior border furrow, gracile genal spines, inconspicuous axial constriction of pygidium and rather narrow postaxial border. The phylogenetic relations of the *M. (Megistaspis)* group are uncertain, but *M. polyphemus* appears closest to *M. limbata* and *M. simon*.

Remarks. – The stratigraphic provenance of the holotype has been the object of some discussion (cf. Brögger 1882; Skjeseth 1952). The specimen is embedded in a fine-grained, compact, light grey limestone, containing common small pyrite nodules, and the sample undoubtedly represents the basal limestone bed of the Hukodden Limestone. The characteristic lithology is distinctly different from the remaining limestone beds of the Hukodden Limestone, as well as from the limestone nodules of the Herramb Member (cf. Skjeseth 1952). Two additional specimens of *M. polyphemus* have been found in the Slemmestad area at the same level (PMO 94538 and PMO 604 (Fig. 109A)).

The sparse material from Herramb, identified with *M. polyphemus* by Skjeseth (1952), is too poorly preserved to be confidently assigned to species, but the original assignment is questioned. The librigena has a prominent genal spine, quite unlike *M. polyphemus*, and is overall very similar to *M. (P.)*

estonica. However, the librigena of *M. ringsakerensis* is unknown, and it cannot be excluded that the specimen in question represents that species. The associated fragmentary pygidial doublure is considerably broader than *M. ringsakerensis*, and reminds strongly of *M. (P.) estonica*.

M. polyphemus (Brögger, 1882) is considered a senior synonym of *M. lata* (Törnquist, 1884); the likeness of these species is obvious from Fig. 108. The only established difference between the southern Norwegian-Bornholm *M. polyphemus* and the Swedish *M. 'lata'* is the size of the eyes. The significance and variability of this feature is uncertain, but it hardly justifies a separation at the species level.

Schmidt (1906) regarded *M. limbata* var. *lata* Törnquist, 1884 as a variant of *M. polyphemus*, and to which he introduced the name var. *Törnquisti*. Brögger (1882), Törnquist (1884), Schmidt (1881 *et seq.*) and other contemporaneous authors used the designations *lata*, *elongata*, *minor*, *major*, *maxima*, *typica* etc. as informal descriptive designations, which explains the introduction of a proper (!) name to *M. limbata* var. *lata* by Schmidt (1906). However, in a modern taxonomic interpretation var. *Törnquisti* Schmidt must be treated as a subjective synonym of var. *lata* Törnquist (see Jaanusson 1956a).

Schmidt (1906) also attributed a var. *minor*, a var. *Laman-skii* and a var. *Knyrkoi* to *M. polyphemus*, all of which were later renamed by Jaanusson (1956a) (= *M. (M.) lepikuensis*, *M. (M.) ingeriensis* and *M. (M.) laine*). According to Schmidt (1906, p. 23) the *M. polyphemus* group is characterized by a highly arched thoracic axis, an elongate mesial impression in the frontal area, a very narrow lateral cephalic border, absence of a posterior cephalic border furrow (= occipital furrow *sensu* Schmidt), and by having an evenly vaulted glabella without protuberance and generally without a tubercle. In Schmidt's interpretation the main character separating the *M. polyphemus* group from *M. limbata* is the absence of a cephalic posterior border furrow. The *M. polyphemus* group, occurring in BII α –BII γ , was regarded as the forerunner of the *M. hyorrhina* group (Schmidt 1906, p. 23). These ideas were adopted by Balashova (1976), who erected *M. (Megistaspinus)* to accommodate *M. polyphemus* (Brögger), *M. lepikuensis* Jaanusson, *M. ingeriensis* Jaanusson, *M. laine* Jaanusson and *M. lawae* (Schmidt). However, the '*M. polyphemus* group' comprises a medley of not closely related species in my interpretation. *M. lepikuensis* Jaanusson appears based on juvenile specimens of *M. polyphemus*, as, in fact, suspected also by Schmidt (1906, pp. 25–27). The claimed diagnostic characters, small size, marked elevation of the palpebral lobes, strong sagittal cephalic relief, distinct and well-defined lateral cephalic border, and presence of a well-developed pygidial border are all typical juvenile features. *M. (M.) ingeriensis* Jaanusson is close or identical to *M. simon*, but the original material is probably mixed (see introductory discussion, and remarks on *M. simon*). *M. laine* Jaanusson is younger and much different from the remaining 'variants' assigned to *M. polyphemus*; it resembles the

early members of *M. (Megistaspidella)*. The original assignment of *laine* [*M. p.* var. *Knyrkoi* Schmidt] to *polyphemus* was based on the presence of a longitudinal depression in the frontal area – the name '*polyphemus*' alludes to the presence of a depression in the frontal area (Brögger 1882) – but this plesiomorphic feature, which seems to reflect the ventral median suture, is present in several megistaspid species, and is of no diagnostic value.

M. lawae (Schmidt), assigned to *M. (Megistaspinus)* by Balashova (1976) – not included in the *M. polyphemus* group by Schmidt (1906) – was originally established to contain a single, rather small entire specimen (see Schmidt 1906); Balashova (1976) listed an additional cranidium. *M. lawae* is very similar to *M. limbata*, except that the glabella is unusually short; the species is certainly a member of *M. (Megistaspis)* Jaanusson, but hardly close to *M. polyphemus*.

The variable border morphology of *M. polyphemus*, noted already by Törnquist (1884, p. 93), may cause identification problems. Balashova (1976) actually stated that *M. (Megistaspis) lata* differs from *M. (Megistaspinus) polyphemus* by exhibiting a pygidial border extending all the way forwards, but this is not so. Smaller pygidia occasionally has a concave border extending to just behind articulating facets, but the border is steeper and narrower than in representatives of the preceding *M. (Paramegistaspis)* group. The largest pygidia seen with a forwards extending concave border are about 30 mm long (sampled from the lower part of the *M. polyphemus* Zone on southern Öland).

The fragmentary megistaspid material from the Finngrundet drill-core, determined by Tjernvik (1980), has been reexamined. The earliest specimen of *M. polyphemus*, which in my opinion can be confidently identified, is a cranidium from level 56.6 m in the core (cf. Tjernvik 1980, Fig. 4). A pygidium from 56.4 m most likely belongs to *M. limbata* type 7. The pygidium found at 57.7 m (cf. Tjernvik 1980, Fig. 4) has a broad and well-defined anterolateral border and belongs to *M. (P.) estonica*; the specimen definitely cannot represent *M. polyphemus*. The tiny anterior fragment of a megistaspid pygidium from level 57.9–58.0 m is impossible to identify even at the subgenus level (cf. Tjernvik 1980, Fig. 4), and cannot be taken as biostratigraphical evidence. It follows that the boundary between the *M. estonica* and *M. polyphemus* Zones is at 56.6–56.7 m in the Finngrundet core, lithologically indicated by a series of yellow-stained discontinuity surfaces.

A pygidium, tentatively assigned to *M. limbata* by Bohlin (1955, Textfig. 3; Pl. 5:1), was later referred to as *M. limbata lata* by Tjernvik (1956, p. 155). This specimen, however, belongs to *M. estonica*. It is misplaced in Textfig. 3 of Bohlin 1955; the correct level is 37.4 m (also apparent from the text to Bohlin 1955, Pl. 5:1). The changed identification suggests that the supposed 'bloody layer' in the Böda Hamn core at 36.85–36.95 m (cf. Bohlin 1955, p. 117 and Textfig. 2) corresponds instead to the 'flowery sheet' i.e. the base of the Volkhov Stage.

Megistaspis (Megistaspis) simon Tjernvik, 1980

Figs. 111–113

Synonymy. – □cf. 1906 *Megalaspis polyphemus* var. *Lamanskiim*. [*partim*] – Schmidt, pp. 27–29; ?Textfig. 8; Pl. 2:8; non Pl. 2:7 [unnamed] (description, occurrence, illustrations of cephalon [holotype of *M. (M.) ingeriensis* Jaanusson] and hypostome). □v 1936 *Megalaspis limbata* Sars & Boeck [*partim*] – C. Poulsen, pp. 48, 50 (listed). □cf. 1956a *Megistaspis (Megistaspis) ingeriensis* n.nom. [*partim*] – Jaanusson, pp. 69–70 (renaming of *M. polyphemus* var. *Lamanski* Schmidt, 1906; designation of lectotype). □1980 *Megistaspis (Megistaspis) simon* n.sp. – Tjernvik, pp. 189, 191, 192, 199; Figs. 7C, 9B–D (diagnosis, occurrence, photographs and drawings of cranidium and pygidium).

Holotype. – Exfoliated small cranidium, SGU Ac 5; a cast is figured by Tjernvik (1980, Fig. 9B–C.).

Material. – One cephalon (juvenile), 4 cranidia, 3 librigenae and 38 pygidia, plus 1 cranidium and 4 pygidia, referred to as *M. (M.) cf. simon*.

List of material. – □Cephalon A 10 (im) (juvenile) [MGUH 22.514]. □Cranidia A 705? (pim), A 709 (im), A 715 (im) [MGUH 22.513], A 746 (im). □Librigenae (All tentatively identified) A 666 (t), A 711 (im), A 778 (im). □Pygidia S 776b (c), S 805 (pim) [MGUH 22.521], S 930 (c), K 88 (c), K 382 (c), K 390 (c) [MGUH 22.525], K 411 (c) [MGUH 22.520], K 543 (c), K 604 (c), K 610 (c) [MGUH 22.516], K 728a (c), K 1349 (c), GM 1988.22 (t) [MGUH 22.523], GM 1888.300 (im) [MGUH 22.515], LU 18b? (im), LU 32a (c), LU 32b (c), LU 41? (im), LU 43b (c), LU 48b (im), LU 49b (im), LU 51a (c), LU 51b (c), LU 69? (im), LU 73 (im), LU 77 (im), A 3 (em), A 6? (im) [MGUH 22.517], A 8 (im), A 20 (pim) [MGUH 22.518], A 700 (im), A 707a (pim), A 707b (im) [MGUH 22.524], A 710 (im), A 721 (im), A 724 (im) [MGUH 22.519], A 732? (im), A 747 (im).

Additional material. – [‘Extra-zonal’ *M. (M.) cf. simon*] □Cranidium A 1024 (im). □Pygidia S 1671 (pim) [MGUH 22.522], A 961b (im), A 976 (pim), A 1055b (c) [MGUH 22.526].

Occurrence. – *M. (M.) simon* is uncommon in the Komstad Limestone at Skelbro, and only a few pygidia have been found in bed interval –13 (upper part) to –5, forming the main part of the *M. simon* Zone. Pygidia GM 1988.22 and GM 1888.300 are from Skelbro, probably bed interval –10 to –13 (most likely bed –10 or –12). A poorly preserved pygidium (S 1671) from bed –15 at Skelbro is referred to as *M. (M.) cf. simon*; this bed is within the *M. polyphemus* Zone.

M. (M.) simon is more frequent in the *M. simon* Zone of SE Scania, where it has been found at Gårdlösa-1 (bed M), Gårdlösa-4a (bed interval 3 to 10) and Killeröd (beds nos. –7 and –6). The listed museum specimens (LU nos.) come from Andrarum, Smedstorp and Komstad. The materials from Andrarum and Smedstorp were collected from loose blocks and cannot be assigned to level, whereas the specimens from Komstad derive from an interval corresponding to beds –10 to –1 at Killeröd, as shown by the lithology. A single pygidium from Gislövshammar originate according to the label from the basal bed of the Komstad Limestone.

M. (M.) simon is fairly frequent in bed interval M-2 to M-6 at Slemmestad, i.e. *M. simon* Zone. Furthermore, three ‘*simon*-type’ pygidia have been found in beds M-9, M-10 and M-13, and a fragmentary cranidium from bed M-11 may also be of *M. ‘simon*-type’. Beds M-9 to M-13 belong to the lower part of the *M. limbata* Zone. The late specimens are treated as *M. (M.) cf. simon*. Additional extra-zonal *simon*-type pygidia are described as *Megistaspis* sp. A.

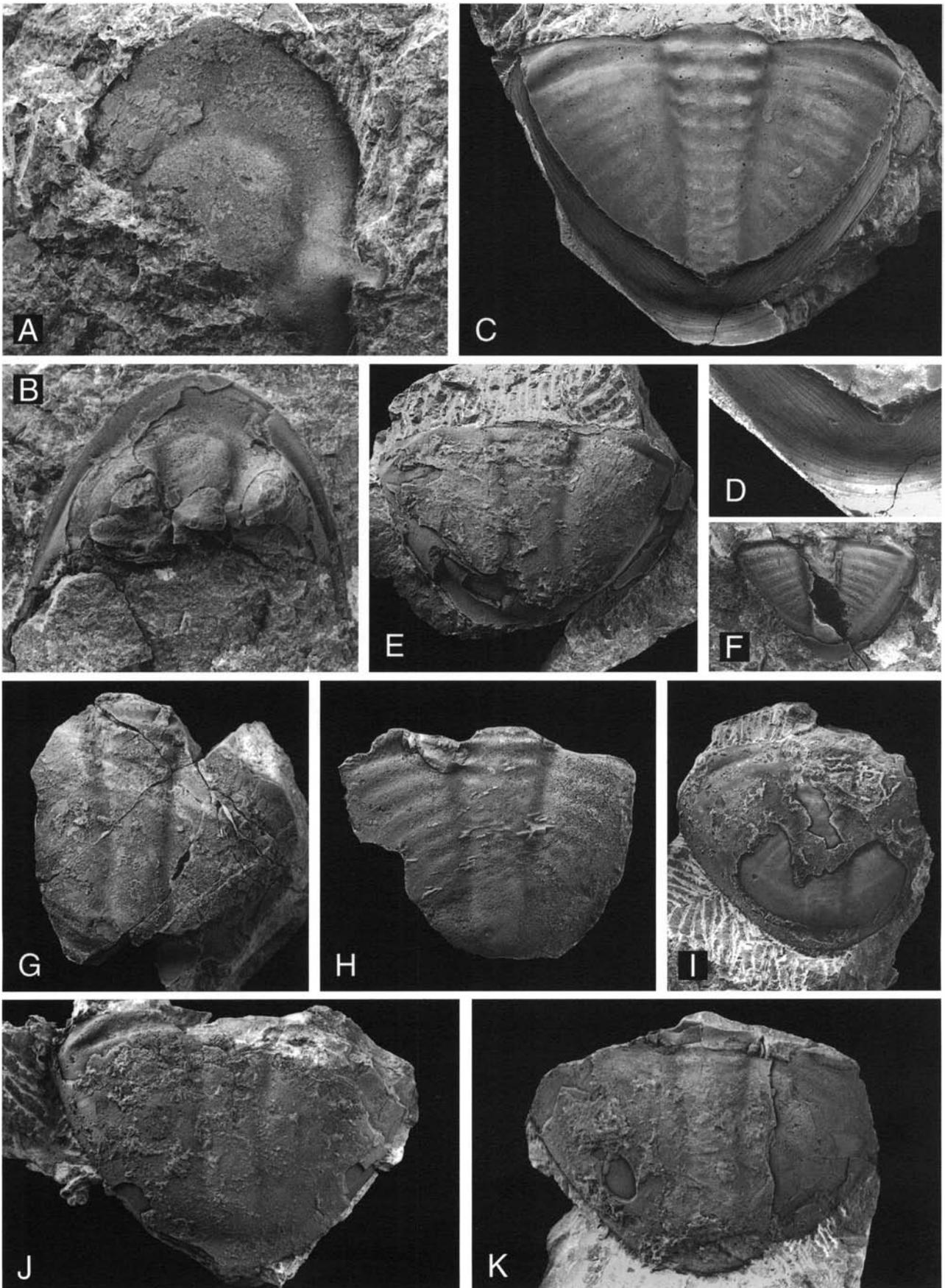
Description. – The observations are complementary to the description published by Tjernvik (1980, p. 199). Medium-sized to large species, largest cranidium ca. 40 mm long, largest pygidium 57 mm long. A 12 mm long cephalon has a stronger sagittal relief, a flatter, almost horizontal frontal area, a better defined lateral border and higher elevated palpebral lobes than adults (Fig. 111B).

L:W ratio of adult pygidia from the Komstad Limestone varies between 0.64 and 0.82 (mean 0.70; $N = 24$), while pygidia from the Hukodden Limestone are narrower, showing L:W ratios between 0.64 and 0.77 (mean 0.72; $N = 8$) (Fig. 113A). Minimum width of axis, approximately at axial ring nos. 8–9, is equivalent to 0.21–0.26 of the pygidial length in pygidia from the Komstad Limestone (mean 0.23; $N = 24$), and to 0.20–0.26 of the pygidial length (mean 0.23; $N = 14$), in pygidia from Slemmestad. Pygidial doublure basically as in *M. limbata* (Fig. 111C), but the terrace lines are less densely spaced and more delicate, though still distinctly impressed; there seem to be about 15 lines across the doublure at pygidial midlength. Behind axis the lines are U-shaped in dorsal view, turned sharply backwards only close to sagittal line.

A juvenile pygidium, 9.7 mm long, has a L:W ratio of 0.67, and shows a strongly inflated axis, distinctly raised above pleural fields, a fairly pronounced segmentation of the pleural fields, and a gently concave border extending all the way to just behind articulating facets (Fig. 111F).

Affinities. – Isolated pygidia of *M. simon* may occasionally be difficult to distinguish from *M. limbata*, but are, at least in the Komstad Limestone, typically broader, besides generally having a broader axis (compare Figs. 111–112 with Fig. 98).

Fig. 111. □A–H, J–K. *Megistaspis (M.) simon* Tjernvik, 1980. □A. Latex cast of fragmentary cranidium, ×2. MGUH 22.513 (A 715), bed M-5, Slemmestad. □B. Juvenile cephalon, ×3. MGUH 22.514 (A 10), bed M-3, Slemmestad. □C–D. Internal mould of pygidium showing doublure. C ×1, D close-up of postaxial area, ×2. MGUH 22.515 (GM 1888.300), Skelbro. □E. Corroded pygidium, ×1. MGUH 22.516 (K 610), bed 11, Gårdlösa-4a. □F. Internal mould of juvenile pygidium showing lateral border all the way, ×2.5. MGUH 22.517 (A 6), bed M-3, Slemmestad. □G. Fragmentary internal mould of pygidium, ×1. MGUH 22.518 (A 20), bed M-6, Slemmestad. □H. Internal mould of small pygidium, ×2. MGUH 22.519 (A 724), bed M-5, Slemmestad. □J. Corroded pygidium, ×1. MGUH 22.520 (K 411), bed M, Gårdlösa-1. □K. Corroded pygidium, ×1. MGUH 22.521 (S 805), bed –11, Skelbro. □L. *Megistaspis (M.) aff. simon* Tjernvik, 1980. Somewhat corroded pygidium, ×1. MGUH 22.522 (S 1671), bed –15, Skelbro.



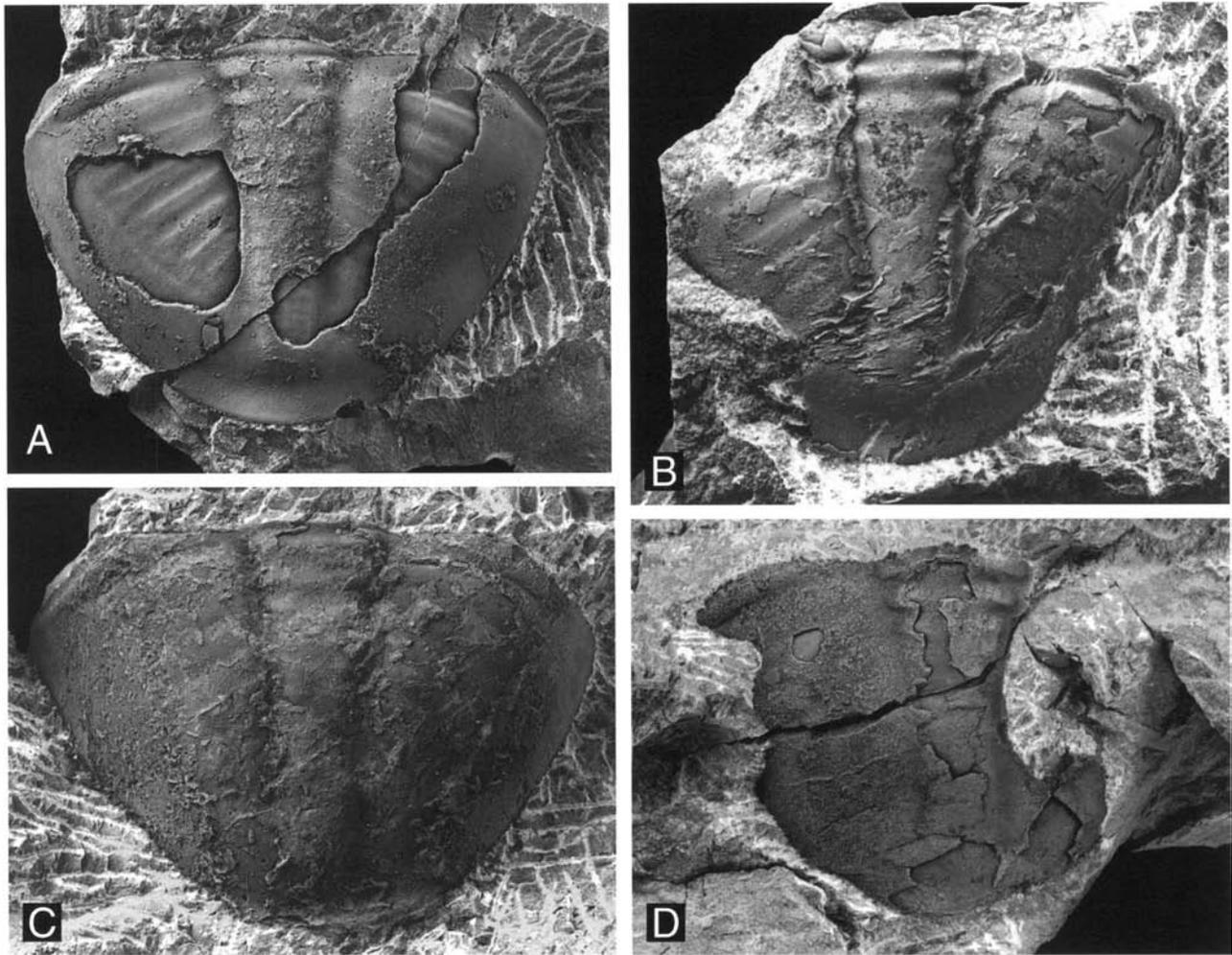


Fig. 112. □A–C. *Megistaspis (M.) simon* Tjernvik, 1980. □A. Partly exfoliated pygidium, $\times 1.2$. MGUH 22.523 (GM 1988.22), Vasegård, Bornholm. □B. Fragmentary internal mould of small pygidium, $\times 2.5$. MGUH 22.524 (A 707b), bed M-4, Slemmestad. □C. Corroded, comparatively narrow pygidium, $\times 1.2$. MGUH 22.525 (K 390), bed-7, Killeröd. □D. *Megistaspis (M.)* aff. *simon* Tjernvik, 1980. Corroded, fragmentary pygidium, $\times 1.2$. MGUH 22.526 (A 1055), bed M-13, Slemmestad.

M. lawae has a very short glabella, stretching for about 0.6 of the cranidial length, and its cranidium is in gross outline rather 'simon-like' although being slightly more elongate. The *M. lawae* pygidium is certainly not of 'simon-type', showing a narrow axis, and it resembles *M. limbata*. The relations between *M. lawae*, *M. simon* and *M. limbata* are obscure.

Remarks. – *M. (M.) simon* is diagnosed by the short, rather broad glabella, and by the broad pygidial axis, which, however, appears less prominent in the rather broad pygidia here assigned to *M. simon*, than in the relatively narrow pygidia figured by Tjernvik (1980, Figs. 7C and 9D), showing L:W ratios of about 0.75. Because of the variable pygidial width, the ratio axial width vs. length of pygidium is found to be a more stable measure. In the material at hand this ratio averages 0.23, which is in accordance with the *simon* pygidia illustrated by Tjernvik (1980).

Tjernvik (1980, p. 191) mentioned that pygidia with a broad axis occur already in the lower half of the *M. lata* [*polyphemus*] Zone; I have found rare 'simon-type' pygidia in the upper part of the *M. polyphemus* Zone, throughout the *M. limbata* Zone, and in the basal part of the *A. expansus* Zone (see *Megistaspis (M.)* sp. A). Stratigraphical interpretations should, accordingly, not be based on isolated pygidia of *M. simon* (s.l.), although the species certainly is most common in the *M. simon* Zone. 'Extra-zonal' *M. simon* cranidia are unknown, except for a damaged specimen from bed M-11 at Slemmestad, tentatively identified with *M. (M.) cf. simon*, because of its short and relatively broad glabella.

A complete specimen from BII α , identified with *M. (M.) ingeriensis* by Balashova (1976, pp. 88–89, Pl. 20:4a–b), has a pygidium with a seemingly very broad axis; the minimum axial width is approximately equivalent to about 0.28 of the pygidial length (cf. Balashova 1976, Pl. 20:4a–b). The cepha-

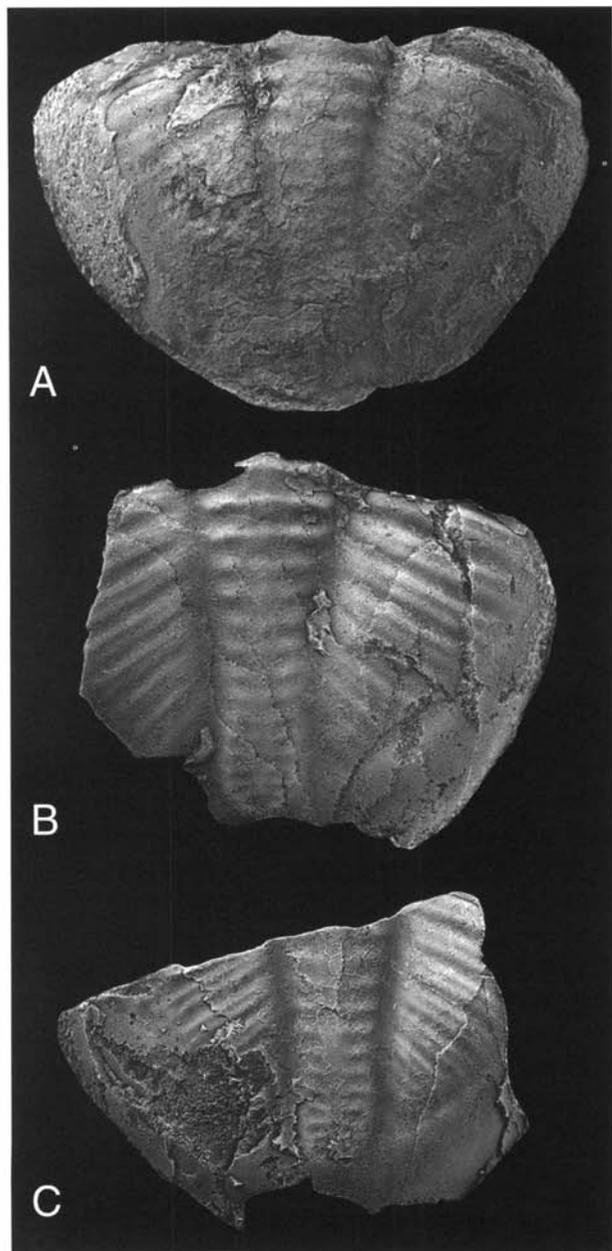


Fig. 114. *Megistaspis* (*M.*) sp. A. □A. Corroded pygidium, $\times 1.2$. MGUH 22.527 (K 412), bed +13, Killeröd. □B. Internal mould of pygidium, $\times 1.2$. MGUH 22.528 (S 1682), bed +13, Skelbro. □C. Fragmentary internal mould of pygidium, $\times 1.2$. MGUH 22.529 (S 1535), bed +13, Skelbro.

(1980), except for the lack of a concave border. Sp. A in fact more closely resemble *M. (M.) simon sensu* Tjernvik than the pygidia of *M. (M.) simon* from the *M. simon* Zone of the Komstad Limestone, because of the circumstance that the latter specimens are relatively broad, hence the axis appears less prominent.

The long range of *M. simon* (*s.l.*) (see remarks on *M. simon*) may be taken to indicate that a *M. simon* branch

existed as a sister group to the *M. limbata* line, but it is for instance very puzzling that sp. A has no concave border and shows the same high number of axial rings and pleural ribs as the associated *M. geminus* n.sp. Speculations on a mutual cause remain purely notional, but either some kind of environmental affect on skeletal morphology may be inferred – or the broad-axed ‘*simon*-types’ just represent a special morph of the ‘standard’ species (*M. limbata s.l.* and *M. geminus* n.sp.). It seems unlikely, however, that the narrow/broad axed types represent sexual dimorphs, as *M. simon* generally is rare except in the *M. simon* Zone. *M. simon* types (*s.l.*) seem fairly consistently to be linked to shallow-water habitats.

Megistaspis (Rhinoferus) Balashova, 1976

pro *Rhinaspis* Remelé, 1885; non *Rhinaspis* Perty, 1830

Type species. – (OD) *Asaphus hyorrhinus* Leuchtenberg, 1843.

Megistaspis (Rhinoferus) cf. hyorrhina (Leuchtenberg, 1843)

Fig. 115

Synonymy. – (Key papers only, see Schmidt 1906 and Balashova 1976 for further references) □cf. 1906 *Megalaspis hyorrhina* [sic] Herz. v. Lencht. – Schmidt, pp. 31–36; Textfig. 12a–b; Pls. 2:10; 3:1–3, 5–8 (description, occurrence, illustrations of complete specimens, hypostome, cephalia, cranidium, pygidia). □cf. 1976 *Rhinoferus (Rhinoferus) hyorrhinus* (Leuchtenberg, 1843) – Balashova, pp. 107–108; Pl. 28:5 (description, occurrence, illustration of pygidium).

Lectotype. – Specimen figured by Leuchtenberg (1843, Pl. 1:4–5), listed as type by Balashova (1976).

Material. – One pygidium (A 181 (pim) [MGUH 22.530]).

Occurrence. – The specimen is from bed A-8 of the Lysaker Member, Slemmestad, which is close to the base of the upper subzone of the *M. limbata* Zone. *M. hyorrhina* occurs frequently in the BII γ zone of the eastern Baltic Region, but ranges from BII β (Balashova 1976); the species is also common in the *Lepidurus* Limestone of northern Öland (Tjernvik 1972), and occurs scattered in the *M. limbata* Zone of mainland Sweden (Tjernvik 1980). The species or a closely similar one also occurs in the *M. simon* Zone of northern Öland (unpublished).

Description. – The pygidium is about 77 mm long, parabolic in outline, L:W ratio slightly below 5:6. Axis gently arched, stretching for slightly less than 0.9 of the pygidial length, and anteriorly occupying about 0.25 of the pygidial width (tr.). Specimen gently compacted, but axis appears to be slightly

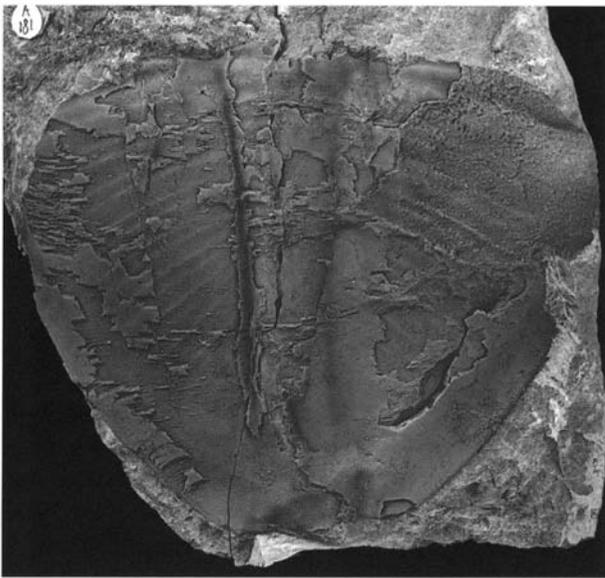


Fig. 115. *Megistaspis (Rhinoferus) cf. hyorrhina* (Leuchtenberg, 1843). Largely exfoliated pygidium, $\times 0.9$. MGUH 22.530 (A 181), bed A-8, Slemmestad.

raised above pleural fields anteriorly and posteriorly, and level with the adjacent pleural fields for the greater, middle part. Anterior $\frac{2}{3}$ of axis tapers, then it becomes roughly parallel-sided; terminal portion slightly expanded; segmentation vestigial. Minimum axial width, $\frac{2}{3}$ the length from front, equivalent to 0.17 of axial length, corresponding to slightly more than half of the axial width at anterior margin. Axis delimited by wide, moderately deep furrows. Segmentation of pleural fields rather faint, and indicated by raised double lines, of which the anterior line generally is more distinct than the posterior line; a total of 10 pairs is present, although the shortest posterior pair is rather effaced and visible only on the left exfoliated side of the pygidium. The lines stop at paradoublural line. A concave border is present all the way, but anterolateral parts are not preserved in the specimen. Border possibly steeper anteriorly to flatten rearwards; greatest width probably attained postaxially.

Remarks. – The pygidium corresponds in all preserved features to *M. hyorrhina* as described by Schmidt (1906) and Balashova (1976), but the isolated Norwegian specimen is treated as *M. (R.) cf. hyorrhina* in the absence of cephalic material. *M. hyorrhina* is a typical eastern Baltic species, which hitherto has been considered absent in the Oslo region (Tjernvik 1980, p. 189). The collection of the Paleontological Museum, Oslo, does, however, contain two more pygidia of *M. cf. hyorrhina* from the Lysaker Member.

Megistaspis (Rhinoferus?) cf. explanata Angelin, 1851

Fig. 116

Synonymy. – \square cf. 1851 *Megalaspis explanata*. n.sp. – Angelin, p. 17; Pl. 15:3 (brief diagnosis, occurrence, illustration of pygidium). \square ? 1882 *Meg. explanatæ*, Ang. aff. – Brögger, p. 77 (occurrence). \square v 1936 *Megalaspis cfr. explanata* Ang. – C. Poulsen, p. 48 (listed).

Type material. – Not designated.

Material. – One pygidium (GM 1984.1800 (pim) [MGUH 22.531]).

Occurrence. – The museum specimen is from Skelbro. A provenance from bed interval 0 to +9 seems most probable, and, tentatively, the pygidium may be assumed to originate from the lower part of the *M. limbata* Zone.

The rare species perhaps also occurs in the Lysaker Member of the Oslo region (Brögger 1882), i.e. *M. limbata* or *A. expansus* Zone, and Angelin (1851) reported it from Kinnekulle, Vestergötland (exact level unknown).

Description. – Pygidium 63 mm long, parabolic in outline; L:W ratio 3:4. Axis long and narrow, stretching for $\frac{5}{6}$ of the pygidial length, and anteriorly occupying about 0.2 of the pygidial width (tr.); it is slightly raised above the pleural fields, except for the central posterior portion, which is at level with the adjacent pleural fields. Axis tapers gently to axial ring no. 9 and then maintains a nearly constant width; axial width at midpoint is 0.7 of the anterior axial width. Axial segmentation fairly distinct (test intact), comprising at least 13 axial rings in addition to the terminal piece and anterior half-ring, but the true number of rings is presumably 14 or, less likely, 15. Axis delimited by wide, rather deep furrows. Ten pairs of well-defined pleural ribs (visible also in areas with preserved test) inside paradoublural line; each rib bifurcated by a shallow interpleural furrow. Concave border present all the way, except immediately behind articulating facets; it is steep anterolaterally to flatten rearwards; greatest width attained postaxially. Test surface of border region carries short, undulating, fine terrace lines with a density of 6–7 lines per 5 mm (Fig. 116B).

Remarks. – *M. explanata* Angelin is a *nomen dubium*. The rare species has, so far, been reported only from the western part of the Baltoscandian area, but the pygidium resembles that of the eastern Baltic *M. hyorrhina* group, and *M. explanata* is here tentatively assigned to *M. (Rhinoferus)*.

The pygidium at hand is similar to the pygidium figured by Angelin (1851, Pl. 15:3), but apparently has fewer axial rings and pleural ribs. Brögger (1882, p. 77) also noted the different number of pleural ribs between a fragmentary pygidium investigated by him, and the diagnosis stated by Angelin. This may indicate that the species is variable, or that the

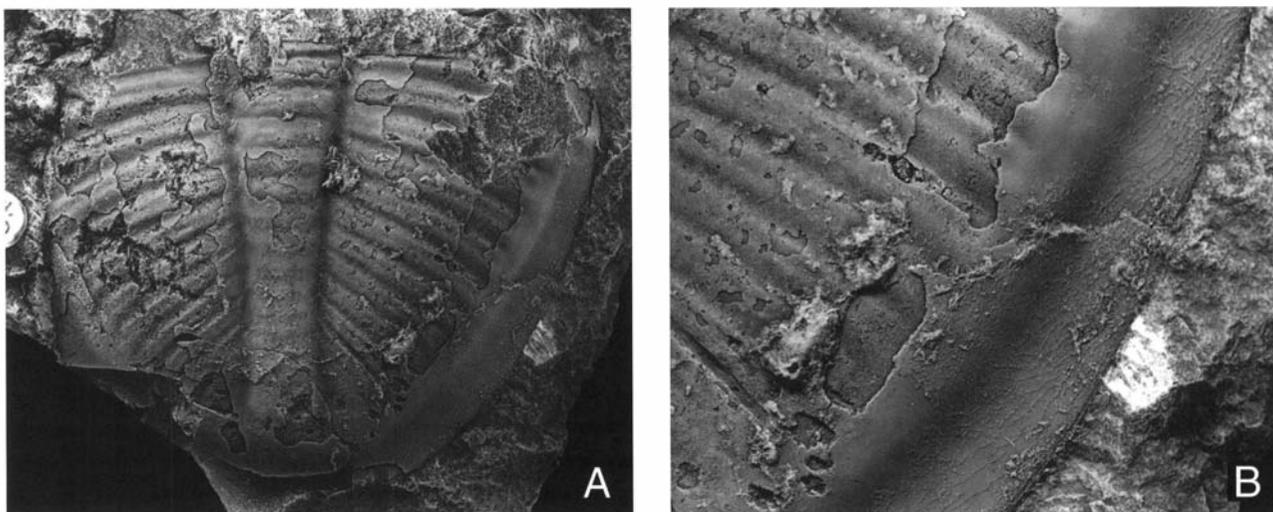


Fig. 116. *Megistaspis* (*Rhinoferus?*) cf. *explanata* (Angelin, 1851). □A. Pygidium, $\times 1$. MGUH 22.531 (GM 1984.1800), Skelbro. □B. Same pygidium, close-up of border region, showing fine terrace lines, $\times 2$.

reconstruction presented by Angelin is inaccurate, or that the sparse Scanian–Norwegian material does not belong to *M. explanata* (*s.str.*)

Megistaspis (*Megistaspidella*)

Jaanusson, 1956

Type species. – (OD) *Entomostracites extenuatus* Wahlenberg, 1821.

Megistaspis (*Megistaspidella*) *extenuata* (Wahlenberg, 1821)

Fig. 117

Synonymy. – □1851 *Megalaspis extenuata*. Wahl. – Angelin, p. 17; Pl. 15:1–1a (brief diagnosis, occurrence, illustrations of entire specimen and pygidium). □1882 *Megalaspis extenuata*, Wahlenberg – Brögger, p. 80 (occurrence). □1906 *Megalaspis extenuata* Dalman – Schmidt, pp. 49–51; Textfig. 28; Pl. 7:1–3 (description, occurrence, illustrations of three complete specimens). □v 1936 *Megalaspis acuticauda* Ang. – C. Poulsen, p. 48 (listed). □v 1956a *Megistaspis* (*Megistaspidella*) *extenuata* (Wahlenberg, 1821) – Jaanusson, pp. 71–73; Textfig. 2; Pl. 1:4–6 (discussion of subgenus, photographs and drawings of complete specimen [lectotype], cephalon, hypostomes). □v 1976 *Megistaspis* (*Megistaspidella*) *extenuata* (Wahlenberg) – Reymont, Fig. 26a–b (illustrations of complete specimen [lectotype]). □1976 *Megistaspidella* (*Megistaspidella*) *extenuata* (Wahlenberg, 1821) – Balashova, pp. 91–92; Pls. 22:3; 23:4; 26:1–3; 27:5–6; 30:5 (description, occurrence, illustrations of complete specimen, cephalon, librigena, hypostome, pygidia).

Lectotype. – Complete specimen Ög 1, figured by Wahlenberg 1821 (Pl. 7:4), designated and refigured by Jaanusson (1956a, Pl. 1:6); also figured by Reymont (1976, Fig. 26a–b).

Material. – One hypostoma, 5 pygidia (two of which are badly preserved).

List of material. – □Hypostoma LU 111 (pim). □Pygidia F 306 (im) [MGUH 22.532], F 307? (c), LU 29a (c), GM 1984.1805 (im/c), GM 1869.881 (im).

Occurrence. – *M. (M.) extenuata* has not been found *in situ* during the present study. Hypostome LU 111 and pygidium GM 1869.881 are from Fågelsång, and the lithology clearly points to a provenance from bed interval 18–22, i.e. the Zone of *A. expansus*. Pygidia F 306 (Fig. 117) and F 307 were collected from loose slabs at Fågelsång; the former is associated with *Asaphus* (*A.*) *acuminatus*, proving an origin from the lower part of the *A. expansus* Zone, and the sample almost certainly represents bed 19. Pygidium LU 29a is from the upper part of the Komstad Limestone at Tommarp (coll. Funkquist), i.e. probably the *A. expansus* Zone. As a matter of fact the specimen is presumably from the topmost 0.1 m of the limestone (cf. Funkquist 1919, p. 22). A rather poorly preserved specimen from Vasegård, GM 1984.1805, listed as *M. acuticauda* by C. Poulsen (1936), is undoubtedly from bed +13, and most likely from the uppermost part (*A. expansus* Zone).

Brögger (1882) stated that *M. extenuata* occurs infrequently in the upper part of the Lysaker Member of the Oslo area, i.e. *A. expansus* Zone; no new material of the species was found at Slemmestad.

M. (Megistaspidella) extenuata is known from the *A. expansus* Zone of Sweden (Jaanusson 1956a) and the East Baltic area (Schmidt 1906; Balashova 1976).

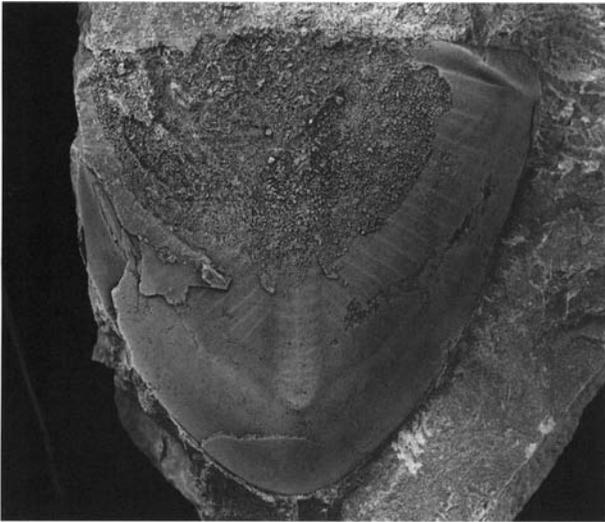


Fig. 117. *Megistaspis (Megistaspidella) extenuata* (Wahlenberg, 1821). Exfoliated, partly corroded pygidium, $\times 1$. MGUH 22.532 (F 306), Fågelsång.

Description. – The hypostome, 11.3 mm long including posterior projection, is fragmentary. Median body rounded, strongly inflated, body W:L ratio about 0.7–0.75. Weakly impressed premacular pits situated very close to rear end of median body; macular surfaces small, narrow, distinctly set off. Median body stretches for almost 0.9 of the hypostomal length, reaching hypostomal margin anteriorly. Anterior hypostomal margin rather straight in the main central part, then distally turns backwards almost at a right angle. Anterolateral margin flexed in ventral direction, forming an anterior border. Anterior wings ascend very strongly in dorsal direction, so the width across anterior wings is only about 0.8–0.85 of the hypostomal length. Lateral border starts ca. 0.4 of the hypostomal length from anterior margin, but is not preserved. Border furrow well-defined throughout, also behind median body. Posterior border narrow, consisting of a somewhat raised (ventral view) strip along posterior margin. Posterior hypostomal margin convex with a small mesial projection. Terrace ridges present anterolaterally on median body, whereas central and posterior part of the body as well as border furrows are smooth; remaining part of hypostome exfoliated. The specimen is not suited for illustration.

The limited new material of pygidia is in accordance with the descriptions published by Schmidt (1906) and Balashova (1976). Specimen F 306 (Fig. 117) is 61 mm long and about 67 mm wide.

Megistaspis (Megistaspidella) acuticauda (Angelin, 1854)

Fig. 118–119

Synonymy. – \square 1854 *Megalaspis acuticauda*. n.sp. – Angelin, p. 50; Pl. 27:4 (brief diagnosis, occurrence, illustration of

pygidium). \square v 1882 *Megalaspis limbata*, Boeck [*partim*] – Brögger, p. 79; Pl. 9:5 (brief description and illustration of hypostome *in situ*). \square 1882 *Megalaspis acuticauda*, Ang. – Brögger, pp. 82–85; Textfig. 5; Pls. 2:1, 1a; 6:1, 1a (description, occurrence, illustrations of complete specimens and pygidia). \square v non 1919 *Megalaspis acuticauda* Ang. – Funkquist, pp. 22, 39 [= *M. (M.) cf. spinulata*]. \square v non 1936 *Megalaspis acuticauda* Ang. – C. Poulsen, p. 48 [= *M. (M.) extenuata*]. \square 1960 *Megistaspis (Megistaspidella) acuticauda* (Angelin, 1854) – Bohlin, pp. 181–186; Textfigs. 17–20; Pl. 8:1–7 (description, occurrence, drawings and figures of cephalon, cranidium, librigenae, hypostome, pygidia). \square 1976 *Megistaspidella (Spinopyge) acuticauda* (Angelin, 1854) – Balashova, p. 104; Pls. 19:7; 23:1–2; 28:7; 29:2 (description of pygidium, occurrence, illustrations of complete specimen, hypostome and pygidia).

Neotype. – Pygidium Ar 21763, chosen and figured by Bohlin (1960, Pl. 8:6).

Material. – Four complete specimens, 5 cranidia, 2 librigenae and 16 pygidia.

List of material. – \square Complete specimens A 451 (pim), A 457 (pim), A 1114 (t) [MGUH 22.534], A 1163 (im/em) [MGUH 22.533]. \square Cranidia K 1133? (t) [MGUH 22.537], A 153 (pim), A 184 (pim), A 299 (t), A 302a (t) [MGUH 22.535]. \square Librigenae A 174 (im/c), A 303a (im/em). \square Pygidia K 1134? (im), K 1156? (t) [MGUH 22.538], K 1209 (im), A 116? (t), A 171 (im), A 320 (im), A 378 (im), A 405 (t) [MGUH 22.536], A 423 (pim), A 427 (im), A 430 (em), A 506 (im), A 545 (im), A 1088 (pim), A 1131 (im), A 1159 (im).

Occurrence. – *M. (Megistaspidella) acuticauda* (*s.l.*) ranges from the upper part of the *M. limbata* Zone and through the *A. expansus* Zone at Slemmestad. It has been found in beds A-4 to A-8, A-19, A-26 (Zone of *M. limbata*) and in beds A-29 to A-55 (Zone of *A. expansus*). The specimens from beds A-4 to A-8 are referred to as *M. cf. acuticauda* (see discussion below), whereas the remaining material is identified with *M. acuticauda (s.str.)*

M. acuticauda is rare in the Komstad Limestone, and has been found only at Killeröd site b in beds 7–8, which is within the lower part of the *A. 'raniceps'* Zone; this is an unusually late occurrence of the species. However, the material is poorly preserved, and is therefore referred to as *M. cf. acuticauda*. The species has previously been reported from the Komstad Limestone at Tommarp, Komstad (Funkquist 1919) and Vasegård (C. Poulsen 1936). The latter occurrence was based on a single poorly preserved pygidium, which belongs to *M. extenuata*, and *M. acuticauda sensu* Funkquist is here assigned to *M. cf. spinulata*.

M. acuticauda is known from the *A. expansus* Zone of Sweden (Tjernvik & Johansson 1980, p. 194), and is, according to Anderberg & Johansson (1981), especially frequent in the lower part of the zone which they actually separated as the *Acuticauda* Limestone; the same distribution is seen at Slemmestad. A form called *M. aff. acuticauda* was listed by Tjernvik & Johansson (1980, p. 192) from the *M. limbata* Zone of

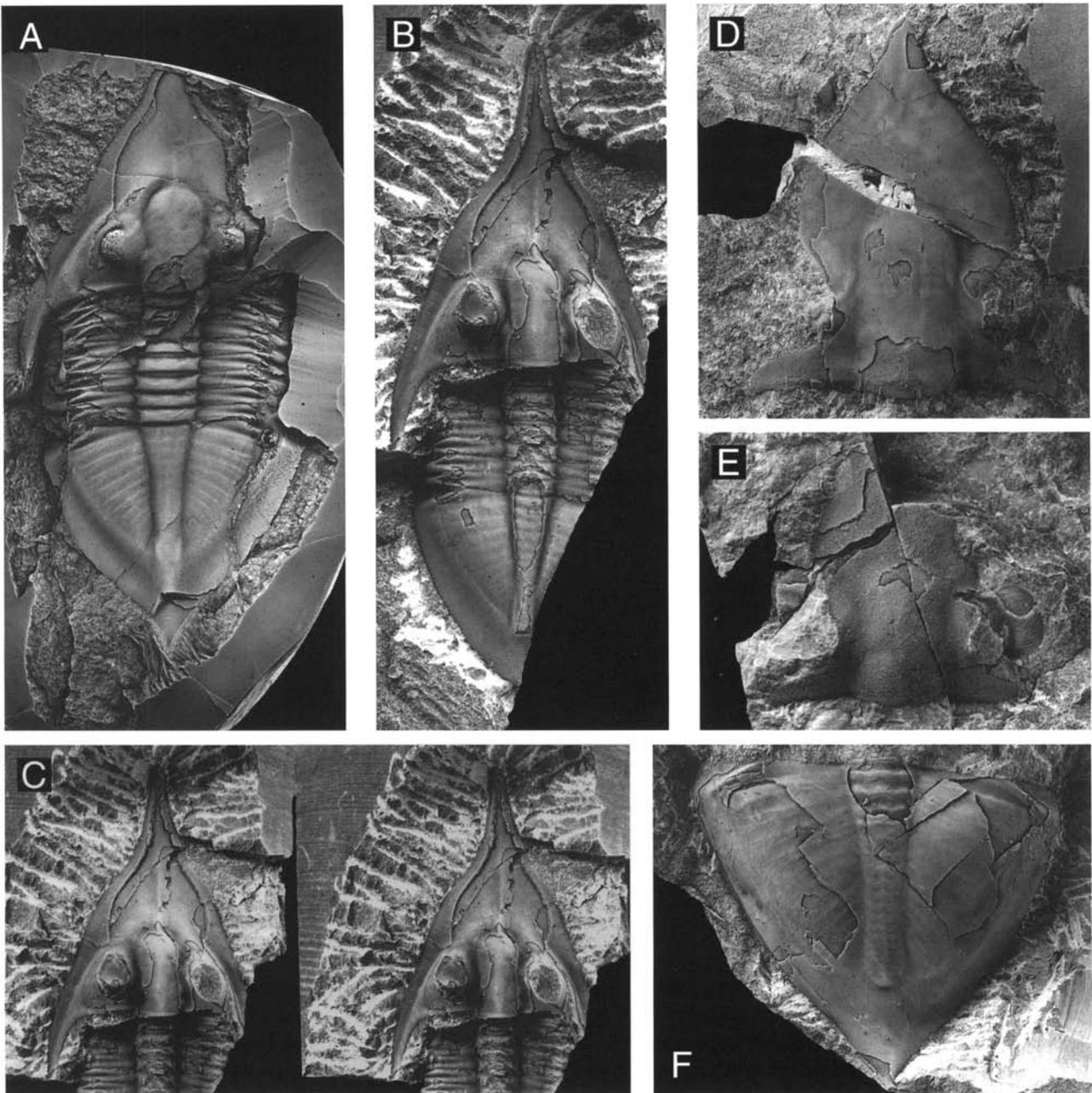


Fig. 118. □A–D, *M. (Megistaspidella) acuticauda* (Angelin, 1854). □A. Latex cast of complete specimen showing anterolateral pygidial border, $\times 1$. MGUH 22.533 (A 1163), Lysaker Member (probably lower part), Slemmestad. □B. Small complete specimen, $\times 2$. MGUH 22.534 (A 1114), bed A-46, Slemmestad. □C. As B, stereo-pair of cephalon showing upturned anterior snout and raised eyes, $\times 1.5$. □D. Large cranidium, $\times 1$. MGUH 22.535 (A 302a), bed A-19, Slemmestad. □E. *M. (M.)* cf. *acuticauda* (Angelin, 1854). Damaged cranidium, $\times 1$. MGUH 22.537 (K 1133), bed 7, Killeröd site b. □F. Partly exfoliated pygidium, $\times 1$. MGUH 22.536 (A 405), Bed A-29, Slemmestad.

Sweden. The occurrence and status of other variants are discussed below.

Description. – See Brögger (1882), Balashova (1976) and especially Bohlin (1960). However, these authors do not to any degree of detail describe the pygidial doublure, which may prove important for distinction between species of *M. (Megistaspidella)* (cf. Balashova 1976). It is strongly concave

and covered with rather openly spaced terrace lines. On the shorter, upturned inner part, the lines descend backwards from the inner margin, while they on the larger, flat outer part run subparallel with outer margin; the inner and outer terrace lines meet discordantly in the doublural flexure. A total of 18 lines was counted across the doublure in three specimens, whereas two less well-preserved pygidia may have only 16 or 17 lines. Axial embayment small; the poste-

rior terrace lines, descending backwardly from the inner margin, are connected across sagittal line.

The material at hand demonstrates that smaller pygidia, up to 30 mm long, may have a concave border the whole way, unlike adults (see also Bohlin 1960).

Remarks. – Schmidt (1906) separated several so-called variants of *M. acuticauda*, viz. var. *Lamanskii*, var. *triangularis* and var. *obtusa*, in addition to var. *typica*. All of these have been treated as separate species by subsequent authors (Bohlin 1960; Balashova 1976). Schmidt (1906) also ranked 'Asaphus' *centron* Leuchtenberg, 1843 as a variant of *M. acuticauda*, but later synonymized it with var. *typica* (see Schmidt 1907). The affinities of the poorly known 'A.' *centron* has been a vexed question, Lamansky (1905) included it in *M. leuchtenbergi*, Bohlin (1960, pp. 185–186) suggested that it might be of *M. heroica* type [= *M. (Heraspis) Wandås*, 1984], while Balashova (1976, p. 114) in part assimilated it within *Rhinoferus (Ropshiaspis) petrowtschinensis*. Further discussion should await a redescription of the type material; until then the inadequately known taxon must be considered a *nomen dubium*.

Bohlin (1960) adopted a very narrow interpretation of *M. acuticauda*, and actually temporarily excluded all non-Oelandian material from the species; *M. acuticauda* var. *typica* Schmidt (1906) was separated as *M. (M.) spinulata* (see below). A narrow interpretation of *M. acuticauda* was maintained by Balashova (1976) (who distinguished *M. triangularis*, *M. lamanskii*, *M. obtusa*, *M. acuticauda*, *M. spinulata* and *M. isovsica*, all of which, broadly speaking, are of *acuticauda*-type), and is also largely upheld in the present paper, owing to the lack of material for a more thorough revision. However, all authors treating *M. (M.) acuticauda* have mentioned that it is quite variable (e.g., Brögger 1882, p. 82; Bohlin 1960, p. 184), and in order to establish a biologically based species concept it appears necessary to undertake a detailed biometric analysis of extensive material. The high intra-specific variability may alternatively lead to taxonomic 'oversplitting', and it is for instance possible that *M. spinulata* merely represents an ecophenotype of *M. acuticauda*, and as such should be classified only at the subspecies or variant level. The sparse presence of *M. cf. spinulata* in the upper part of the Komstad Limestone supports this conjecture, and most of the differences separating *spinulata* from *acuticauda* are actually analogous to the differences separating the assumed shallower–deeper-water ecophenotypes of *M. limbata* (compare Table 5).

The status of *M. obtusa* is also suspect; introducing the variant, Schmidt (1906, p. 47) mentioned that it perhaps simply comprises rare pathological specimens of *acuticauda* in which the snout is injured. This seems to be a plausible inference, judging from the figures and description of *M. obtusa* presented by Balashova (1976), and the species(?) is assumed to just represent impaired specimens of *M. acuticauda/spinulata*.

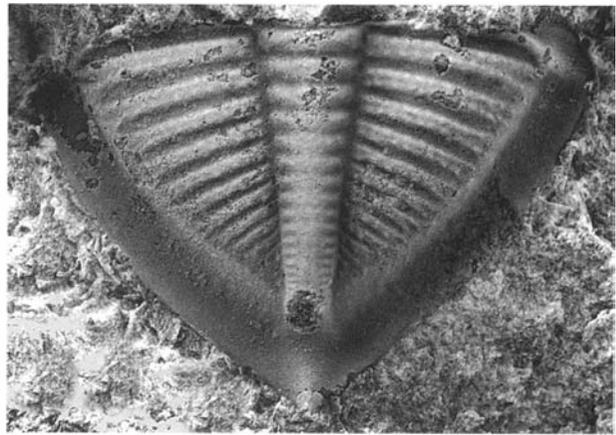


Fig. 119. *M. (Megistaspidea) cf. acuticauda* (Angelin, 1854). Juvenile pygidium showing well-developed concave border all the way and pronounced segmentation of pleural fields, $\times 6$. MGUH 22.538 (K 1156), bed 7, Killeröd site b.

The bulk of the available material comes from Slemmestad. The early representatives from bed interval A-4 to A-8 are poorly preserved, but have a strongly vaulted glabella and pygidial axis (which furthermore appears proportionally broader), compared to the later specimens, and perhaps a lateral cephalic border extends all the way to the genal spine. It is tempting to regard these specimens as slightly transitional towards *M. spinulata*, although they by far most closely resemble *M. acuticauda*. Thus the cranidia have a smooth glabella without segmentation and are similar in other preserved features to *M. acuticauda (s.str.)*, the pygidia do not show an especially distinct segmentation and their doublure is similar to *M. acuticauda* from higher levels; it is uncertain whether a pygidial border continues all the way forwards. Because of the poor preservation and the possible minor differences, the early specimens are treated as *M. (M.) cf. acuticauda*.

Brögger's (1882) distinction of a narrow and a broad form of *M. acuticauda*, mainly depending upon whether or not the pygidial L:W ratio exceeds 1:1, is not evident in the material at hand. Tentative measurements of the rather fragmentary pygidia indicate a continuous variation range of L:W ratios from around 0.75 to 1.0 ($N = 12$; length includes posterior spine); judging from the measures reported by Brögger (1882, p. 83), the pygidial L:W variation range even goes to about 1.2 (all in adult specimens). The present material is much too limited to estimate whether or not there is a relation between environment and skeletal width similar to the one displayed by *M. (Megistaspis) limbata* (Fig. 53).

A few poorly preserved specimens from the lower part of the A. 'raniceps' Zone at Killeröd site b probably belong to *M. (M.) acuticauda*. Except for a juvenile specimen (Fig. 119), all of the pygidia from this locality are fragmentary, so the distinctness of the pleural segmentation and the border

outline are unknown. The pygidial doublure is covered with 18 terrace lines, like the Norwegian material. The juvenile pygidium, 11 mm long, shows distinct pleural ribs, a fairly pronounced axial segmentation, a markedly arched, raised axis, and a concave border all the way (Fig. 119), but these features are typically juvenile. The cranidium (Fig. 118E) has a very low, entirely smooth glabella, and is very similar to the Norwegian material, except that the preocular width seems slightly smaller (which, however, hardly is a significant difference). Compared to the coeval *M. (H.) heros*, the Scanian specimen is more elongate, narrower (tr.), and the sagittal relief is much lower. Compared to *M. (M.) convexa*, also known from the *A. 'raniceps'* Zone (Bohlin 1960), the sagittal cranidial relief is markedly lower, and the cranidium is distinguished from *M. (M.) curvispina* by the lack of a mesial depression in front of glabella, the glabella is less inflated, and the anterior branches of facial suture are less forward diverging. The fragmentary material from the Komstad Limestone is treated as *M. (M.) cf. acuticauda*, but it most likely does represent *M. (M.) acuticauda (s.str.)*, which therefore seems to enter the base of the *A. 'raniceps'* Zone.

Megistaspis (Megistaspidella) cf. spinulata Bohlin, 1960

Fig. 120

Synonymy. – (Key papers only, see Bohlin 1960 for additional references) □v 1919 *Megalaspis acuticauda* Ang. – Funkquist, pp. 22, 39 (occurrence). □cf. 1960 *Megistaspis (Megistaspidella) spinulata* n.sp. – Bohlin, p. 186 (diagnosis). □cf. 1976 *Megistaspidella (Spinopyge) spinulata* (Bohlin, 1960) – Balashova, pp. 104–105; Pls. 31:7; 33:1 (description, occurrence, illustration of thoracic doublure and close up of librigena).

Holotype. – Complete specimen, figured by Schmidt (1901, Pl. 5:1).

Material. – One pygidium (LU 28 (im) [LO 7087]).

Occurrence. – The specimen is from the uppermost part of the Komstad Limestone at Tommarp (coll. Funkquist), i.e. *A. expansus* Zone. *M. (M.) spinulata* is characteristic of the BIII α Zone of the eastern Baltic area (Schmidt 1906; Bohlin 1960; Balashova 1976).

Description. – The exfoliated pygidium is 84 mm long, including posterior spine. Pygidium moderately strongly vaulted; L:W ratio, including spine, 0.82, and about 0.75 excluding the spine. Axis gently arched, delimited by wide and moderately deep furrows. Middle part of axis approximately level with adjacent pleural fields, while the anterior and posterior portions rise above the pleural fields. Axial segmentation vestigial, and only 6 to 7 anterior rings can be distinguished. Pleural fields exhibit fairly distinct segmentation; 12 pairs of bifurcate ribs present inside paradoublural

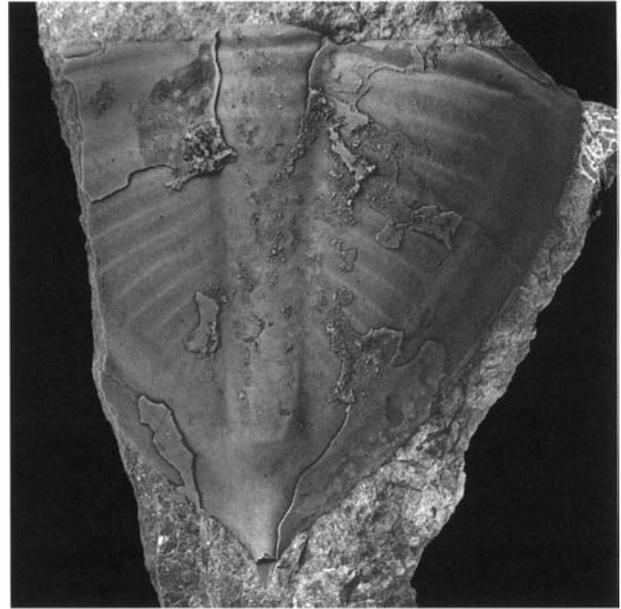


Fig. 120. *Megistaspis (Megistaspidella) cf. spinulata* Bohlin, 1960. Internal mould of large pygidium, $\times 0.9$. LO 7087 (LU 28), Tommarp.

line, of which the posterior pair is almost effaced. Anterior crest of each rib more distinct than crest behind the interpleural furrow. Paradoublural line indicated by a low, wide crest, and by the termination of pleural ribs. Concave border continues all the way to anterolateral corner, interrupted only by the crest delimiting articulating facet to the rear; border widest posteriorly. Axis continues into a low crest which is projected backwards into a short, slightly upwards directed spine.

Remarks. – Bohlin (1960) separated *M. acuticauda* var. *typica sensu* Schmidt (1906) as a new species, *M. (M.) spinulata*, distinguished from *M. (M.) acuticauda* by having a more convex and distinctly segmented glabella, a well-defined border along cephalon as well as pygidium, stronger ribs on the pleural fields of pygidium and perhaps also a different hypostome (Bohlin 1960, p. 185). Balashova (1976) described both *M. spinulata* and *M. acuticauda* from the eastern Baltic area.

Pygidium LU 28 agrees well with *M. spinulata*, but the relationship between *M. spinulata* and *M. acuticauda* is uncertain. The border outline and presumably also the distinctness of the pleural ribs were very likely affected by the environment (compare resembling variation displayed by representatives of *Megistaspis (Megistaspis)*, notably *M. limbata*), and *M. spinulata* / *M. acuticauda* may turn out to represent ecophenotypes of the same species. If so, they should be separated only as subspecies or variants.

Pending investigation of more material, and especially findings of matching cranidia, the pygidium at hand may conveniently be treated as *M. (M.) cf. spinulata*. It is rather

like the pygidia from Fågelsång assigned to *M. (M.) cf. triangularis*, but differs by having a narrower axis with a lowered central part and a more effaced segmentation, a comparatively distinct anterior crest of the bifurcated pleural ribs, and by being relatively slightly longer. Compared to *M. (M.) acuticauda*, the described pygidium has more conspicuous pleural ribs, a concave border all the way, a proportionally broader axis and a less prominent postaxial spine, which, furthermore, is less distinctly upturned.

Megistaspis (Megistaspidella) cf. triangularis (Schmidt, 1906)

Fig. 121

Synonymy. – □*cf.* 1906 *Megalaspis acuticauda* Ang. var. *triangularis* – Schmidt, pp. 42–49; Pl. 6:3–6 (short description, occurrence, illustrations of complete specimen, cephalon, pygidia). □*cf.* 1976 *Megistaspidella (Spinopyge) triangularis* (F. Schmidt, 1906) – Balashova, pp. 98–100; Pls. 23:3a–v; 26:6a–g; 27:3; 29:3; 30:4; 32:1, 2a–v; 33:5 (description, occurrence, illustrations of complete specimens and pygidial doublure).

Lectotype. – Enrolled specimen 250/52-18478, figured by Schmidt (1906, Pl. 6:4, 4a), listed as type by Balashova (1976).

Material. – One cranidium and 3 pygidia.

List of material. – □Cranidium LU 108 (pim) [LO 7115]. □Pygidia GM 1950.134 (im) [MGUH 22.539], LU 31b (im) [LO 7089], LU 31c (im) [LO 7090].

Occurrence. – The material comprises museum specimens only. Samples LU 31 and LU 108 from Fågelsång undoubtedly originate from bed interval 18–22 (most likely beds 18–20), which corresponds to the lower part of the *A. expansus* Zone. Pygidium MGUH 22.539 is from Skelbro, and probably derives from bed +10 or, less likely, from the lower part of bed +13; both beds are within the upper part of the *M. limbata* Zone.

M. (Megistaspidella) triangularis (Schmidt, 1906) has been reported from the *A. lepidurus* Zone (BIγ) of the East Baltic area (Balashova 1976).

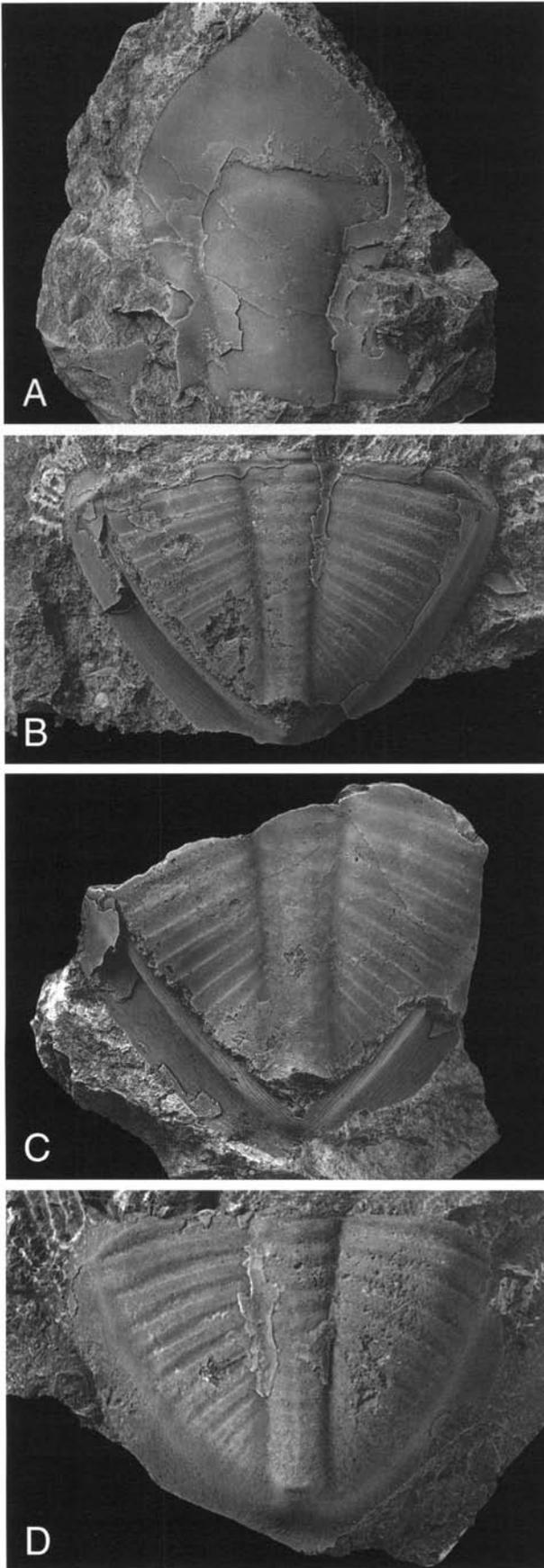
Description. – Available cranidium 63.5 mm long, largest pygidium approximately 60–65 mm long. Cranidium rather elongate, PW:L ratio close to 2:3; sagittal relief moderately strong. Glabella subcylindrical, fairly arched and stretches for 0.6 (including occipital region) of the cranidial length; it has a slight constriction between the eyes, minimum width equals about 0.45 of the glabellar length (incl. occipital region), maximum glabellar width (anteriorly) corresponds to 0.60 of the glabellar length. Lateral glabellar furrows and occipital furrow effaced; occipital ring barely raised, flat, virtually not set off from glabella. Two pairs of very indistinct lateral muscle insertion sites present on posterior part of

frontal glabellar lobe (internal mould); small mesial tubercle situated on posterior part of glabella, level with inner posterior corner of palpebral lobes. Axial furrows shallow, wide, but augmented by the change of slope between genae and glabella; preglabellar furrow even more shallow. Frontal area gently concave with two diffuse rounded wide impressions on sagittal line; a nebulous mesial keel stretches from glabellar front to tip of cranidium. Lateral part of anterior fixigena bent gently downwards. Anterior branches of facial suture diverge strongly forwards in front of eyes at an angle of about 30° to sagittal line, then, level with glabellar front, begin to turn gently inwards, converging at an angle of about 130° to sagittal line, to bend a little forwards immediately before meeting in an angulate junction. Palpebral lobes presumably small, positioned below level of glabellar crest. Judging from the preserved inner base of lobe, distance between posterior cranial margin and posterior inner corner of lobe is equivalent to about 1.3 times the lobe length (exsag.). The preserved proximal part of right posterior fixigena shows a wide, shallow and indistinct border furrow, which seems to run gently obliquely backwards from anterior level of occipital ring. A narrow strip along posterior margin is slanting backwards.

Available pygidia damaged, but width clearly exceeds length; estimated L:W ratios, exclusive of the posterior spine, are about 0.70–0.75. Pygidia broadly triangular in outline and fairly strongly vaulted. Axis moderately narrow, fairly convex and slightly raised above pleural fields for the whole length; it consists of 15 axial rings in addition to the terminal piece and anterior half-ring, but the rather indistinct segmentation fades rearwards, and may be difficult to recognize posteriorly; the available pygidia are all internal moulds. Axis delimited by wide and fairly deep axial furrows. Pleural fields show 11 pairs of well-defined, bifurcate ribs, of which the posterior pair, though, is short and almost effaced. A concave border is present the whole way, but is presumably widest posteriorly (rear part of all specimens damaged). Posterior spine not preserved. Doublure strongly concave, main outer part flattened, subhorizontal; very small axial incision. Terrace lines most dense on inner part, descending backward-downward from inner margin; lines on outer part less dense and run subparallel with outer margin. The inner and outer lines meet discordantly on outer side of the sharp doublural bend. A total of 20–21 lines was counted across the middle lateral part of doublure in two pygidia.

Affinities. – The cranidium differs from *M. (M.) acuticauda* by lacking an anterior snout and by having a more strongly inflated glabella with a better defined mesial tubercle, while the pygidia are more broadly triangular in outline, show well-marked pleural ribs, a forwardly extending concave border, a relatively slightly broader and stronger inflated axis and a doublure with more densely spaced terrace lines.

Judging from the description presented by Balashova (1976), the pygidium of *M. lamanskii* differs from the material at hand by being less vaulted, the axis is less elevated



relative to the pleural fields and exhibits a more indistinct segmentation, the axial furrows are shallower, and the doublure is less concave and carries about 30 terrace lines.

M. laine [= *M. polyphemus* var. *Knyrkoi* Schmidt, 1906] also has a short frontal area and a mesial depression in front of glabella, but the cranidium described here shows a more distinctly vaulted and broader glabella (compare Balashova 1976, p. 90; Pl. 20:1), and the palpebral lobes are positioned well below the sagittal level of glabella (since this feature may be assumed to be influenced by growth it is remarked that the holotype of *M. laine*, described by Balashova 1976, is approximately of the same size as the specimen under discussion). The cranidium at hand may be described as intermediate between *M. laine* and *M. triangularis*.

Remarks. – Cranidium LU 108 is clearly of *acuticauda* type (*s.l.*), and is tentatively taken to match the only two *acuticauda*-like pygidia presently known from Fågelsång. The pygidium from Skelbro is similar in all features to those from Fågelsång. The cranidium is stored together with a fragmentary ptychopygid pygidium, and perhaps the specimens were originally from the same sample. According to an adjoining label, the material was studied by Schmidt in April 1906, and although he noted the resemblance of the cranidium to *M. acuticauda*, the specimens were identified with *Ptychopyge lata* Angelin. This assignment of the cranidium is evidently wrong, and Schmidt's identification must refer to the pygidium.

Cranidium LU 108 is quite similar to *M. triangularis*, as described by Balashova (1976, pp. 98–100), e.g., with regard to the lack of an anterior snout, the gently concave frontal area, showing an indistinct longitudinal keel and mesial depressions, the comparatively wide glabella, the diffuse posterior border furrow, situated slightly behind the anterior level of the occipital ring, the presence of a mesial tubercle, and the relatively large eyes. In comparison to Balashova's description of *M. triangularis*, the available cranidium has a shorter frontal area, and the facial suture diverge less strongly in front of the eyes. The pygidia also matches the description of *M. triangularis* (see Balashova 1976, pp. 99–100), for example with regard to the triangular outline, the degree of convexity, the height of axis above the pleural fields, the number and distinctness of pleural ribs, the concavity of the doublure and the doublural terrace-line density (the number of lines stated by Balashova is close to axis, whereas the above stated total number of lines were counted laterally, as the rear part of all pygidia are damaged). The only obvious difference

Fig. 121. *Megistaspis* (*Megistaspidella*) cf. *triangularis* (Schmidt, 1906). □A. Partly exfoliated large cranidium, $\times 1$. LO 7115 (LU 108), Fågelsång. □B. Internal mould of pygidium showing part of doublure, $\times 1.5$. LO 7089 (LU 31b), Fågelsång. □C. Internal mould of pygidium showing doublure, $\times 1$. LO 7090 (LU 31c), Fågelsång. □D. Internal mould of pygidium, $\times 1.5$. MGUH 22.539 (GM 1950.134), Skelbro.

is the number of axial rings, stated to be about 20 by Balashova, but this number may include the terminal piece and the anterior half-ring.

As no reference material has been available, and as there might be minor differences between *M. triangularis* and the material at hand, the latter is referred to as *M. (M.) cf. triangularis*. Furthermore, it is disturbing that the cranidium was not identified by Schmidt, the author of *M. triangularis*.

Megistaspis (Megistaspidella) sp. I

Fig. 122

Material. – One fragmentary cranidium (K 166a, corroded [MGUH 22.540]).

Occurrence. – The specimen was found in bed +1 at Killeröd, belonging to the lowermost part of the *M. limbata* Zone.

Description. – Fragment of a very large cranidium showing a ca. 45 mm long glabella, so the original length of cranidium presumably exceeded 65–70 mm, and may have been up to about 80–90 mm, depending on the size order of the snout. Cranidium rather effaced; overall relief very low. Glabella weakly inflated, broad, with gentle constriction level with the eyes; minimum width equivalent to slightly more than half of the glabellar length (incl. occipital region). Axial furrows shallow, preglabellar furrow almost effaced. Occipital and lateral glabellar furrows not defined; occipital ring insignificantly inflated (visible only in oblique light); baculae barely outlined. The preserved proximal parts of posterior fixigenae inconclusively indicate the presence of a wide and shallow border furrow. Eye most likely small, not raised above glabella; judging from the inner base of palpebral lobe, the distance to posterior cranial margin is presumably about 1.5 times the palpebral length (exsag.). Facial suture diverge in front of eye at an angle of about 35° to sagittal line.

Remarks. – The specimen is an early representative of *M. (Megistaspidella)*. The preserved parts quite well match the rather effaced cranidium of *M. lamanskii* (compared description by Balashova 1976), also showing strongly diverging anterior facial sutures in front of the eyes (note that the 70° stated by Balashova (1976, p. 100) is the angle between the branches). The distance between the eyes and the posterior margin seems to be slightly higher in the Scanian specimen than in *M. lamanskii*, but the difference cannot be verified as the lobes are not preserved. Besides, Schmidt (1906, p. 47) wrote that the distance between posterior cranial margin and the lobes of var. *lamanskii* is equivalent to 1.5–2 times their length, which, as far as can be established, is in agreement with specimen K 166a. Accordingly, the isolated specimen seems close to and may even represent this species, reported from the *A. lepidurus* Zone (BIIγ) of the eastern Baltic area (Balashova 1976).

Megistaspis (Heraspis) Wandås, 1984

Type species. – (OD) *Megistaspis heroica* Bohlin, 1960.

Megistaspis (Heraspis) cf. heroica Bohlin, 1960

Fig. 122B

Synonymy. – (Key papers only; see Bohlin 1960 for additional references) □cf. 1960 *Megistaspis heroica* n.sp. – Bohlin, pp. 174–179; Textfigs. 15, 16; Pl. 7:1–8 (description, occurrence, illustrations of cranidia, librigenae, pygidium, drawings of cephalon and pygidial relief). □cf. 1976 *Megistaspidella (Spinopyge) heroica* (Bohlin, 1960) – Balashova, pp. 102–104, Pl. 34:6 (description, occurrence, illustration of cranidium). □cf. 1984 *Megistaspis (Heraspis) heroica* Bohlin, 1960 –

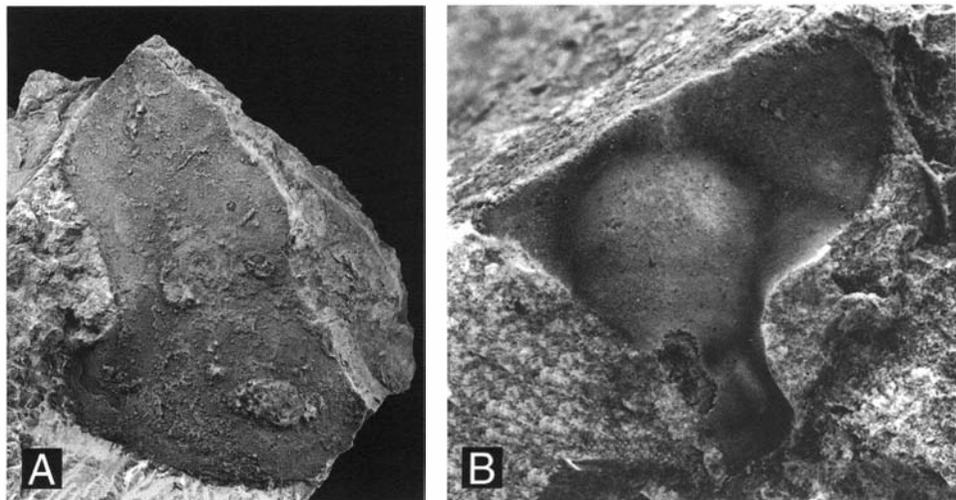


Fig. 122. □A. *Megistaspis (Megistaspidella) sp. I*. Fragment of large cranidium, ×1. MGUH 22.540 (K 166), bed +1, Killeröd. □B. *Megistaspis (Heraspis) cf. heroica* Bohlin, 1960. Fragmentary internal mould of cranidium, ×6. MGUH 22.541 (K 1164), bed 8, Killeröd site b.

Wandås, pp. 223–224; Pls. 5C, E, G; 6A, C (occurrence, illustrations of cranidia, librigena, pygidia).

Holotype. – Almost complete specimen figured by Schmidt (1906, Pl. 7:4, 4a).

Material. – One fragmentary cranidium, K 1164 (t) [MGUH 22.541].

Occurrence. – The cranidium was found in bed 8 at Killeröd site b, i.e. within the basal part of the *A. 'raniceps'* Zone. *M. (H.) heroica* is characteristic of the *A. 'raniceps'* Zone of Baltoscandia (Bohlin 1960; Balashova 1976).

Remarks. – The specimen is too fragmentary to be confidently identified, but it resembles *M. (H.) heroica* in all preserved features.

Species not assigned to subgenus

Megistaspis cf. *knyrkoi* (Schmidt, 1906)

Fig. 123

Synonymy. – □cf. 1906 *Megalaspis Knyrkoi* m. – Schmidt, pp. 37–38, Textfig. 16 (description, occurrence, illustration of pygidium). □non 1906 *Megalaspis polyphemus* var. *Knyrkoi* m. – Schmidt, pp. 29–31, Textfig. 10, Pl. 2:9. [= *M. laine* Jaanusson, 1956]. □v 1936 *Megalaspis stenorhachis* Ang. – C. Poulsen, pp. 48–49 (listed, stratigraphical distribution discussed). □v 1965 *Megistaspis (Megistaspis)* sp. no. 1 – V. Poulsen, pp. 67–68; Pl. 1:8 (description, occurrence, illustration of pygidium). □cf. 1976 *Rhinoferus (Lawiaspis) knyrkoi* (F. Schmidt, 1906) – Balashova, pp. 112–113 (description, occurrence).

Holotype. – By monotypy, pygidium 250/78-18448, described and figured by Schmidt (1901, Textfig. 16).

Material. – Two pygidia (internal moulds), comprising MGUH 22.542 (S 1771, donated by Mr. Niels Mogensen, Rønne), and MGUH 9423, previously figured by V. Poulsen (1965, Pl. 1:8).

Occurrence. – S 1771 is from Skelbro and MGUH 9423 is from the Duegård quarry of Bornholm. They originate either from bed –21 or –20, i.e. the lower part of the *M. polyphemus* Zone.

Description. – By comparison to the smaller pygidium (Fig. 123B), described by V. Poulsen (1965, pp. 67–68), the larger specimen, 43 mm long, is less fragmentary (Fig. 123A); both specimens are exfoliated. The present account is complementary to Poulsen's description. Pygidium broad parabolic in outline, L:W ratio 3:4. Axis narrow, delimited by narrow, well-impressed furrows. Axis tapers backwards to axial ring nos. 9–10; posterior part insignificantly expanded; minimum axial width equivalent to 0.16 of the pygidial length. Axis slightly elevated above pleural fields all the way; there are at least 14, but probably 15 axial rings in addition to terminal

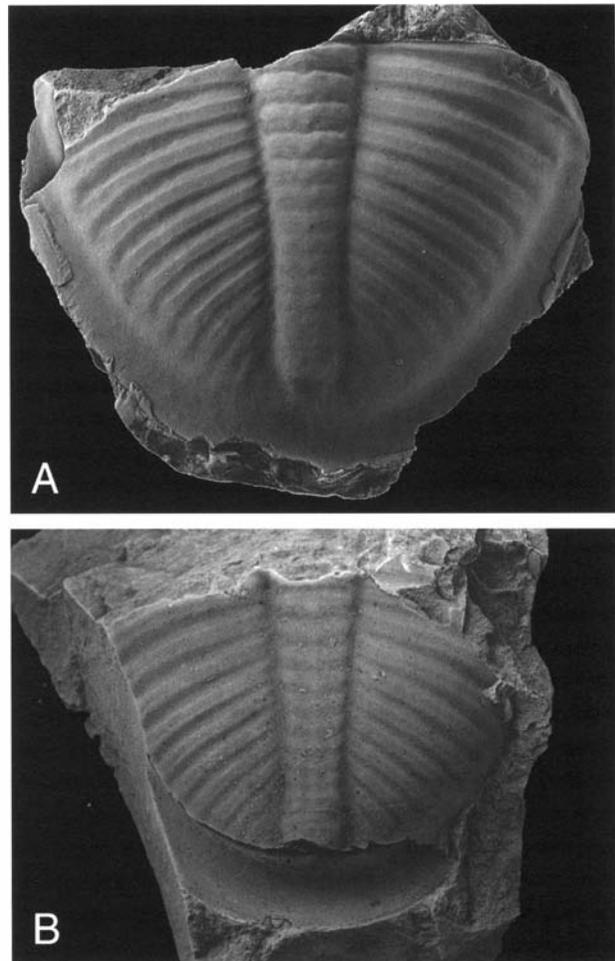


Fig. 123. *Megistaspis* cf. *knyrkoi* (Schmidt, 1906). □A. Internal mould of pygidium, $\times 1.4$. MGUH 22.542 (S 1771), Skelbro. □B. Internal mould of small pygidium showing doublure, $\times 2$. MGUH 9423, Skelbro. Previously figured by V. Poulsen (1965, Pl. 1:8).

piece and anterior half-ring. Axis stretches for slightly less than 0.8 of the pygidial length. A narrow, indistinct postaxial ridge continues across the border. Pleural fields show 11 pairs of ribs, of which the posterior pair is very faint, and most likely not visible on testaceous material. A well-defined concave border continues to anterolateral corners. The exfoliated state possibly amplifies the concavity of the border, but it must be defined anterolaterally also when the test is intact.

Remarks. – The two specimens strongly resemble the somewhat younger *M. knyrkoi*, reported from the BII α Zone of the Leningrad area (Schmidt 1906), and of which only two isolated pygidia are known (Balashova 1976). *M. knyrkoi* has a narrow axis, 10 to 11 pairs of moderately distinct pleural ribs, a gently concave border extending forwards, and a rather sigmoidal doublure (cf. Schmidt 1906, pp. 37–38, Textfig. 16). The pleural fields of the Russian pygidium, ca. 38 mm long, are possibly slightly more conspicuously segmented than in the large specimen at hand (cf. Schmidt 1906,

Textfig. 16), but the available smaller pygidium seemingly has a comparable distinct segmentation. No other differences can be pointed out.

M. cf. knyrkoi somewhat resembles *M. ringsakerensis*, reported from the upper part of the Tøyen Shale at Herramb, Zones 3Bγ–δ (Skjeseth, 1952), but the exact levels in the section are unknown. The bulk of the material of *M. ringsakerensis* is sampled from small limestone nodules, probably from the upper part of the *M. estonica* Zone, but a *M. polyphemus* Zone age cannot be excluded. The two pygidia from Bornholm are thus approximately contemporaneous with *M. ringsakerensis*; they differ by being slightly more convex (tr.) and relatively narrower, by having an extra pleural rib, by showing a more strongly concave doublure, and, most importantly, by having a concave anterolateral border. It also appears that the largest specimen has an extra axial segment, compared to *M. ringsakerensis*; when Skjeseth (1952) stated the number of axial rings to be 16, he included the terminal piece and the anterior half-ring.

In the absence of cephalic material it is impossible to verify the affinities of *M. knyrkoi* and *M. ringsakerensis*, but they are believed related to the forms informally referred to as *Megistaspis* spp. B and C. All of these poorly known species may belong to a new subgenus, possibly closer related to *M. (Paramegistaspis)* than to *M. (Megistaspis)* (see discussion of *Megistaspis* sp. B).

Megistaspis sp. B ? aff. *ringsakerensis*

Fig. 124

Synonymy. – □? 1883b *Megalaspis planilimbata* Ang. – Tullberg, p. 245 (listed).

Material. – One cranium, 8 pygidia.

List of material. – □Cranidium K 18 (im) [MGUH 22.543]. □Pygidia K 21 (im) [MGUH 22.545], K 34 (im), K 37 (pim) [MGUH 22.544], K 42 (im), K 471 (doublure) [MGUH 22.546], K 472 (t), K 473 (im), K 475? (im).

Occurrence. – *Megistaspis* sp. B has been found only in beds C, D and E at Gårdlösa-1. These beds are believed to represent the top of the *M. polyphemus* Chronozone, but the correlation is tentative and the interval may alternatively represent the lower part of the *M. simon* Zone.

Megistaspis sp. B is close to sp. C, described from the top of the *M. polyphemus* Zone in the Oslo region.

Description. – Small to medium-sized megistaspid, available cranium 27.5 mm long, largest pygidium ca. 40 mm long. The rather poorly preserved cranium (Fig. 124A) is exfoliated; it appears narrow, but the PW:L ratio is 0.8, whereas the FW:L ratio is about 1.15; sagittal relief moderate. Mesial depression in frontal area distinct; frontal area dominated by periglabella crest, from which the remaining frontal area concavely slopes downwards-outwards. Glabella gently vaulted, narrow (tr.), only slightly expanding forwards, anterior margin rounded; it is delimited by well-impressed dorsal

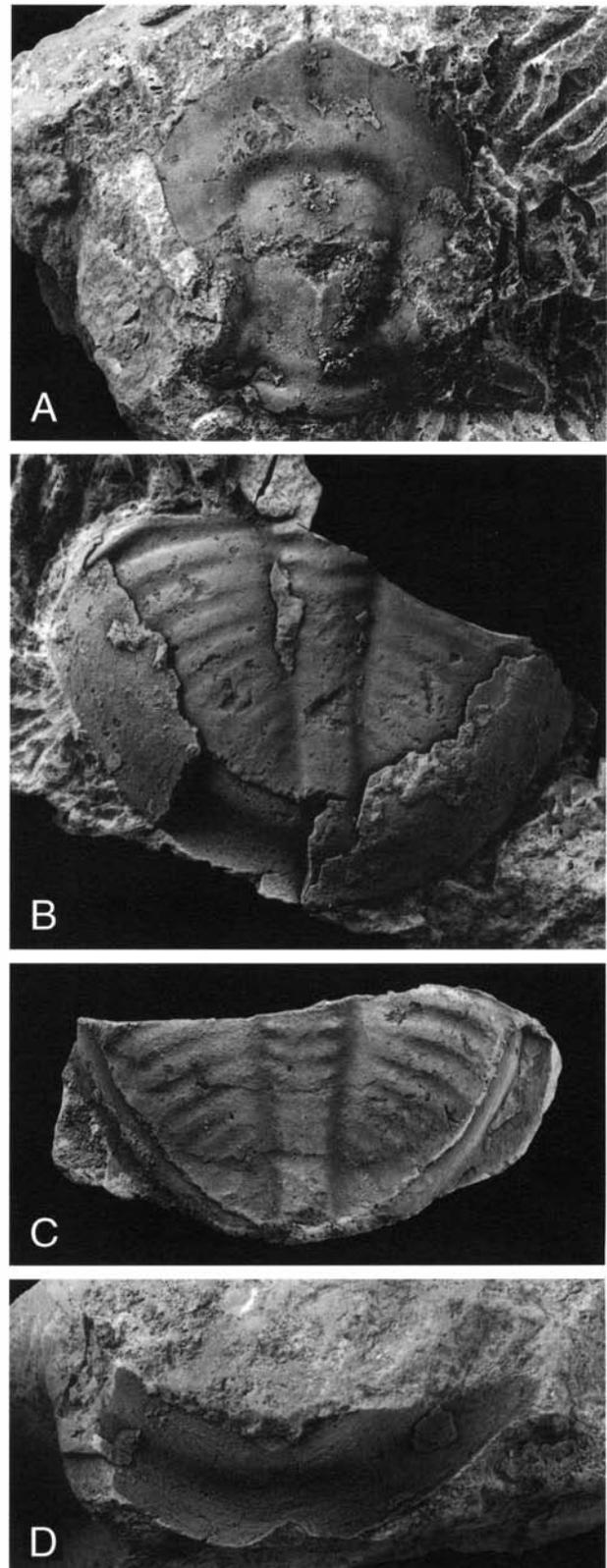


Fig. 124. *Megistaspis* sp. B. □A. Internal mould of damaged cranium, $\times 2$. MGUH 22.543 (K 18), bed C, Gårdlösa-1. □B. Largely exfoliated pygidium, $\times 1.5$. MGUH 22.544 (K 37), bed C, Gårdlösa-1. □C. Fragmentary internal mould of pygidium showing doublure, $\times 1.5$. MGUH 22.545 (K 21), bed E, Gårdlösa-1. □D. Fragment of pygidium showing posterior part of doublure, $\times 1.5$. MGUH 22.546 (K 471), bed E, Gårdlösa-1.

and preglabellar furrows. Especially the preglabellar furrow is unusually well-defined. Glabella (including occipital ring) stretches for 0.66 of the cranidial length. Lateral glabellar furrows shallow, elongate, converging backwards. Occipital furrow deep laterally, shallow mesially. Occipital ring short (sag.), slightly raised above rear part of glabella. Faint, minute mesial tubercle indicated in front of occipital furrow. Baculae fairly inflated. Palpebral lobes not preserved. Posterior fixigenae with wide, shallow border furrow; posterior margin seems raised (poorly preserved). Anterior branches of facial suture diverge in front of the eyes at an angle of about 35° to sagittal line, then turn sharply inwards to converge at an angle of 120° to sagittal line, meeting at a pointed angle.

Pygidium gently vaulted, rather broad and parabolic to almost semicircular in outline. L:W ratio 0.72 in two pygidia from bed H, ca. 0.65 in a pygidium from bed G, and presumably about 0.62 in a pygidium from bed F. Axis unusually narrow (tr.), tapering very gently backwards for 2/3 of the axial length, then becomes approximately parallel-sided; terminal portion may be slightly expanded. Minimum axial width at the more or less imaginary constriction is 0.17–0.18 of the pygidial length ($N=2$). Axial segmentation faint, even on internal moulds, fades out in posterior direction and is effaced behind axial ring nos. 6–8, hence the number of segments cannot be verified, but there is a likely total in the range of 12–16 rings. They appear to be more simple than in *Megistaspis* (*Megistaspis*) (see Tjernvik 1980, p. 197) and are mostly indicated only as lateral, paired knobs. Axis approximately level with pleural fields; it is delimited by wide furrows, which shallow up posteriorly at intersection with paradoublural line, which is also marked by a wide, shallow furrow. Pleural fields gently vaulted, and carries 8 to 9 pairs of low ribs inside paradoublural line; segmentation also visible on testaceous material. Each rib is bifurcated by a shallow longitudinal pleural furrow as typical for *Megistaspis*. A moderately wide, gently sloping concave border is developed posteriorly, but lateral parts of pygidium are actually slightly concave the whole way, except close to anterolateral corners; the gentle concavity is best defined on internal moulds. Crest behind articulating facet narrow, but slightly more raised than in species of *M. (Megistaspis)*; articulating facet has a very moderate anterior slope.

Doublure appears rather wide in dorsal view because of the low convexity of the pygidia, but its relative width is of common size-order; an equal width is approximately maintained the whole way. It is pronouncedly sigmoidal in cross-section with a flattened main outer part and a narrower inner part, separated by a fairly steep middle part. Axial incision small, inner margin insignificantly upturned around the tip of axis. There is apparently no upturning of the outer post-axial part. Terrace lines sparse, especially on the flattened outer part and in the flexure between steep part and inner flattened part; the line density is higher close to inner margin and in the basal flexure between steep middle part and outer flattened part. The lines run subparallel with inner and outer

margins anterolaterally; posterolaterally they run obliquely backwards-outwards from inner margin; mesial portion poorly preserved in all specimens at hand showing the doublure. The material inconclusively indicates the presence of about 17–18 terrace lines anterolaterally, while there seem to be a few more lines posterolaterally (?19–20).

Affinities. – *M. ringsakerensis* (Skjeseth, 1952) also has a narrow axis and a similar large number of ribs on the pleural fields; the matching cranidium is unknown. Skjeseth (1952, p. 162) stated the number of pleural ribs to be 12, but the material of *M. ringsakerensis* has been reexamined, and no more than 9 or at the most 10 rib pairs in addition to the anterior half rib can be counted (cf. Skjeseth 1952, Pl. 2:2). The pygidia of *M. ringsakerensis*, figured by Skjeseth (1952, Pl. 2:1–4), are all very broad, the holotype has a L:W ratio of about 0.6. However, pygidia of sp. B from the lowermost levels of the Komstad Limestone are presumably equally broad. The pygidia of *M. ringsakerensis* differ from sp. B by being markedly less vaulted, and the doublure is clearly narrower and less pronouncedly sigmoidal; only 11–12 lines are present at pygidial midlength across the doublure.

Megistaspis spp. B and C may also be compared to the slightly younger *M. knyrkoi* (Schmidt, 1906) [*non Megalaspis polyhemus* var. *Knyrkoi* Schmidt, 1906 = *M. laine* Jaanusson, 1956], but of which only two pygidia are known (Schmidt 1906, pp. 37–38; Balashova 1976, pp. 112–113). In the absence of a cranidium the affinities of the species cannot be confidently established. Like the eastern Baltic material, the two somewhat older pygidia from Bornholm, referred to as *M. cf. knyrkoi*, share with sp. B a narrow axis, posteriorly parallel-sided, and a forwards-extending concave border. However, by comparison *M. cf. knyrkoi* seems to have a higher number of pleural ribs and the border is better defined anterolaterally than in sp. B.

The cranidia of *Megistaspis* spp. B and C in some respects resemble *M. (Paramegistaspis)* Balashova, 1976, especially with regard to the course of the facial suture and the development of a preglabellar crest, while the presence of an occipital furrow and weakly impressed lateral glabellar furrows brings members of *M. (Megistaspis)* Jaanusson, 1956 to mind. The fairly steep, concave anterolateral pygidial border is intermediate between the two subgenera; the axial segmentation of the pygidium is of *Paramegistaspis* type. If the hypostome of *M. ringsakerensis* is correctly identified (see Skjeseth 1952, pp. 161–162, Pl. 2:6), it suggests an affinity to *M. (Paramegistaspis)*, but the isolated specimen (which has been examined) may alternatively belong to *M. (P.) estonica*.

Remarks. – *Megistaspis* spp. B–C represent a new species, which, however, is treated in open nomenclature until better preserved material becomes available. Spp. B–C are considered conspecific, and they should be separated as no more than subspecies, but a separation may eventually prove unwarranted altogether. Compared to sp. C, the cranidium of sp. B is broader, the sagittal relief is lower (perhaps owing to

size difference of the studied specimens), glabella is shorter, and the facial sutures diverge more strongly in front of the eyes. The cranidia of spp. B and C both have a periglabbellar crest on the frontal area, strongly impressed preglabbellar furrow, a narrow and slightly vaulted glabella, facial sutures of 'Paramegistaspis outline', mesially indistinct occipital furrow, and comparatively strongly inflated bacculae. The pygidia of sp. B are less triangular in outline, compared to sp. C, but the pygidial L:W ratio of megistaspids is normally quite variable, and the difference is probably unimportant. The axis of sp. B is slightly wider, but pygidia of both species are characterized by an unusually slender axis, 8–9 pairs of moderately distinct pleural ribs, and a markedly sigmoidal doublure with a comparatively broad inner flat part.

Tullberg (1883b) listed *M. planilimbata* from SE Scania. This erroneous report may be based on findings of 'planilimbata-like' *M. sp. B* pygidia; *M. limbata* was on the other hand not listed, and the Tullberg collection from SE Scania (University of Lund) contains no sp. B pygidia, but several specimens of *M. limbata* type 9.

Megistaspis sp. C (cf. sp. B)

Figs. 125–126

Synonymy. – □? 1882 *Megalaspis planilimbata*, Ang.? – Brøgger, pp. 76–77 (occurrence). □v cf. 1952 *Megalaspis limbata* (Boeck) [partim] – Skjeseth, p. 161; Pl. 1:3; non Pl. 1:7 [*Megistaspis limbata* type 7] (occurrence, illustration of cranidium).

Material. – One cranidium, 1 fragmentary librigena and 7 pygidia.

List of material. – □Cranidium A 629a (pim) [MGUH 22.547]. □Librigena A 580? (im). □Pygidia A 587 (im) [MGUH 22.548], A 588 (im), A 597 (im) [MGUH 22.549], A 604 (im), A 629b (im), A 631 (im), A 640 (im).

Occurrence. – *Megistaspis* sp. C has been found solely at Slemmestad in bed M-1, which is correlated with the *M. polyphemus* Zone. *M. limbata sensu* Skjeseth (1952) from the *M. estonica* or *M. polyphemus* Zone of Herramb, southern Norway, covers a mixed material, including sp. C or a closely related form.

Megistaspis sp. C is considered closely related to *M. sp. B*, occurring at the base of the Komstad Limestone of SE Scania.

Description. – Available cranidium 13.5 mm long, largest pygidium 28.5 mm long. The fragmentary small cranidium is poorly preserved (Fig. 125A); it is narrow, PW:L ratio about 2:3, and has a moderately strong sagittal relief, but which presumably reflects the small size. Preserved parts resemble the cranidium of sp. B, except that the mesial impression in preglabbellar area is faint (preservational artefact?), a mesial keel is presumably present immediately in front of glabella, and glabella is relatively longer, stretching (including occipital region) for slightly more than 0.7 of the cranidial length. Occipital furrow impressed only laterally and faintly so, effaced mesially. Median glabellar tubercle cannot be seen, but this may relate to poor preservation. Palpebral lobes damaged, but presumably only slightly to moderately raised above glabella. Anterior branches of facial suture diverge in front of eyes at an angle of about 25° to sagittal line, then turn inwards and converge strongly forwards at an angle of about 120° to sagittal line; mesial part damaged.

Librigena too fragmentary to serve as basis for a description; it appears broad and at least the inner part is only gently vaulted.

Pygidium slightly to moderately convex, more or less triangular in outline. L:W ratio range from 0.65 to 0.82, most specimens show 0.65–0.69 ($N = 5$). Except for the deviating L:W ratio the pygidia are like described for sp. B; minimum axial width at constriction equivalent to 0.15–0.17 of the

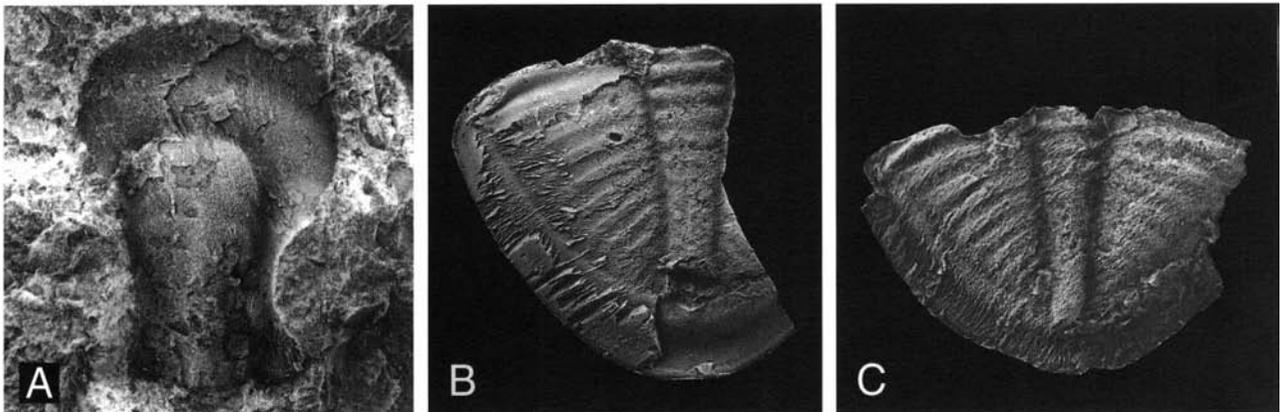


Fig. 125. *Megistaspis* sp. C. □A. Fragment of poorly preserved, exfoliated small cranidium, $\times 4$. MGUH 22.547 (A 629a), bed M-1, Slemmestad. □B. Internal mould of pygidium, $\times 1.5$. MGUH 22.548 (A 587), bed M-1, Slemmestad. □C. Internal mould of juvenile pygidium showing well-defined anterolateral border, $\times 4$. MGUH 22.549 (A 597), bed M-1, Slemmestad.



Fig. 126. *Megistaspis* sp. C. Small, well-preserved cranidium, $\times 5$. PMO 66 330, Herramb. Previously figured by Skjeseth (1952, Pl. 1:3).

pygidial length (mean 0.16; $N = 5$). Regarding the forwards extending border it should be noted that the test apparently is thickened in the bending zone towards the border, so the border concavity is better defined on internal moulds. A juvenile pygidium also shows a better defined border (Fig. 125C). It is inconclusively indicated by the material that the inner flat part of the doublure is narrower than in sp. B. Postaxial outer part of doublure very slightly upturned. No details of the terrace-line pattern are revealed.

Remarks. – The material clearly resembles *Megistaspis* sp. B (see remarks on that species for details and enumeration of differences), and spp. B–C should most likely be separated only at the subspecies level or not at all. The small cranidium of *M. limbata* reported from Herramb by Skjeseth (1952, Pl. 1:3; refigured Fig. 126) is very similar to the cranidium of sp. B and must represent a closely related or identical form. The preglabellar furrow is well-impressed, there is a gently inflated paradoublural crest in front of glabella, the posterior fixigenae show a shallow border furrow and the posterior margin of the fixigenae is slightly raised. The matching pygidium was apparently not found by Skjeseth – or the cranidium may be speculated to represent a juvenile *M. ringsakerensis*.

Brögger (1882, pp. 76–77) wrote that *M. planilimbata* probably occurs in the Hukodden Limestone, a statement which may have been based on findings of *Megistaspis* sp. C.

For comments on the possible affinities to *M. ringsakerensis* (Skjeseth, 1952) and *M. knyrkoi* (Schmidt, 1906), see *Megistaspis* sp. B.

Subfamily Niobinae Jaanusson, 1959

Niobinid material. – Eight complete specimens, 4 cephalae, 60 cranidia, 27 librigenae, 45 hypostomata and 233 pygidia, of which 1 cranidium, 1 hypostoma and 3 pygidia are indeterminate at the species level.

Remarks on Baltoscandian genera

Tjernvik (1956) divided the Scandinavian species till then attributed to *Niobe* Angelin, 1851 among *Niobe* (*s.str.*), *Niobella* Reed, 1931, and a third group, holding only *Niobe explanata* Angelin, 1851, which was stated to be in an uncertain taxonomic position. The latter was transferred to *Gogby* Fortey (1975a). The distinction at generic level between *Niobe* and *Niobella* was adopted by Jaanusson (1959), when he defined the niobinids as a subfamily. Balashova (1976, pp. 122–123) elevated *Niobinae* Jaanusson, 1959 to family rank, comprising *Niobininae* Balashova, 1976, accommodating a medley of genera, and a modified *Niobinae* Jaanusson, 1959, including only *Niobe* and *Niobella* Reed, 1931. The latter two genera are undoubtedly closely related, whereas the *Niobininae* hardly encompasses a monophyletic group, and the diagnostic characters enumerated by Balashova (1976, pp. 130–131) cannot be taken as synapomorphies. It is, accordingly, suggested to abandon *Niobininae* Balashova, 1976.

Niobella was originally distinguished from *Niobe* by hypostomal differences (Reed 1931, p. 462), but the hypostome of *Niobella* changes considerably during evolution (cf. Lake 1942, p. 330; Tjernvik 1956, p. 228; Sdzuy 1958, p. 266), and similar transformations are seen within *Niobe* (cf. Lake 1942; Tjernvik 1956, 1980). Hypostomes of *Niobe* and *Niobella* species from approximately the same stratigraphic level are actually most often very alike, and exhibit no consistent features to serve the distinction between the two taxa. Tjernvik (1956, p. 228) emended the diagnosis of *Niobella* to focus on pygidial features, and it appears that these characters are the only consistent separating characters, valid throughout the ranges of *Niobe* and *Niobella*. Tjernvik (1956) moreover pointed out that the doublure of early *Niobella* species is narrow, whereas *Niobe* always has a wide doublure (see also Tjernvik 1980, pp. 200–201). Also Balashova (1976) emphasized the difference in doublure width, but it is not a consistent feature, as late species of *Niobella* have a wide doublure equal to that of *Niobe* (e.g., *N. lindstroemi*, *N. imparilimbata*, *N. cf. plana*, and, presumably, *N. laeviceps*). The cephalae exhibit no features of proven use to separate *Niobella* from *Niobe*. The idea of Whittington (1965) that poorly developed baculae possibly characterizes *Niobella* is disproved by several late species such as *N. imparilimbata* and *N. plana*.

I prefer to rank *Niobella* as a subgenus of *Niobe*, in accordance with Lake (1942), Sdzuy (1958), Whittington (1965), and Lisogor (*in* Zhuravleva & Rozova 1977); for a different opinion, see Shergold & Sdzuy (1984, pp. 104–106). It is

pointed out that the names *Niobe* (*Niobellina*) Petrunina, 1966 and *Niobe* (*Paraniobe*) Petrunina, 1966 are *nomina nuda*. *Niobe* (*Niobe*) (*s.str.*) is rare outside Baltoscandia (occurring in France, Turkey, s. China) and the bulk of the species hitherto attributed to *Niobe* belong to *N.* (*Niobella*) (see list of non-Baltoscandian species below).

Discussion of Baltoscandian species

With a few exceptions, the subgenus *Niobe* (*Niobella*) characterizes the Billingen–Volkhov Stages and *N.* (*Niobe*) the Hunneberg and Kunda Stages (Fig. 127). *Gog* is an infrequent member of the Komstad Limestone fauna; it ranges through the *M. simon* to *A. expansus* Zones.

Baltoscandian representatives of *Niobe* and *Gog* are listed in Fig. 127 (exclusive of Cambrian and early Tremadocian taxa). Non-Baltoscandian species of *Niobe* at least includes *N.* (*Niobella*) *asiatica* Ivshin, 1956, *N.* (*Niobella*) *baikonurensis* (Ergaliev, 1983), *N.* (*Niobella*) *bajkadamica* Lisogor in Zhuravleva & Rozova, 1977, *N.* (*Niobella*) *bella* Peng, 1984, *N.* (*Niobella*?) *brevicauda* Poulsen, 1937, *N.* (*Niobella*) *chui* (Sheng, 1934), *N.* (*Niobella*) *ciliensis* Liu in Zhou et al., 1977, *N.* (*Niobella*?) *ellipticaudata* (Burskij, 1970), *N.* (*Niobella*?) *feitleri* Holliday, 1942, *N.* (*Niobella*) *flabellifera* Fortey, 1975, *N.* (*Niobella*) *fourneti* Thoral, 1946, *N.* (*Niobella*?) *groenlandica* Poulsen, 1937, *N.* (*Niobella*) *homfrayi homfrayi* Salter, 1866, *N.* (*Niobella*) *homfrayi preciosa* Lu & Zhou, 1981, *N.* (*Niobella*) *homfrayi smithi* Stubblefield, 1933, *N.* (*Nio-*

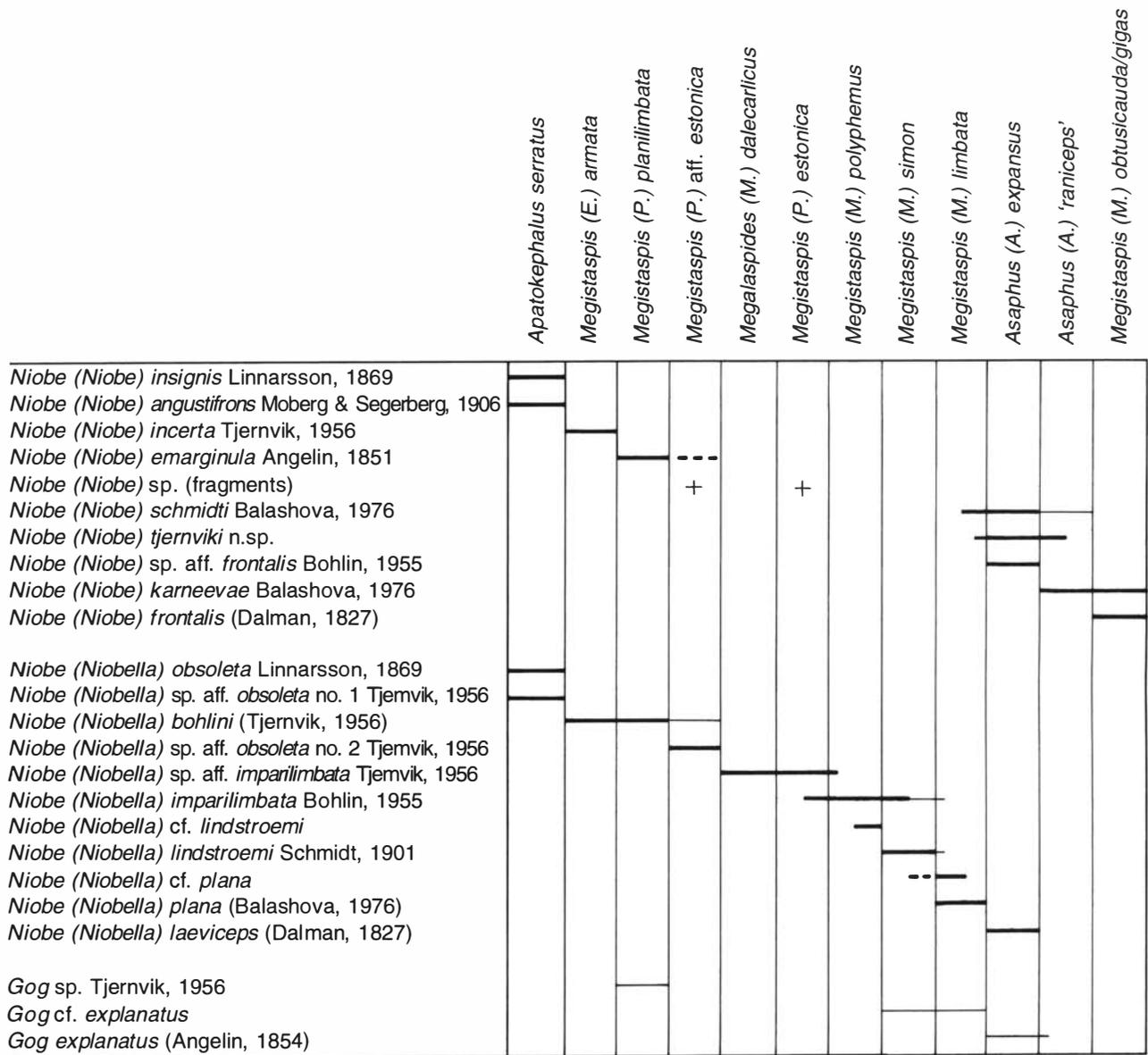


Fig. 127. Stratigraphical distribution of Baltoscandian species of *Niobe* and *Gog* (includes data from Bohlin 1955; Balashova 1976; Tjernvik & Johansson 1980).

bella) *innotata* (Barrande, 1868) [various synonyms discussed by Sdzuy 1955], *N. (Niobe) lignieresi* (Bergeron, 1895) *sensu* Thoral (1935), *N. (Niobella) minor* Liu *in* Zhou *et al.*, 1977, *N. (Niobella) morrissi* (Billings, 1865), *N. (Niobella) oblonga* Lu & Lin, 1984, *N. (Niobella) occulta* Fortey, 1975, *N. (Niobella?) ornata* (Reed, 1945), *N. (Niobella) pamirica* Balashova, 1966, *N. (Niobella) parvula* (Burskij, 1970), *N. (Niobella?) quadratica* (Billings, 1865), *N. (Niobella) sanduensis* Chien, 1961, *N. (Niobella) saryarkensis* Ivshin, 1956, *N. (Niobella) shenjiawamensis* Peng, 1990, *N. (Niobe) sobovana* Dean, 1973, *N. (Niobella) subinsignis* Thoral, 1935, *N. (Niobella) taojiangensis* Liu, 1982, *N. (Niobella) tianjiapingensis* Liu, 1982, *N. (Niobella) yangjiawanensis* Chien, 1961, *N. (Niobe) yangtzeensis* Lu, 1975, and *N. (Niobella) ziyangensis* Zhou *in* Zhou *et al.*, 1982. However, the list is not likely to be complete. Some of the Chinese and Russian species are difficult to evaluate from the published descriptions and figures. Lisogor (*in* Zhuravleva & Rozova 1977) also attributed *Ogygia peltata* Salter, 1866 and *Ogygia discreta* Barrande, 1872, to *Niobe*; both species are now transferred to *Bohemopyge* (see Morris 1988 and Horný & Bastl 1970). For remarks on *Niobella kozhuchensis* Petrunina, 1973, see Shergold & Sdzuy (1984, p. 104). *O. lignieresi* Bergeron, 1895 was assigned to *Niobella* by Dean (1966) and Berard (1986), but the material illustrated by Thoral (1935, Pl. 24:2–4) certainly resembles *N. (Niobe)*, and so does the specimen referred to in open nomenclature (Thoral 1935, Pl. 24:6). *Niobe tenuistriata* Chugaeva, 1958 is here attributed to *Gog*.

Some of the non-Baltoscandian species listed above show a comparatively very broad doublure, e.g., *N. quadratica* (Billings, 1865), *N. elliptica* Burskij, 1970, and *N. groenlandica* Poulsen, 1937, and these taxa may not belong to *Niobella* (*s.str.*) However, this issue is a Pandora's box, and will not be addressed; whatever the circumstances, these species do not belong to *Niobe (Niobe)* (*s.str.*)

NIOBE (NIOBE) Angelin, 1851

Niobe frontalis (Dalman, 1827) was for long a collective name of Lower Ordovician niobinids; the species was re-described by Bohlin (1955, pp. 143–148), and he emphasized that it occurs only in the *M. gigas* Zone. Wandås (1984) described and figured *N. (Niobe) frontalis* from the Killingen Member of the Oslo Region. The species is not present in the East Baltic region according to Balashova (1976), who assigned *N. frontalis sensu* Schmidt (1901) to the new species *N. (Niobe) schmidtii* and *N. (Niobe) karneevae*. Bohlin (1955, pp. 146–148) discussed a form from the 'Expansus' Limestone of Sweden, resembling *N. frontalis sensu* Schmidt (1901). It presumably belongs to a new species according to Bohlin (the relationship to *N. schmidtii* Balashova is unknown). The material of *N. frontalis* reported from the Komstad Limestone of Bornholm by Johnstrup (1891), Grönwall (1916), Funkquist (1919), C. Poulsen (1936), and

others is here identified with *N. (Niobella) imparilimbata* Bohlin, 1955. *N. frontalis* listed by Angelin (1851) from the Komstad Limestone of Fågelsång probably covers *N. (Niobe) tjernviki* n.sp.

N. emarginula Angelin (1851) is another former collective name for various niobinids. A modern description was published by Tjernvik (1956); the species is characteristic of the *P. planilimbata* Zone. Brøgger (1882, pp. 66–71) reported *N. emarginula* from the Hukodden Limestone and Lysaker Member of the Oslo area, but subsequently changed the identification to *N. frontalis* (see Brøgger 1886, p. 51). *N. emarginula frontalis sensu* Brøgger is here identified with *N. (Niobe) schmidtii* Balashova and *N. (Niobella) cf. plana* Balashova.

Niobe volborthi (see Schmidt 1907, pp. 76–77, 102–103) was chosen as type species of *Pogrebovites* by Balashova (1976). *Pogrebovites* largely covers the species group assigned to *Ottenbyaspis* by Bruton (1968) (see discussion of *Ottenbyaspis* and *Panderia*).

NIOBE (NIOBELLA) Reed, 1931

N. (Niobella) laeviceps (Dalman, 1827) was for long a wastebasket designation for a variety of forms (see Hisinger 1837; Brøgger 1882; Holm 1882; Törnquist 1884; Wiman 1905; Moberg & Segerberg 1906, etc.); it was briefly re-described by Bohlin (1955) and Tjernvik (1956), and the latter author emphasized that it is typical of the *A. expansus* Zone. A neotype was designated by Balashova (1976), but, still, *N. laeviceps* is a poorly known species. *N. laeviceps sensu* Brøgger (1882, pp. 66–71) is presumably identical to *N. (Niobella) bohlini* (see Tjernvik 1956). *N. laeviceps sensu* Schmidt (1898, 1901) was divided among *N. laeviceps*, *N. imparilimbata* and *N. plana* by Balashova (1976); *N. laeviceps* (*s.str.*) does not occur in the eastern Baltic area according to her. *N. laeviceps sensu* Moberg & Segerberg (1906, pp. 94–96) represents *Niobella bohlini* and *Platypeltoides serus* (see Tjernvik 1956). The material from the 'Umbonata' Limestone of Bornholm [= Skelbro beds], listed as *Niobe laeviceps* by C. Poulsen (1936, p. 49), is here identified with *N. imparilimbata* Bohlin (see also V. Poulsen 1965). *N. laeviceps sensu* Skjeseth (1952, pp. 169–170), described from Herramb, Norway, was transferred to *N. imparilimbata* by V. Poulsen (1965).

Bohlin (1955, pp. 149–151) defined *Niobe imparilimbata*, based on a pygidium from the Böda Hamn core, northern Öland. The holotype specimen was assumed to originate from the lower part of the 'Limbata' Limestone, but it actually seems to be derived from the upper part of the *M. estonica* Zone (see remarks on *M. polyphemus* for stratigraphic details). *N. (Niobella) imparilimbata* has been subjected to much discussion (cf. Tjernvik 1956, 1980; V. Poulsen 1965; this study); it is here concluded that the range of variation displayed by *N. imparilimbata* is considerable, but even so, *N. imparilimbata* (*s.l.*) comprises two species.

Burskij (1970) described *Niobella parvula* (*A. serratus* Zone) and *N. ellipticaudata* (Billingen – Volkhov equivalent) from Paj-Choj, northern Urals, i.e. still the Baltic-Russian plate. *N. parvula* has an unusually wide border and short axis, and is probably closest to *N. bohlini*. *N. ellipticaudata* has a very broad axis and is not a typical representative of *Niobella*. It may be compared to the North American species *N. quadraticaudata* (Billings, 1865) (see Whittington 1965).

Sexual dimorphism

It has occasionally been suggested that different niobinid taxa possibly just represent sexual dimorphs, see, e.g., *Niobe quadraticaudata* (Billings) vs. *N. morrisoni* (Billings) (Whittington 1965, p. 353) and *Niobe flabellifera* Fortey vs. *N. occulta* Fortey (Fortey 1975a, p. 30). (See also discussion of ‘*Niobe*’ *menapiensis* and ‘*N.*’ *solvensis* by Whittard 1964 and Bates 1969, p. 20). Dimorphism seems to be present within the closely related species *Niobe* (*Niobella*) *imparilimbata* Bohlin and *N. (N.) cf. plana* (Balashova), each embracing a short and a long morph. The short form of *N. cf. plana* (Fig. 138C, E) has a broad glabella, emarginate at front, the anterior glabellar lobe is trapezoidal, the anterior branches of the facial suture meet at a very blunt angle, the paradoublural crest is narrow and its surface is covered with coarse, densely spaced pits, and the pygidium is short with only 6 axial rings and 4 pairs of ribs (Fig. 140F). The long form has an evenly rounded frontal glabellar lobe (Fig. 138A–B), the anterior branches of the facial suture meet at a slightly less blunt angle, the paradoublural crest is wider and exhibits a smooth surface, the pygidium is longer and shows 7 axial rings and 5 pairs of ribs (Fig. 140G).

The dimorphism displayed by *N. imparilimbata* is similar, but less pronounced (Fig. 133A vs. B). The pygidia of *N. imparilimbata* contain a short type with 7 axial rings and 5 pairs of ribs (e.g., Fig. 136D), and a long type with 8 axial rings and 6 pairs of ribs (e.g., Fig. 136A).

It appears most straightforward to interpret the short/long types of *N. cf. plana* and *N. imparilimbata* as sexual dimorphs; the differences do not relate to growth, environment or evolution. The dimorphism of *N. cf. plana* and *N. imparilimbata* resembles *N. flabellifera* vs. *N. occulta*, and I share Fortey’s (1975a) suspicion that these ‘species’ represent sexual dimorphs. The differences between *N. morrisoni* and *N. quadraticaudata*, as discussed by Whittington (1965), are much greater, and these taxa are not believed to represent dimorphs. However, *N. morrisoni*, which basically is similar to *N. imparilimbata*, seems to contain a long and a short type of pygidium (cf. Whittington 1965, Pl. 27:10 vs. Pl. 27:12), differing not only in relative length, but also with regard to the number of pleural ribs (four or five, see also Whittington 1965, p. 353). The figures inconclusively indicate that the number of axial rings may be different as well.

The analogous differences between *N. schmidtii* Balashova and *N. tjernviki* n.sp. cannot be another case of dimorphism,

as these species never occur together, even when being present at the same locality. In general, they are characteristic of separate geographical regions.

The fairly strong variation displayed by various Scandinavian niobinids, e.g., *Niobe insignis* (see Linnarsson 1869, p. 75; Brögger 1882, p. 66; Moberg & Segerberg 1906, p. 94; Tjernvik 1956, p. 225), *N. emarginula* Angelin, *N. obsoleta* Linnarsson, and *N. bohlini* (see Tjernvik 1956), perhaps reflects an unrecognized dimorphism, but much larger materials than hitherto studied are needed to check this notion.

Niobe (*Niobe*) Angelin, 1851

Type species. – *Asaphus frontalis* Dalman, 1827 (SD Vogdes 1890).

Niobe (*Niobe*) *tjernviki* n.sp.

Figs. 128–130

Synonymy. – □1851 *Niobe frontalis* Dalm. [*partim*] – Angelin, p. 14 (occurrence). □v 1886 *Niobe explanata* Ang. [*partim*] – Brögger, Pl. 2:35 (illustration of hypostome). □v ?1901 *Niobe frontalis* Ang. – Lindström, p. 63; Pl. 5:19–21 (brief comments on hypostome, illustrations of hypostome).

Derivation of name. – In honour of the late Dr. Torsten Tjernvik, who has made an outstanding contribution to the investigation of the Lower Ordovician of Sweden.

Holotype. – Cranidium LO 7112 (LU 105) (Fig. 129C) from Fågelsång, bed interval 18–23 (basal part of the *A. expansus* Zone).

Paratypes. – Cranidium MGUH 22.551 (F 162a) (Fig. 129B) with disarticulated librigena MGUH 22.550 (F 162b) (Fig. 129A); pygidium LO 7111 (LU 102) (Fig. 130A), both from the basal part of the *A. expansus* Zone, Fågelsång. The former sample is from bed 19, the latter originates from bed interval 18–23.

Other material. – Nine cranidia, 6 hypostomata and 31 pygidia.

List of additional material. – □Cranidia S 1610 (im), K 1005 (pim), K 1117 (pim), K 1211 (t), F 76 (im), F 108 (im), F 301 (im), LU 6 (im), LU 129 (im) [LO 7119]. □Hypostomata S 1506 (im) [MGUH 22.552], K 1212 (im), F 86 (im), F 103 (im), LU 144b (im) [LO 7123], LU 144c (im). □Pygidia S 1703 (im), S 1727 (im), K 297 (c), K 827 (t), K 877 (im), K 883? (im), K 885? (im), K 1010 (t) [MGUH 22.553], K 1098 (im), K 1109 (em), K 1115 (is), K 1126? (t), K 1128 (t), K 1129 (pim), K 1136 (t), K 1195 (im), F 39 (c), F 43? (im), F 84 (im) [MGUH 22.554], F 90 (im) [MGUH 22.555], F 114 (em), F 127 (im), F 160 (im), F 163 (im/is), F 179 (im), F 182 (im), LU 3 (im), LU 67 (t), LU 87 (em), LU 136 (im), LU 158 (im) [LO 7126].

Occurrence. – *Niobe* (*N.*) *tjernviki* n.sp. ranges from the upper part of the *M. limbata* Zone (bed 9) and into the *A. expansus* Zone (bed 20) at Fågelsång, but is rare below bed 18 (base of

the *A. expansus* Zone). The species first appears at the base of the *A. expansus* Zone at Skelbro (bed +13) and Killeröd (bed +22). *N. (N.) tjernviki* n.sp. is rather frequent at Killeröd site b in bed interval 0 to 9 (upper part), which is correlated with the *A. 'raniceps'* Zone.

The new species is currently unknown outside the Komstad Limestone domain (but see remarks below).

Diagnosis. – Large for a *Niobe*, and with extensive dorsal terrace lines (cephalon and pygidium). Facial sutures unite in an ogive at front; cephalic axial furrows show outwards flare between palpebral lobes; occipital furrow straight; posterior fixigena pronouncedly broad (exsag.), with large, elongate baccula, pointing obliquely forwards-inwards. Pygidium with six pairs of pleural ribs showing no, or just a faint backwards deflection outside paradoublural line, no inflation of distal rib ends; test surface with minute pits arranged at random and in rows adjacent to the terrace lines.

Description. – Rather large for a *Niobe*, largest cranium (holotype) about 32 mm long, largest pygidium 36 mm long. The specimens from the *A. 'raniceps'* Zone are generally smaller than those from the base of the *A. expansus* Zone. Cranium of low convexity, FW:L ratio about 0.7, PW:L ratio slightly below 1.2. Glabella rather broad (tr.), and stretches (including occipital ring) for about 0.9 of the total cranial length. Glabella only slightly expanding forwards, maximum width is just in front of the eyes, about 0.3 of the glabella length (including occ. ring) from glabellar front, minimum width, shortly in front of occipital furrow, is about 0.75 of the maximum glabellar width. Glabella moderately vaulted, delimited by fairly deep axial furrows confluent with preglabellar furrow. Axial furrow makes a slight, but characteristic outward bulge at level with anterior half of the palpebral lobe; the flare is most distinct on internal moulds. Glabellar front truncate with a faint mesial impression, most distinct on internal moulds; frontal lobe of glabella assumes a trapezoidal outline owing to the truncate front. Four pairs of faint lateral glabellar furrows visible on internal moulds (Figs. 128, 129C). F4 most distinct, situated immediately in front of anterior corner of palpebral lobe, running transversely almost from axial furrow to a point near sagittal line, then shallows up, not joining across glabella. F3 slightly less impressed, situated level with the midline of palpebral lobes, close to sagittal line; this pair appears as fairly wide, shallow, rounded impressions. F2 very faintly impressed, situated about level with the mesial tubercle, resembling F3 in outline and relative position, but situated slightly lower on glabella. F1 situated level with minimum glabellar width, running transversely from axial furrows, fading out short off sagittal line. F1 is, compared to F4, somewhat less impressed, subtriangular in outline, with a straight posterior margin. Minute mesial tubercle situated at the imaginary transverse line connecting posterior corners of palpebral lobes; a single specimen indicates that the tubercle appears relatively larger when the test is intact. Occipital furrow fairly well-im-

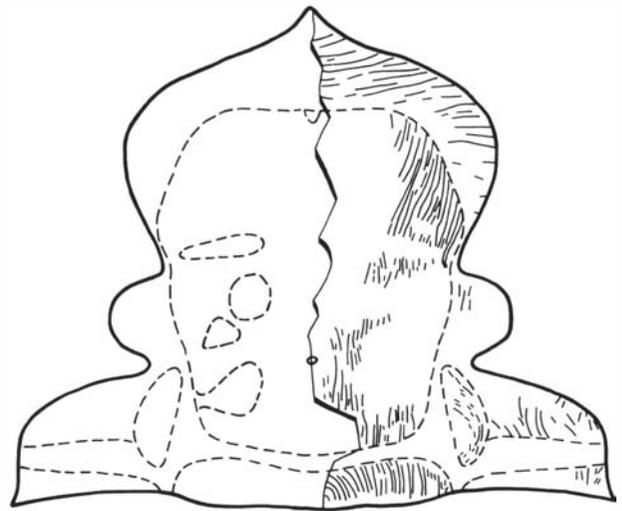
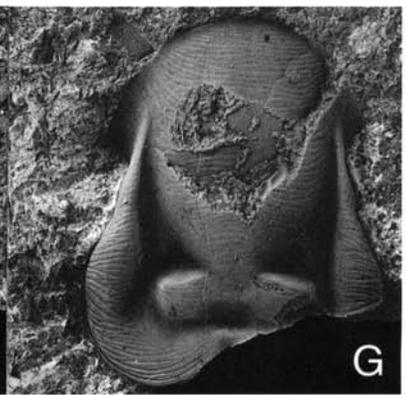
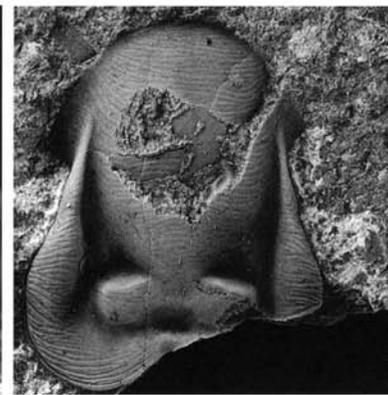
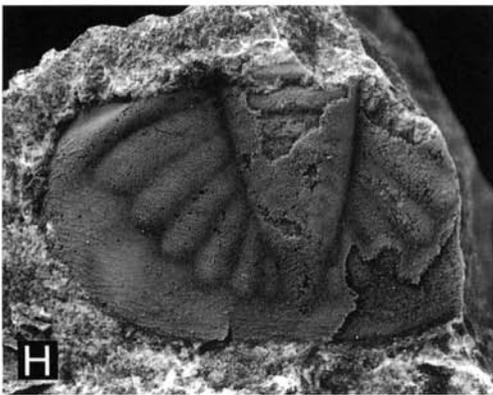
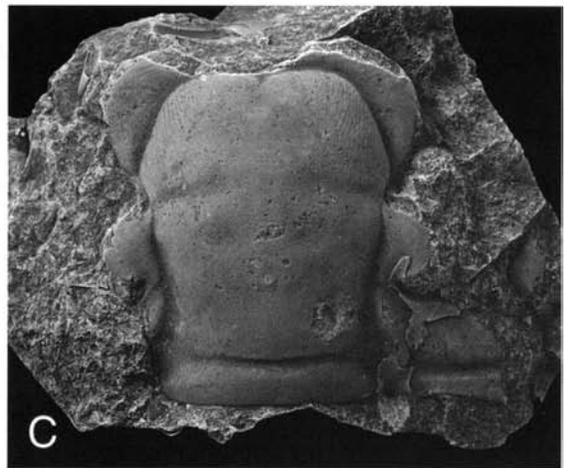
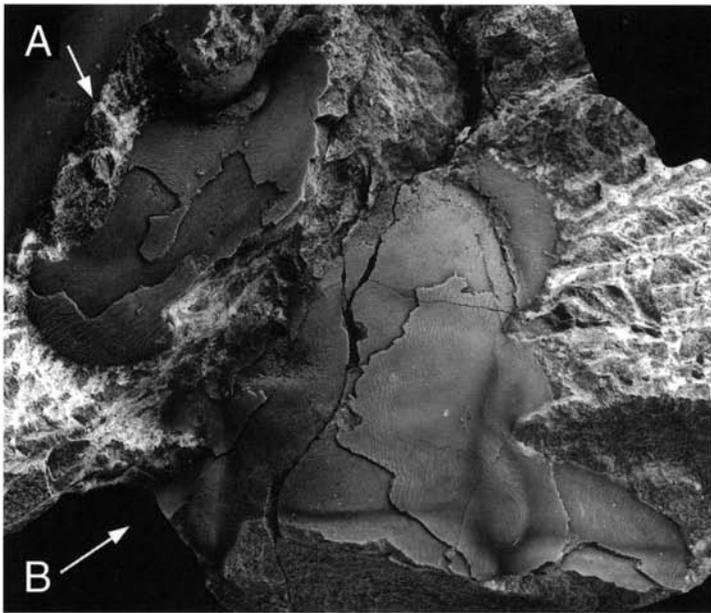


Fig. 128. Reconstruction of cranium of *Niobe (N.) tjernviki* n.sp., left half exfoliated. Based on specimens LO 7112 (LU 105), MGUH 22.551 (F 162) and K 1211, supplemented by K 1005, F 108 and F 301.

pressed, narrowest mesially; close to axial furrows it widens markedly, forming shallow triangular depressions at the junctions with the axial furrows. Occipital furrow almost straight with only a gentle and even backwards curvature, and, accordingly, the occipital ring is but slightly narrower mesially, as the posterior cranial margin is straight. Occipital ring comparatively wide (sag.), sagittally occupying slightly less than 0.15 of cranial length; it is flat and level with the rear part of glabella. Frontal area entirely occupied by flat border, sloping in lateral directions away from sagittal line. Anterior area of fixigena tapers out in posterior direction and stops immediately in front of eye. Palpebral area of fixigena almost flat, very gently downsloping in abaxial direction; it is narrow (tr.), corresponding to only about 0.25 times the width of the adjacent part of glabella. Palpebral lobes small, length (exsag.) equivalent to about 0.2 of the cranial length; posterior corner situated about 0.4 of the

Fig. 129. *Niobe (Niobe) tjernviki* n.sp. □A. Paratype. Fragmentary, partly exfoliated librigena showing terrace-line sculpture; $\times 2.5$. MGUH 22.550 (F 162b), bed 19, Fågelsång. □B. Paratype. Fragmentary cranium with partially preserved cuticle showing delicate terrace-line sculpture (cf. Fig. 128), $\times 2.5$. MGUH 22.551 (F 162a), bed 19, Fågelsång. □C. Holotype. Internal mould of cranium, $\times 1.5$. LO 7112 (LU 105), Fågelsång. □D. Internal mould of detached cephalic doublure (ventral view), $\times 1.5$. LO 7119 (LU 129), Fågelsång, loc. E21b. □E. Exfoliated hypostome showing imprints of cuticle terrace-line sculpture, $\times 2$. Ar 24 082, Fågelsång. The specimen has previously been figured by Brögger (1886, Pl. 2:35). □F. Fragmentary exfoliated hypostome, $\times 3$. LO 7123 (LU 144b), Fågelsång, loc. E21b. □G. Exfoliated hypostome, stereo-pair, $\times 3$. MGUH 22.552 (S 1506), bed +13, Skelbro. □H. Small pygidium, $\times 5$. MGUH 22.553 (K 1010), bed 0, Killeröd site b. □I. Internal mould of large pygidium, $\times 1.5$. MGUH 22.554 (F 84), bed 18, Fågelsång. □J. Latex cast of pygidium showing cuticle terrace-line sculpture, $\times 2$. LO 7108 (LU 98), Fågelsång.



cranial length from posterior margin. Posterior area of fixigena slopes outwards; it is comparatively broad (exsag.) and short (tr.), stretching for about 0.25 (middle of fixigena) of the total cranial length, and transversal width corresponds to less than 0.6 times the width of the occipital ring. Posterior margin runs straight out from axial furrow, then, at one third of the genal length (tr.) from axial furrow, turns very slightly backwards. Posterior border virtually flat and shows the same slope as the remaining part of posterior fixigena; greatest border width is attained distally. Posterior border furrow wide, moderately impressed, straight, running outwards, very slightly oblique-backwards; the furrow is not continuous with occipital furrow, but join axial furrow behind the baccula. Bacculae elongate, pointing obliquely forward-inward (strike ca. 165°). Anterior sections of facial suture diverge forwards in front of the eyes, then curve uniformly inward-forwards, to meet in an ogive forming a short V-shaped snout. Posterior section of facial suture runs almost straight forward from posterior margin, then turns sharply inwards, describing a very flat curve, running to posterior inner corner of palpebral lobe.

The cranial terrace-line pattern is comparatively extensive (Fig. 128); the terrace lines are short, but well-impressed, and can also be seen on well-preserved internal moulds. The sagittal area between F4 and the occipital furrow is presumably also covered with terrace lines, but this area is exfoliated in all specimens available. The entire cranium, except axial and posterior border furrows, is covered with densely spaced small pits, which are not impressed on internal moulds. The pits on glabella and bacculae tend to form rows immediately adjacent to the terrace lines at their inner side, but pits are also randomly distributed.

The librigena at hand is impaired (Fig. 129A). Lateral border flat, delimited by a shallow, wide border furrow. The lateral border changes slope posteriorly and the border furrow shallows up, so no border is defined posterolaterally. Genal angle obtusely rounded. Doublure broad; paradoublural furrow shallow, wide, and connects with posterior border furrow of the fixigena; paradoublural ridge only gently inflated and comparatively wide. Well-defined, small eye socle present. Test surface covered with densely spaced terrace lines in the genal angle region, arranged subparallel to outer margin, but close to the edge the lines bend steeply forwards and intersect margin. Paradoublural ridge with short, moderately spaced lines. Densely spaced, short lines, running obliquely forwards-outwards, present on the posterior part inside paradoublural crest; almost no lines occur in front of the eye. The surface is also covered with densely spaced, well-impressed pits, more dense and better impressed than on the cranium.

A detached cephalic doublure (Fig. 129D) most likely belongs to *N. tjernviki* n.sp. It is strongly concave anterolaterally, inner part subvertical, outer part almost horizontal. Inner margin flexed down mesially, forming a flattened socle for the hypostome; socle bounded anteriorly by a wide, fairly

deep furrow. The doublure extends inwards for a short stretch along posterior margin; inner limit of doublure appears here to coincide with posterior border furrow of cephalon. Doublure covered with coarse, continuous terrace lines, also impressed on the surface of internal moulds. Rearmost lines are finer, bending inwards. A total of 18–19 lines were counted across the doublure anterolaterally; 8 lines are present sagittally.

Hypostome rather large, largest specimen about 17 mm long. Outline roughly rectangular, W:ML ratio close to 3:4; greatest width is across posterolateral borders. Median body subrectangular in outline, reaching the rather strongly curved anterior margin; deep, triangular premacular pits situated close to posterior end. Anterior lobe of median body gently vaulted, long, and constitutes main part of the median body; W:L ratio of anterior lobe is about 7:10. The conspicuous premacular pits form a marked constriction of the median body, thereby delimiting the much shorter posterior lobe (= consoles *sensu* Lindström 1901; maculae *sensu* Balashova 1976). Posterior slope of premacular pits smooth, elongate, flat surfaces, interpreted as maculae following Lindström (1901); they are strongly inclined in anterior direction, with an oblique-backwards strike of about 110° to sagittal line. Anterior wings, ascending steeply in dorsal direction, merge with median body anteriorly. Lateral border commences at a point about 0.4 the length of the anterior lobe of median body from anterior margin. Anterior part of lateral border is a narrow (tr.) crest, raised (ventral view) considerably above the lateral furrow, it widens slightly backwards and descends level with the maculae and merges with the posterior border. The wide, flat posterior border is bilobate, as posterior margin is provided with a rather deep mesial notch stretching inwards for about 0.1 of maximum hypostomal length. Lateral border furrows shallow anteriorly, but deepen considerably backwards and are confluent with premacular pits. Posterior border furrow wide and shallow, deepest mesially. The test is not preserved in any of the specimens available, but internal moulds show imprints of external terrace lines. Entire hypostome covered with closely spaced, continuous terrace lines, except (apparently) in the furrows, in the premacular pits, and on the macular surfaces; line configuration is apparent from Fig. 129E–G. Specimen K 1212 has minute patches of test preserved in the lateral furrows, and it appears that terrace lines actually are present, but more weakly impressed than on the remaining part of the hypostome. These lines seem to be quite densely spaced, running along the furrows, with irregularities close to the premacular pits.

Pygidium parabolic in outline, L:W ratio about 0.6. Axis prominent and distinctly vaulted, except posteriorly; axial width at anterior margin averages 0.3 of the total pygidial width. Axis tapers evenly all the way back to terminal piece, axial ramp then tapers more strongly and descends to the border. Axial rings separated by undulating furrows, which are moderately impressed anteriorly, but progressively fade

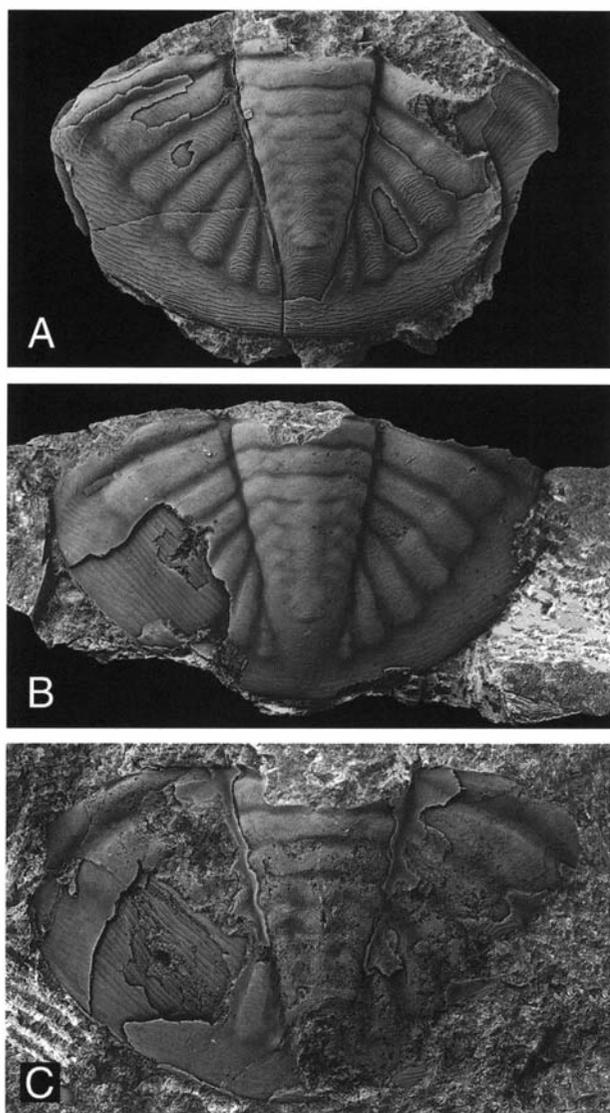


Fig. 130. *Niobe (Niobe) tjernviki* n.sp. □A. Paratype. Partly exfoliated pygidium showing cuticle terrace-line sculpture, $\times 1.5$. LO 7111 (LU 102), Fågelsång. □B. Internal mould of pygidium, $\times 1.5$. MGUH 22.555 (F 90), bed 18, Fågelsång. □C. Internal mould of pygidium showing part of doublure, $\times 1.5$. LO 7126 (LU 158), Tommarp.

rearwards, particularly in the mesial part, which is smooth behind axial rings nos. 5–6. Anterior ring furrow, delimiting anterior half-ring, is straight, successive furrows undulate (e.g., Fig. 129I); there is a total of 8 rings in addition to the anterior articulating half-ring and the terminal piece. The rings are swollen into a low knob immediately above the axial furrows. Axial segmentation rather effaced on testaceous material. Terminal piece shaped as a very small, cuesta-like platform, with a convex posterior edge vertically descending to the axial ramp. Axial furrows wide and shallow, but the axis is well set off by a marked change of slope. Pleural fields show 6 pairs of conspicuous ribs, separated by wide interpleural furrows; a well-defined anterior half rib is

bounded by a wide, moderately impressed furrow. The pleural ribs are almost straight, but some specimens show a very slight backwards deflection outside the intersection with paradoublural line (Fig. 130B). Anterior pair of pleural ribs almost transverse, successive pairs point more steeply backwards, and the very short posterior pair is almost parallel to sagittal line. Wide, flat, almost horizontal border set off by a change of slope and the terminating pleural ribs; a border furrow is practically absent. The boundary between pleural fields and border is gently scalloped as the lobed ends of the pleural ribs bulge slightly onto the border; the interpleural furrows are basically confluent with the border. It appears that the interpleural furrows, particularly the anterior two pairs, occasionally have an extremely faint strongly backward deflected continuation on the border, outlined by the lack of surface ornamentation. Maximum border width attained at midline across pygidium, level with the end of second and third rib pair, occupying about 0.3 of the transverse pygidial width at that level. Minimum border width is postaxially. Anterolateral parts of border show a slight increase in outwards slope. Articulating facets long (tr.), slanting only moderately forwards, inclined at an angle of about 30° .

U-shaped terrace lines, opening backwards, occur on the sagittal part of the axis, even continuing across the transverse furrows. Short terrace lines are present in narrow bands on the anterior lateral flanks of each axial ring (Fig. 129J). Roughly transverse lines are densely spaced on the axial ramp; slightly concave terrace lines run across the pleural ribs. The border is covered with dense lines, shorter on the inner part, more continuous and more abundant along the outer margin. The lines are subparallel to the margin of the pygidium, the inner ones with a slight inward direction. The pygidial surface is also provided with numerous small pits, except in the axial furrows. The pits are randomly dispersed where terrace lines are absent, i.e. laterally on axis and in the interpleural furrows; where terrace lines are present, and particularly on the pleural ribs and the border, the pits are arranged in rows on the outer side of, but immediately adjacent to each terrace line. The terrace lines, but not the pits, are impressed on internal moulds.

Doublure concave, very wide, anteriorly occupying about half of the pygidial width, presumably with a deep V-shaped notch in the axial region. Paradoublural line is indicated dorsally by a very faint constriction of the pleural ribs (e.g., Fig. 129I). The doublure is covered with 18–20 coarse, continuous terrace lines.

Affinities. – *Niobe (Niobe) tjernviki* n.sp. is readily separated from the smaller *N. (N.) schmidtii* Balashova by being more elongate, the facial sutures are less strongly diverging in front of the eyes, and meet in an ogive anteriorly, the palpebral lobe is less arcuate, the occipital furrow is basically straight, not gently undulating, the baccula is less prominent and more elongate, the posterior fixigena is broader (exsag.), the para-

doublural ridge on librigena is wider and less inflated, the eye socle is smaller and the cephalic terrace-line pattern is much more extensive. The hypostome of *N. tjernviki* n.sp., compared to *N. schmidtii*, is smaller and less elongate, which is peculiar, as the species overall is more elongate and larger. Furthermore, it has larger premacular pits, less backward striking maculae, the terrace lines are finer, the posterior lobe of the median body is less pronouncedly bilobate, and the posterior border lobes are wider (tr.), and so overall, the hypostome appears wider. *N. tjernviki* n.sp. has a downflexed socket for the hypostome, whereas *N. schmidtii* has a lunate incision in the cephalic doublure. The pygidium has 6 pairs of ribs, instead of 5 as in *N. schmidtii*; the ribs show almost no backward deflection outside the paradoublural line and no distal swelling, and the pygidial surface ornamentation is much more extensive. The pygidial doublure of *N. tjernviki* n.sp. is also wider and not quite as concave.

N. (Niobe) karneevae Balashova is rather similar to *N. (N.) schmidtii*, and is therefore distinguished from *N. tjernviki* n.sp. mainly on the same characters. Furthermore, *N. karneevae* has up to 27 terrace lines on the pygidial doublure, compared to about 20 in *N. tjernviki* n.sp..

N. tjernviki n.sp. is separated from *Niobe* cf. *frontalis* sensu Bohlin (1955) by the more distinctly trapezoidal anterior glabella lobe, the slightly different outline of the facial suture anterior to the eyes (no minute incision) and at front ('nose'); the elongate bacculae strike obliquely forward-inward, not forward-outward as in *N. cf. frontalis*, the distal end of posterior fixigena is slightly pointed rearwards, and the external terrace-line pattern is more extensive. The pygidium of *N. tjernviki* n.sp. is more elongate, compared to *N. cf. frontalis*, the axis and the border are comparatively narrower (tr.), and the external terrace lines are finer and much more abundant, particularly on the pleural fields. It should, however, be noted that the pygidium figured by Bohlin (1955, Pl. 6:10) is tiny (about 6 mm long), and juvenile pygidia are often relatively broader and with more restricted terrace-line ornamentation than adults.

The cranidium of *N. tjernviki* n.sp. is distinguished from *N. (Niobe) frontalis* (Dalman) by the comparatively smaller palpebral lobes, the smaller mesial tubercle, the less distinct glabellar muscle scars (well-impressed in *N. frontalis*), the straight occipital furrow (mesial 'loop' in *N. frontalis*), the less inflated bacculae, the distinctly broader (exsag.) posterior fixigena with less impressed border furrow and less raised posterior border, and the somewhat different and slightly more extensive external terrace-line pattern. Judging from the figures of the *N. frontalis* hypostome in Angelin (1851, Pl. 11:2b), Brögger (1886, Pl. 2:37), and Wandås (1984, Pl. 10D), the hypostome of *N. tjernviki* n.sp. is distinctly less elongate, broader, with less partitioned posterior lobe of median body (clearly bilobate in *N. frontalis*, divided by a mesial depression), the posterior border is shorter (exsag.), and the median notch in the posterior margin is likewise shorter (sag.). The pygidium of *N. tjernviki* n.sp. is

clearly more elongate than the pygidium of *N. frontalis*, which is the most obvious difference. Furthermore, the pleural ribs are marginally less inflated, compared to *N. frontalis*, there are 8 axial rings (7 in *N. frontalis*), and they are but slightly less well-defined. The border is slightly wider in *N. frontalis*. The terrace-line patterns are basically similar, but more dense in *N. tjernviki* n.sp. *Niobe tjernviki* n.sp. is clearly of '*frontalis* type', and is believed to be closer to this species, than to *N. schmidtii* and *N. karneevae*.

Exfoliated cranidia of *N. tjernviki* n.sp. strongly resemble those of the Turkish species *N. sobovana* Dean, 1973, but the Scandinavian species shows less strongly forward-diverging facial sutures in front of eyes, and F4 appears to be more transverse, whereas it goes obliquely forward-inwards in *N. sobovana* (cf. Dean 1973, Pl. 10:10). However, the best distinguishing character between cephalia is the more extensive terrace-line sculpture on the Scandinavian species (cf. Dean 1973, Pls. 10:1 and 11:1). The pygidium of the Turkish species is on the other hand rather different from that of *N. tjernviki* n.sp., as it has clearly backward-deflected lobes outside paradoublural line, and the border is rather poorly set off from the pleural fields.

The pygidia called *N. (Niobe) yangtzeensis* by Lu (1975) (upper Arenig, s. China) are distinguished from those of *N. tjernviki* n.sp. by showing a more distinct axial segmentation and the border is broader.

Remarks. – The hypostome from Östergötland, central Sweden, assigned to *Niobe frontalis* by Lindström (1901, Pl. 5:19) is remarkably similar to *N. tjernviki* n.sp., the only difference regards a slightly smaller backward strike of the maculae than typical for *N. tjernviki* n.sp. The specimen cannot belong to *Niobe frontalis* (s.str.), as it is much broader (tr.), the anterior margin is more strongly curved, and the posterior marginal notch is shallower (cf. Angelin 1851, Pl. 11:2b; Brögger 1886, Pl. 2:37). The hypostome of *Niobe* sp. (cf. *frontalis*) sensu Bohlin (1955) is unknown, and the hypostome in question perhaps represents that form. The specimen has been examined, but the small preserved part of the dorsal exoskeleton does not permit a confident identification.

One of the hypostomes from Fågelsång, identified with *N. explanata* by Brögger (1886, Pl. 2:35), belongs to *N. tjernviki* n.sp. The specimen was drawn too narrow by Brögger; it is refigured on Fig. 129E.

Niobe (Niobe) schmidtii Balashova, 1976

Fig. 131

Synonymy. – □v 1882 *Niobe emarginula*, Ang. [*partim*] – Brögger, pp. 68–71; Pls. 7:7–7a; 8:7; 12:13 (description, occurrence, illustrations of cephalon, pygidia, doublure). □1901 *Niobe frontalis* Dalm. sp. [*partim*] – Schmidt, pp. 107–110; Textfigs. 61–64; non Pl. 9:11; non Pl. 10:8 [= *Niobe karneevae* Balashova] (description, occurrence, illustrations of enrolled specimen, cephalon, pygidia). □1976 *Niobe*

schmidti sp.n. – Balashova, pp. 127–129; Pls. 38:8; 39:1–2 (description, occurrence, illustrations of complete specimen, cephalon, hypostome, pygidium).

Holotype. – Enrolled specimen figured by Schmidt (1901, Textfigs. 61–63).

Material. – Four complete specimens, 1 cephalon, 1 hypostoma, and 5 pygidia.

List of material. – □ Complete specimens F 294 (flattened (c)), A 448 (thorax missing (pim)) [MGUH 22.556], A 469 (fragmentary (pim)), A 1160 (c). □ Cephalon PMO 83321 (t). □ Hypostoma A 452 (pim) [MGUH 22.557]. □ Pygidia K 356 (t), F 292 (pim) [MGUH 22.559], A 437 (im), A 561 (pim), GM 1919.51 (pim) with thoracic segments [MGUH 22.558].

Occurrence. – *N. schmidti* occurs sparsely in bed interval A-31 to A-37 at Slemmestad; a single specimen is from bed A-51. These beds belong to the *A. expansus* Zone. A pygidium was found at Fågelsång in bed 1, which represents the top of the lower subzone of the *M. limbata* Zone. Complete specimen F 294 is from a loose slab (Fågelsång, E21a). The lithology shows that the sample is from the *M. limbata* Zone, perhaps bed 6 (in case the upper subzone of the *M. limbata* Zone). Pygidium K 356 is from bed +27, Killeröd, which belongs to the lower part of the *A. expansus* Zone.

The presence in the *M. limbata* Zone of western Scania is unusual, as *Niobe* (*Niobe*) has been reported from the Volkhov Stage nowhere else in Baltoscandia (cf. Tjernvik 1980, p. 202). *N. (N.) schmidti* is characteristic of the BIII α Zone of the eastern Baltic area, but also ranges into the BIII β Zone (Balashova 1976). The species may have a wide distribution in the *A. expansus* Zone of Scandinavia (cf. Tjernvik 1980, p. 202).

Description. – The new material is insufficient for a redescription; the reader is referred to Brögger (1882, pp. 68–70), Schmidt (1901, pp. 107–110) and Balashova (1976, pp. 127–129). For comparative purposes the most important characteristics of the species may be summarized as follows. *Niobe schmidti* is relatively broad (tr.), cephalon and pygidium are up to twice as wide as long. Cephalon short with wide glabella, faintly emarginate at front; palpebral lobes strongly arcuate, wide (tr.); eye socle well-developed; anterior branches of facial suture diverge very strongly in front of the eyes, then turn inwards and merge smoothly in front of glabella. Baculae conspicuous, oval; mesial glabellar tubercle comparatively prominent, albeit small; occipital furrow gently undulating; paradoublural ridge narrow, quite well-defined; cephalic terrace lines sparse, present only on anterior lobe of glabella and on librigenae. Hypostome narrow (tr.), elongate, large; anterior lobe of median body rather rectangular, posterior lobe deflected slightly backwards laterally, maculae with a pronounced lateral-backward strike; anterior wings flexed moderately in dorsal direction; posterior border well-developed with a deep central notch; terrace lines coarse. Pygidium transverse with only 5 pairs of pleural ribs, which show a slight, but characteristic constriction at

paradoublural line followed by a gentle backward deflection outside the line. Distal part of pleural ribs, outside paradoublural line, are gently inflated. Surface of test with few, widely spaced terrace lines, in addition to small pits. Pygidial doublure pronouncedly concave and rather narrow, stretching for about one third of the pygidial width at anterior margin; inner doublural edge faintly scalloped with impressions of pleural furrows; total number of terrace lines on doublure less than 20.

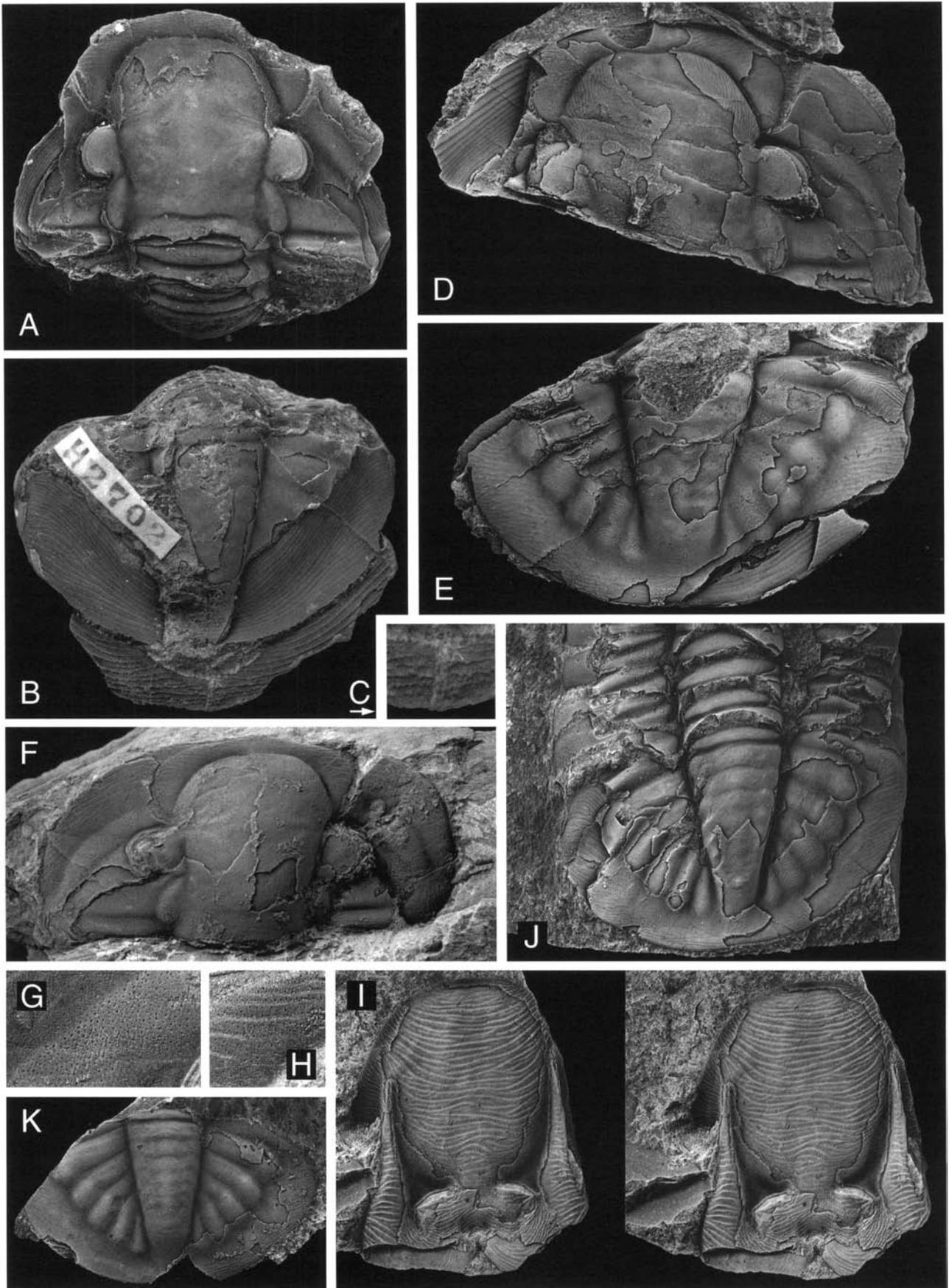
Affinities. – *N. (Niobe) schmidti* Balashova is distinguished from *N. (N.) frontalis* (Dalman) by being relatively shorter and broader, the anterior branches of the facial sutures do not meet in an ogive in front of glabella, hence the frontal area is shorter (sag.), the anterior fixigena is wider (tr.), the anterior lobe of glabella is more strongly trapezoidal, the palpebral lobes are wider (tr.) and more arcuate, the distribution of dorsal terrace lines on cephalon is much more restricted, and the glabellar muscle areas are less impressed. The pygidium of *N. schmidti*, compared to *N. frontalis*, has only five pairs of pleural ribs instead of six, and the distal ends, outside the paradoublural line, are gently inflated and backwards deflected. Furthermore, the axis of *N. schmidti* is less funnel-shaped.

N. schmidti is distinguished from the contemporaneous *Niobe* sp. (cf. *frontalis*) *sensu* Bohlin (1955) by the different outline of the facial suture, particularly with regard to the posterior parts of anterior branches, the palpebral lobes are larger, the posterior fixigenae are longer (tr.), the cephalic terrace lines are more restricted; the pygidium has a more slender axis (tr.) and only 5 pairs of pleural ribs with backward deflected distal ends, and the terrace lines on the border are presumably less abundant (the juvenile state of the pygidium figured by Bohlin (1955, Pl. 6:10) excludes confident conclusions regarding the terrace-line pattern).

The differences from *N. (Niobe) karneevae* are discussed by Balashova (1976, p. 130) and from *N. (Niobe) tjernviki* n.sp. in the section on that species (pp. 171–172).

Remarks. – Brögger (1882) assigned the niobinid material from the Huk Formation ['3c'] of Oslo to *Niobe emarginula* Angelin; later the identification was changed to *Niobe frontalis* Dalman (Brögger 1886, p. 51). *N. 'emarginula'* was stated to occur at least in subunits 3c α and 3c β , being most common in the latter. Brögger's description of *Niobe 'emarginula'* refers chiefly to material of *Niobe (Niobe) schmidti*; all specimens illustrated represent this species. The material listed from 3c α belongs largely or entirely to *Niobe (Niobella) cf. plana* (Balashova), but may theoretically have included *N. (Niobella) lindstroemi* Schmidt as well (see remarks on that species below). Brögger's distinction of a relatively shorter and a relatively longer form of *N. 'emarginula'* may reflect the mixed state of his material.

The enrolled specimen figured by Brögger (1882, Pl. 12:13) is drawn incorrectly with regard to the median suture. The 'suture' is an artefact, caused by a crack (Fig. 131A–C).



N. schmidti has nowhere been found together with the coeval *N. tjernviki* n.sp. This circumstance seems to exclude the possibility that these species merely represent sexual dimorphs, although the features separating them essentially are similar to the character set separating the dimorphs of, respectively, *N. (Niobella) cf. plana* and *N. (Niobella) imparilimbata*.

Niobe (Niobella) Reed, 1931

Type species. – (OD) *Niobe homfrayi* Salter, 1866.

Niobe (Niobella) lindstroemi Schmidt, 1901

Fig. 132A–I

Synonymy. – □1898 *Niobe laeviceps* Dalm. – Schmidt, p. 35 (listed). □1901 *Niobe Lindströmi* n.sp. – Schmidt, pp. 105–107; Pls. 9:12; 10:1–4, 7; 12:1, ?non Pl. 12:2 (description, occurrence, illustrations of complete specimens, cephal, hypostome, pygidia). □1905 *Niobe Lindströmi* F.S. – Lamansky, pp. 54, 169 (occurrence). □v non 1936 *Niobe lindströmi* Schm. – C. Poulsen, p. 49 (listed). [= *Niobe (Niobella) imparilimbata* Bohlin 1955]. □1976 *Niobella lindströmi* (F. Schmidt, 1901) – Balashova, pp. 124–125; Pl. 37:1–5, 7–10 (description, designation of lectotype, occurrence, illustrations of cephal, hypostome, pygidia). □1980 *Niobella lindstroemi*–Tjernvik, pp. 191, 192, 202, Figs. 10I–J (occurrence, illustrations of cranidium with fixigena, pygidium).

Lectotype. – Complete specimen, figured by Schmidt (1901, Pl. 10:1–2), designated by Balashova (1976).

Material. – Two cephal, including one with hypostome, 1 cranidium with thoracic segments, 5 cranidia, 1 librigena, 1 hypostoma and 16 pygidia. Five additional pygidia are referred to as *N. cf. lindstroemi*.

List of material. – □Cephal A 660a (t) (fragmentary) [MGUH 22.562], A 672b (fragmentary, (t)) with hypostoma (pim) [MGUH 22.560]. □Cranidia A 9 (im) with thoracic segments, A 624 (pim), A 662 (t), A 688 (pim), A 689 (im) [MGUH 22.561], A 709a (im). □Librigena A 652a (t). □Hypostoma A 658 (im). □Pygidia A 613 (t), A 647 (t) [MGUH 22.563], A 652b (t), A 654 (t), A 660b (t), A 661 (t), A 672a (pim), A 673 (t), A 680 (im) [MGUH 22.564], A 683 (t) A 709b (im), A 710 (im), A 722a (pim), A 735 (t), A 739 (im), A 761 (t).

Additional material. – [*Niobella cf. lindstroemi*] □Pygidia K 27 (t), K 188 (t) [MGUH 22.567], K 226 (t) [MGUH 22.565], K 442? (pim), K 458 (t) [MGUH 22.566].

Occurrence. – The species is frequent at Slemmestad in beds M-2 to M-5, single specimens have been found in bed M-6. This interval constitutes the *M. simon* Zone.

The material listed as *N. cf. lindstroemi* are from Gårdlösa-1 (beds H and K), Gårdlösa-2 (bed L) and Killeröd (beds –3 and +7). The latter occurrence is surprising, as it is within the lower part of the *M. limbata* Zone; the remaining specimens are from the *M. simon* Zone (for further remarks, see below).

N. (Niobella) lindstroemi Schmidt is a stratigraphically important and very frequent member of the fauna in the *M. simon* Zone of Sweden and BIIβ of the eastern Baltic area (Lamansky 1905, p. 169; Tjernvik 1980, pp. 178–179, 192); the species possibly ranges from the upper part of the *M. polyphemus* Zone (Tjernvik 1980, p. 191).

Description. – See also Schmidt (1901). Small for a *Niobella*, largest cranidium 16 mm long, largest pygidium 13 mm long. Cranidium almost as long as wide and of low convexity. Glabella rather elongate, narrow (tr.), and stretches (including occipital ring) for about 0.9 of the cranidial length. Glabella only slightly expanding forwards, maximum width attained shortly in front of the eyes, about 0.3 of the glabellar length from front; minimum width, halfway between the eyes and occipital furrow, is about 2/3 of maximum glabellar width. Glabella gently vaulted, front truncate and may show a very faint mesial impression. Only one pair of weakly indicated lateral glabellar furrows on internal moulds, situated at the narrowest part of glabella behind the eyes; the lateral furrows run from axial furrows, but fade out and are not joined across glabella. A small mesial tubercle, visible also on testaceous specimens, is situated level with posterior inner corners of palpebral lobes. Internal moulds show an indistinct mesial keel running from a point just in front of the palpebral lobes almost to occipital furrow. Occipital furrow shallow, best defined on internal moulds, sagittally showing a gentle backwards curve; abaxially it shallows up and does not join axial furrows. Occipital ring occupies slightly more than 0.1 of the cranidial length; it is flat and not raised above the rear of glabella. No preglabellar field; frontal area entirely occupied by the flat border, sloping very gently away from sagittal line. Anterior area of fixigena tapers out immediately in front of eye. Palpebral area of fixigena relatively wide (tr.), corresponding to about 0.35–0.40 of the width of the adjacent portion of glabella. Palpebral lobe length (exsag.) equivalent to or slightly less than 0.25 of the cranidial length, inner posterior corner situated about 0.4 of the cranidial

Fig. 131. *Niobe (Niobe) schmidti* Balashova, 1976. □A–C. Exfoliated enrolled specimen, dorsal views of cephalon and pygidium, ×2. The mesial crack in the cephalic doublure (close-up in C, ×4) was drawn as a median suture by Brögger (1882, Pl. 12:13). PMO 2702, Lysaker Member, Oslo. □D–E. Fragmentary, largely exfoliated enrolled specimen, dorsal views of cephalon and pygidium, ×2. MGUH 22.556 (A 448), bed A-34, Slemmestad. □F–H. Cephalon slightly distorted by compaction, ×1.5. G, close-up of paradoublural ridge, showing punctate cuticle, ×6. H, close-up of frontal area, showing cuticle terrace-line sculpture, ×6. PMO 83321, Lysaker Member, Huk, Bygdøy, Oslo (Størmer coll.). □I. Internal mould of hypostome, stereo-pair, ×1.5. MGUH 22.557 (A 452), bed A-35, Slemmestad. □J. Partly exfoliated pygidium with thoracic segments, ×2. MGUH 22.558 (GM 1919.51), Lysaker Member, Huk, Bygdøy, Oslo. □K. Internal mould of pygidium, ×2. MGUH 22.559 (F 292), bed 1, Fågelsång.

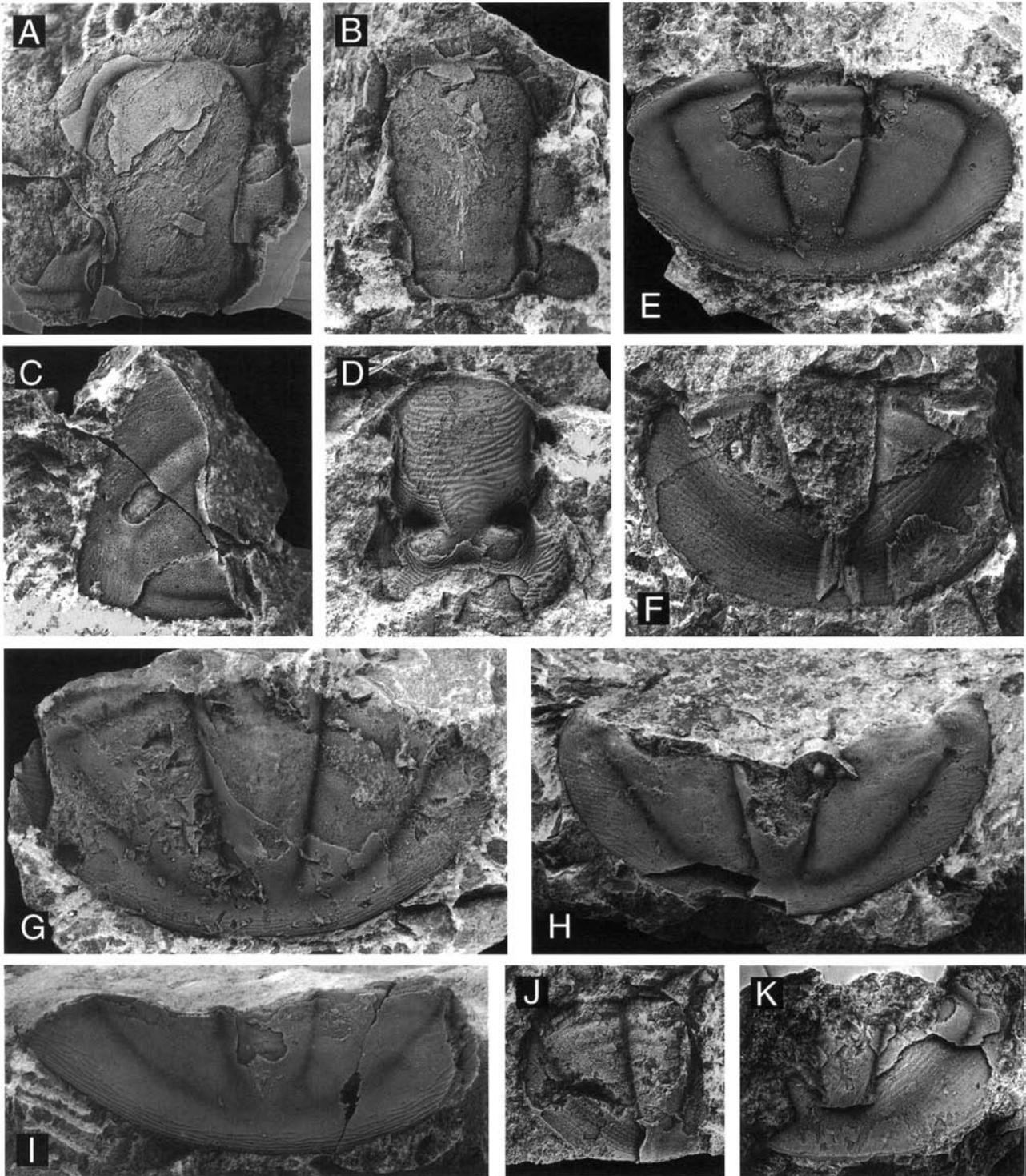


Fig. 132. □A–F. *Niobe (Niobella) lindstroemi* Schmidt, 1901. □A. Latex cast of largely exfoliated fragmentary cephalon, $\times 3$. MGUH 22.560 (A 672), bed M-4, Slemmestad. □B. Damaged internal mould of cranidium, $\times 4$. MGUH 22.561 (A 689), bed M-4, Slemmestad. □C. Fragmentary cephalon showing most of librigena, $\times 4$. MGUH 22.562 (A 660a), bed M-4, Slemmestad. □D. Partly exfoliated hypostome, $\times 4$. MGUH 22.560 (A 672), bed M-4, Slemmestad. □E. Pygidium with intact cuticle showing sparse terrace-line sculpture, $\times 4$. MGUH 22.563 (A 647), bed M-2, Slemmestad. □F. Internal mould of pygidium showing doublure, $\times 3$. MGUH 22.564 (A 680), bed M-4, Slemmestad. □G–I. *Niobe (Niobella) cf. lindstroemi* Schmidt, 1901. □G. Partly exfoliated pygidium, $\times 2.5$. MGUH 22.565 (K 226), bed +7, Killeröd. □H. Fragmentary pygidium, $\times 2.5$. MGUH 22.566 (K 458), bed H, Gärdlösa-1. □I. Fragmentary pygidium, $\times 2.5$. MGUH 22.567 (K 188), bed -3, Killeröd. □J–K. *Niobe (Niobella) aff. lindstroemi*. □J. Fragmentary internal mould of pygidium, $\times 3$. MGUH 22.568 (A 602), bed M-1, Slemmestad. □K. Latex cast of fragmentary internal mould of pygidium showing the doublure, $\times 3$. MGUH 22.569 (A 599), bed M-1, Slemmestad.

length from posterior margin. Posterior area of fixigena fairly short (exsag.), equivalent to about 0.2 (middle of fixigenae) or slightly less of the total cranial length, the width (tr.) corresponds to $\frac{2}{3}$ the width of the occipital ring. Bacculae slender, elongate, pointing obliquely forward-inward (strike in the size order of 170°). Posterior border barely convex, sloping gently in anterior direction; abaxially the border widens slightly. Border delimited by an almost straight, wide and moderately impressed furrow, which join the axial furrow behind the baccula. Anterior sections of facial suture diverge strongly forwards, then curve inward-forwards, meeting at an angle of about 145° in front of glabella. Posterior section of facial suture runs almost straight forward from posterior margin for a short way (generating a truncate appearance of the posterior fixigena), then turns in adaxial direction, describing a gentle curve all the way to the posterior corner of palpebral lobe. A few longitudinal terrace lines occur laterally on frontal glabellar lobe, and transverse lines are present on the anterior border; terrace lines are otherwise absent. The cranial surface is covered with densely spaced, moderately impressed small pits.

Librigena quite wide (tr.), lateral margin almost straight from genal angle to a position just in front of the eye, then curves evenly inwards. Flat anterolateral border delimited by shallow furrow; the border tapers rearwards, and disappears posterolaterally. No posterior border. Genal angle obtusely rounded. Eye socle narrow. Paradoublural ridge narrow, only gently inflated, anteriorly reaching eye socle. Paradoublural furrow shallow, wide, and runs to the posterior border furrow of the fixigena, but becomes indistinct posteriorly. Terrace lines occur only near outer margin, but the entire surface is covered with densely spaced, moderately impressed pits.

A hypostome, 10.8 mm long, was found inside cephalon A 672b (Fig. 132D), another hypostome is 8 mm long. General hypostomal outline as described for *Niobe tjernviki* n.sp.; W:L ratio about 9:10; greatest width is across posterolateral borders. Median body subrectangular in outline, reaching the anterior, gently curved and very faintly pointed margin, no anterior border. Anterior lobe occupies main part of the median body, and shows W:L ratio of 7:10; anterior lobe is separated from the short posterior lobe by small, but very deep premacular pits. Maculae slope moderately forwards, and strike obliquely backwards-outwards at an angle of about 110° . Posterior lobe divided into two moderately inflated swellings by a weakly impressed mesial depression; the swellings are sloping backwards from the maculae. Anterior wings appear to be narrow (tr.), but are defective in the specimens. Lateral and posterior border and furrows as in *N. (Niobe) tjernviki* n.sp. Mesial notch in posterior margin deep, stretching for 0.10–0.15 of the maximum hypostomal length. Terrace-line pattern generally as in *N. tjernviki* n.sp.. The lines are comparatively coarse, and somewhat irregular

posteriorly on anterior lobe of median body, anastomosing. About 20 lines per 5 mm were counted on the anterior lobe of median body in the largest specimen.

Pygidium transverse elliptical in outline, posterior margin occasionally slightly truncate, L:W ratio averages 0.55 ($N = 7$). Axis fairly prominent, distinctly vaulted and well-elevated above pleural fields; axial width at anterior margin occupies about 0.25–0.30 of the pygidial width. Axis tapers evenly all the way back to paradoublural line, thence the postaxial ramp tapers more strongly, and descends rapidly to the border, thereby generating a somewhat funnel-shaped axial appearance. Well-preserved pygidia, and in particular juveniles, may possess a faint postaxial ridge (Balashova 1976, p. 125; Tjernvik 1980, p. 192); such a ridge has not been seen in the specimens at hand. Axial segments usually nebulous on testaceous material, a single internal mould shows the presence of at least 6 axial rings in addition to the anterior articulating half-ring and terminal piece, but the true number of axial rings is presumably 7 or 8 (8 according to Schmidt 1901, p. 106, and Balashova 1976, p. 125, but this number may include the anterior half-ring, cf. Schmidt 1901, Pl. 10:2). Axial furrows wide and shallow, but axis is well set off by a marked change of slope. Axial furrows posteriorly confluent with lateral border furrows; hence there is no postaxial border furrow, and the postaxial ramp merges imperceptibly with border. Pleural fields gently convex, sloping slightly in lateral direction; they are typically smooth, but a few specimens exhibit vague traces of ribs in the anterior part. Internal moulds show one to three pairs of low ribs inside paradoublural line. Anterior half rib well-defined, bounded by a moderately impressed, rather wide furrow; the half rib is somewhat elevated above pleural fields, except close to axis. Border almost flat, virtually horizontal, delimited by a shallow, wide, but relatively well-defined border furrow, which stops at the intersection with the axial furrows, and no border furrow is present postaxially. Maximum border width attained anterolaterally, level with interpleural furrow between first and second pair of pleural ribs; border width decreases gradually rearwards. Anterolateral margins of pygidium flexed slightly downwards. Articulating facets long (tr.), triangular, inclined about 45° . Terrace lines occur only close to the outer pygidial margin, but the test surface is covered with densely spaced, moderately impressed small pits. Doublure moderately wide, stretching inwards for about one third of the pygidial width at anterior margin; it is strongly concave, with a steeply inclined inner part and a flat, horizontal outer part, and provided with a deep V-shaped axial notch. Paradoublural line is indicated on internal moulds by the termination of the faint pleural ribs. The doublure is covered with 18–20 coarse terrace lines.

Affinities. – *Niobe (Niobella) lindstroemi* is readily separated from most other species of *Niobella* as it is relatively small, the glabella is elongate and shows only one pair of faint lateral

furrows, the occipital furrow is weak, the bacculae are slender, the eyes are positioned relatively rearwards and the posterior fixigenae are narrow (exsag.); the pygidium has a highly vaulted axis with obsolescent segmentation, the pleural fields are nearly smooth, and the postaxial border furrow is effaced. Besides, the external surface ornamentation consists of densely spaced small pits with only local presence of terrace lines.

N. laeviceps (Dalman) resembles *N. lindstroemi* with regard to the general lack of terrace lines and also shares a rather smooth, unsegmented pygidium, but *laeviceps* is characterized by a markedly broader (tr.), comparatively short glabella, larger palpebral lobes situated more anteriorly, a more forwards position of the mesial glabellar tubercle (situated slightly in front of transverse line connecting the posterior corners of the palpebral lobes), broader (exsag.) posterior fixigenae, and a pygidium showing a less distinctly vaulted axis, a less marked boundary between the pleural fields and border, and a well-defined axial termination without axial ramp. *N. laeviceps* has a surface ornamentation consisting of alternating small and large pits (Tjernvik 1956, p. 234), whereas the pits are of uniform size in *N. lindstroemi*.

N. bohlini (Tjernvik) is distinguished from *N. lindstroemi* by having larger eyes, glabella fails to reach the facial suture in front of the eyes, the bacculae are ill-defined, the pygidium shows four pairs of ribs (albeit faint on the external side of test), and the greatest border width of pygidium is attained posterolaterally. However, the two species have many features in common, such as an elongate glabella, short (exsag.) posterior fixigenae and weakly developed occipital furrow, the cephalic surface ornamentation mainly consists of pits with only subordinate terrace lines (present on the borders and frontal glabellar lobe), and the pygidia are almost similar. It is reasonable to assume a close relationship, and *N. bohlini* is a possible ancestor to *N. lindstroemi*.

Remarks. – Five pygidia from SE Scania probably belong to *N. lindstroemi*, as indicated especially by the axial termination with a postaxial ramp (Fig. 132G–I), but the specimens, up to 17 mm long, are somewhat larger than typical for *N. lindstroemi* (this study, see also Schmidt 1901, p. 107). In the absence of matching cephalic material the specimens are referred to as *N. cf. lindstroemi*.

Niobe (*N.*) *lindstroemi* has not previously been reported from Norway, but it was possibly included in *Niobe* ‘*emarginula*’ by Brögger (1882, p. 70). However, only one pygidium of *N. lindstroemi* was noted in the collections of the Paleontological Museum, Oslo, and it appeared to have been collected recently.

The peculiar ‘*Lichas*-like’ furrows on the glabella, described by Schmidt (1901, p. 105, Pl. 12:2), have not been seen in any of the available specimens. Balashova (1976, p. 124, vide synonymy list) excluded this and another specimen (Schmidt 1901, Pl. 12:1) from *N. lindstroemi*, but she did not explain why. These specimens, however, are certainly niobinids.

Niobe (*Niobella*) sp. aff. *lindstroemi*

Fig. 132J–K

Material. – Pygidia A 599 [MGUH 22.569], A 602 [MGUH 22.568], and A 606?, which all are very poorly preserved internal moulds.

Occurrence. – The material is from bed M-1 at Slemmestad (*M. polyphemus* Zone). Tjernvik (1980, p. 191) listed *N. lindstroemi* from the top of the *M. polyphemus* Zone of Sweden.

Remarks. – The pygidia have a smooth axis and nearly smooth pleural fields, and thereby resemble *N. (Niobella) lindstroemi*. One of the specimens also shows a faint, very narrow postaxial ridge, a feature which is unusual among Scandinavian species of *Niobe*, and has been reported only from small pygidia of *N. lindstroemi* (Balashova 1976, p. 125; Tjernvik 1980, p. 192). However, maximum border width of the discussed pygidia is attained posterolaterally, thence the border tapers markedly forwards, and the well-developed anterior half rib is raised considerably above the pleural fields. This combination is distinctive of *Niobe (Niobella) bohlini* (see Tjernvik 1956, p. 231). Settlement of the taxonomic status must await collection of better preserved specimens.

Niobe (Niobella) imparilimbata Bohlin, 1955

Figs. 133–137

Synonymy. – □? 1901 *Niobe laeviceps* Dalm. [*partim*] – Schmidt, p. 103, Textfig. 60 (occurrence, illustration of pygidium). □v 1936 *Niobe explanata* Ang. [*partim*] – C. Poulsen, pp. 49, 50 (listed). □v 1936 *Niobe frontalis* (Dalm.) [*partim*] – C. Poulsen, pp. 49, 50 (listed). □v 1936 *Niobe laeviceps* (Dalm.) – C. Poulsen, pp. 49, 50 (listed). □v 1936 *Niobe lindströmi* Schm. – C. Poulsen, pp. 49, 52 (listed). □v 1936 *Niobe* sp. – C. Poulsen, p. 49 (listed). □v 1936 *Niobe* n.sp. – C. Poulsen, p. 49 (listed). □v cf. 1952 *Niobe laeviceps* (Dalman) 1827 – Skjeseth, pp. 169–170; Pl. 2:5, 12, 13 (description, occurrence, illustrations of cranidium and pygidia). □v 1955 *Niobe imparilimbata* nov. sp. – Bohlin, pp. 149–151, Pl. 6:11–12 (description, occurrence, illustrations of librigena and pygidium). □1956 *Niobella imparilimbata* (Bohlin, 1955) – Tjernvik, p. 232, Pl. 5:10 (short description, occurrence, illustration of pygidium). □? 1956 *Niobella* sp. aff. *imparilimbata* (Bohlin) [*partim?*] – Tjernvik, p. 233, non Textfig. 37C; non Pl. 5:11–14 (description, occurrence). □v 1965 *Niobella imparilimbata* (Bohlin, 1955) – V. Poulsen, pp. 69–72; Pls. 2:2–5; 3:1–2 (description, discussion of species, occurrence, illustrations of cranidia, hypostome and pygidia). □1976 *Niobella imparilimbata* (Bohlin, 1955) [*partim*] – Balashova, pp. 123–124; non Pl. 37:6 [= ? *Niobe lindstroemi* Schmidt]] (short description, occurrence).

□1980 *Niobella imparilimbata sensu stricto*—Tjernvik, p. 191 (occurrence). □v 1980 *Niobella imparilimbata sensu lato [partim]*—Tjernvik, pp. 187, 188, 191 (occurrence).

Holotype.—Pygidium Ar 4230, figured by Bohlin (1955, Pl. 6:12). See remarks below for comments on the stratigraphical level of the type specimen.

Material.—Twenty-seven cranidia, 22 librigenae, 23 hypostomata, 1 detached cephalic doublure, 2 thoracic segments, and 115 pygidia.

List of material.—□Cephalic doublure S 186 (im) [MGUH 22.578]. □Cranidia S 63 (im) [MGUH 22.572], S 78 (im) [MGUH 22.570], S 91 (im), S 108 (em), 110 (im), S 113 (im), S 117? (im), S 119? (im), S 132 (t, fragmentary), S 135a (im), S 145 (im), S 157 (t), S 184a (im), S 205 (em), S 208a? (im), S 319 (im), S 436a (im) [MGUH 22.571], S 436b (im), S 520a (pim), S 762? (im) fragment, S 839 (pim), S 857? (t), S 1115? (im), K 614 (c), K 768 (t) [MGUH 22.576], GM 1884.1626 (t) [MGUH 22.573], LU 88b (pim). □Librigenae S 98 (im), S 135b (im), S 139a (im), S 139b (im), S 185 (im), S 214 (im), S 241 (im), S 250 (pim), S 298 (im), S 368 (pim) [MGUH 22.575], S 371b (im), S 520c (pim), S 534 (im) [MGUH 22.574], S 607 (im), S 639 (im), S 697 (c), S 709 (im), S 697 (c), S 844 (im), S 857 (c), S 1681 (c), LU 52 (pim). □Hypostomata S 48 (im), S 82 (im), S 90 (im), S 146 (im), S 195 (im) [MGUH 22.579], S 210 (im), S 230 (im), S 256a (im), S 256b (em), S 281b (im), S 296 (im), S 300a (im), S 341 (pim) [MGUH 22.577], S 374 (im), S 595 (im), S 611 (im), S 1681d (im), K 87 (t), GM 1951.41 (im) [MGUH 22.580], DGU-6 (im), LU 21 (em), LU 43b (t) [LO 7092], LU 50-10 (c). □Thoracic segments S 80 (t) [MGUH 22.581], S 647 (im). □Pygidia S 3 (im), S 18 (im), S 25 (pim) [MGUH 22.590], S 37 (im) [MGUH 22.592], S 45 (im), S 55a (im) [MGUH 22.588], S 55b (im), S 69 (pim), S 93 (pim), S 96 (im), S 109 (im), S 133a (im) [MGUH 22.585], S 133b (em), S 141 (im) [MGUH 22.589], S 152 (im), S 172a (pim), S 172b (t), S 175? (pim) [MGUH 22.593], S 184b (im), S 187 (im), S 196 (im), S 198 (c), S 208b (em) [MGUH 22.583], S 210a (pim) [MGUH 22.582], S 254 (im), S 255 (im), S 281a (im), S 282? (c), S 294 (im), S 297a (im), S 297b (im), S 299 (im), S 300b (im), S 306a (im), S 306b (im), S 308 (im), S 352 (pim), S 354 (im), S 371a (im), S 372? (im), S 373? (im), S 376 (im), S 403 (im), S 414? (im), S 431 (im), S 446 (im), S 454 (t), S 493 (im), S 520b (im), S 532 (im), S 555 (c), S 615 (im), S 654 (t), S 657 (c), S 660 (im), S 674 (im), S 679 (c), S 708 (im), S 711 (c) [MGUH 22.586], S 712a (pim), S 712b (pim), S 712c (pim), S 721 (im), S 736 (im), S 739? (im), S 746 (c), S 757 (im/em), S 787 (c), S 795 (c), S 799 (t, fragmentary), S 803 (t, dissolved), S 804? (pim), S 831 (t), S 851? (em), S 857 (pim), S 875 (c), S 943? (c), S 1247? (c), S 1678 (im), S 1681a (pim), S 1681b? (im), K 12? (im), K 43 (c), K 48 (t), K 66 (im), K 230 (im) (c), K 441 (im), K 679 (t), K 735 (t) [MGUH 22.587], K 744 (c), MGUH 23.080A (im), GM 1869.1429 (im), GM 1874.32 (im), GM 1874.69 (im) [MGUH 22.591], GM 1874.70 (t), GM 1875.1488 (im), GM 1877.1942 (t) [MGUH 22.584], GM 1885.660a (im), GM 1885.660b (im), GM 1938.44 (c), GM 1987.3419 (im), GM 1988.13 (im), DGU 2-1 (im), DGU 2-2 (em), DGU 2-3 (c), DGU 2-5 (im), LU 9 (em), LU 88a (im), LU 25 (t), LU 43a (c), LU 43c (pim), LU 50-3? (im), LU 50-16 (t), LU 95? (im), LU 96 (im).

Occurrence.—*N. imparilimbata* is frequent in the lower half of the *M. polyphemus* Zone at Skelbro, but ranges through at least half of the succeeding *M. simon* Zone (beds nos. –21 to –6). Three poorly preserved specimens from beds –4, +2 and +5 may also represent *N. imparilimbata*, in case extending the range into the lower subzone of the *M. limbata* Zone.

The species also occurs in the *M. simon* Zone at Killeröd and Gårdlösa-1 and -4a, ranging from the base of the zone (beds nos. K to –6). A poorly preserved, tentatively assigned pygidium was found in bed +7 at Killeröd (lower subzone of *M. limbata* Zone).

N. imparilimbata seems to be restricted largely to the lower half of the *M. polyphemus* Zone in mainland Sweden (Tjernvik 1980), but is present also in the uppermost part of the *M. estonica* Zone at least on northern Öland and in the Finngrundet core (see discussion below). *N. imparilimbata* has been reported from the eastern Baltic BII α –BII β Zones by Balashova (1976).

Diagnosis.—Large for a *Niobella*; doublure wide. Facial suture meet in an ogive at front, so frontal area is long (sag.); bacculae well defined; posterior fixigenae broad (exsag.). Paradoublural ridge wide, moderately inflated. Pygidium shows variable L:W ratio, seven to eight axial rings, well defined postaxial ramp, five to six pairs of pleural ribs, generally with extremely faint, or no pleural furrows; broad, flat border tapers backwards. External terrace lines of cra-

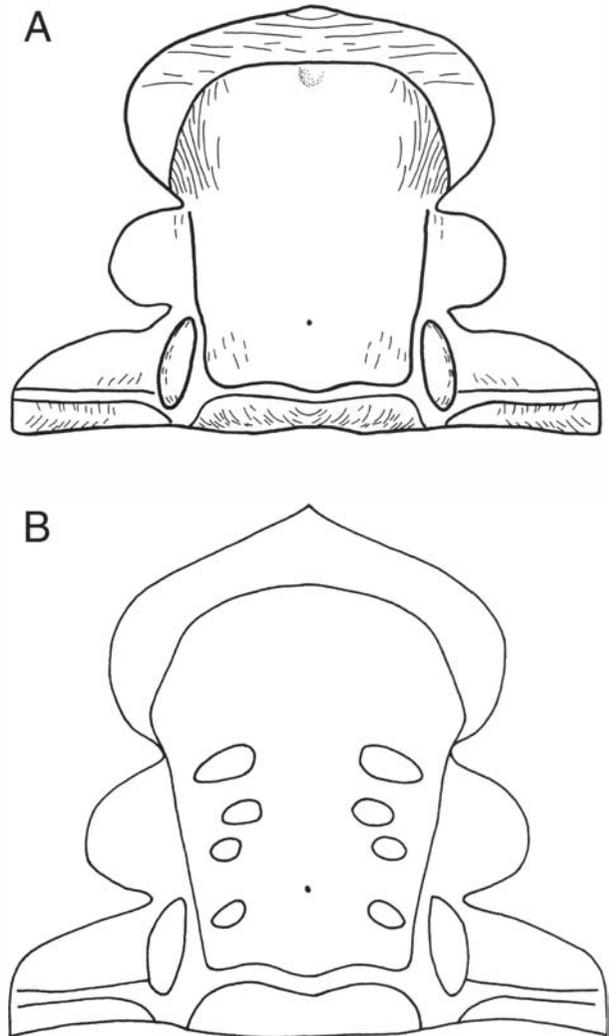
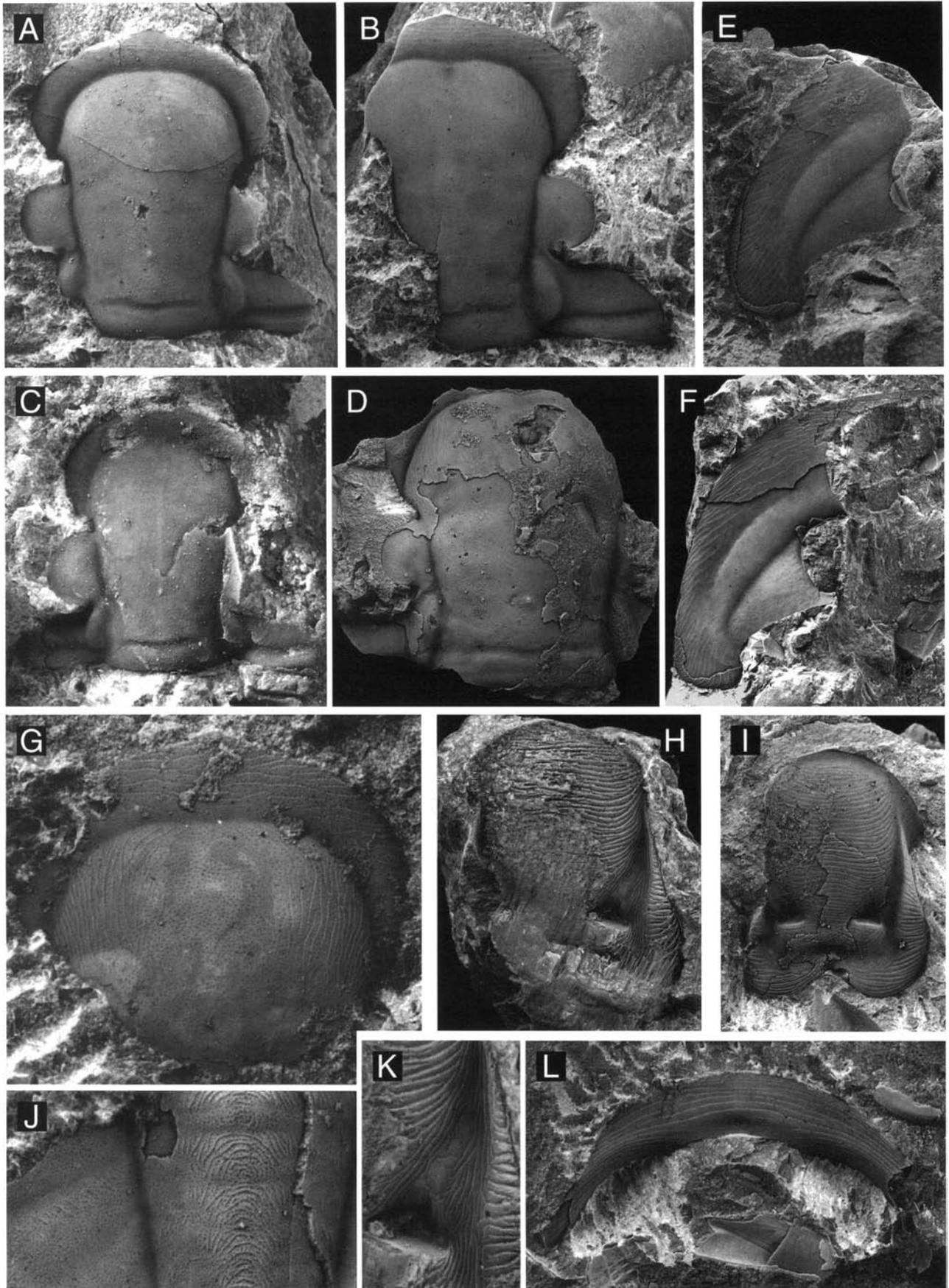


Fig. 133. Cranidia of *Niobe* (*Niobella*) *imparilimbata*. □A. Broad form. Distribution of terrace lines on exterior surface. □B. Narrow form. The reconstructed exfoliated specimen shows the configuration of muscle scars on glabella.



nidium and pygidium fine, associated with densely spaced, weakly impressed small pits; lines always present anterolaterally on glabella, and on anterior two pairs of pleural ribs of pygidium. [Emended from Bohlin 1955.]

Description. – The description is complementary to the account of *N. imparilimbata* published by V. Poulsen (1965, pp. 70–71). Large for a *Niobella*, largest cranidium about 40 mm long, largest pygidium 35 mm long. Glabella front evenly rounded (Fig. 134A) or with gentle mesial impression, generating a more truncate appearance (Fig. 134B). Frontal area relatively long, sagittally occupying about 0.14 of the cranidial length. Posterior fixigena comparatively broad (exsag.), medial width corresponds to about 0.2 of the cranidial length, length (tr.) equal to about 0.8 times the width of occipital ring. Baculae fairly inflated, elongate, pointing forwards, slightly inwards (strike in the size order of 170–175°). Posterior border furrow moderately impressed, delimiting very gently convex border, widest distally, showing almost the same slope as the remainder of posterior fixigena. Anterior sections of facial suture meet (sag.) at an angle close to 140° ($N = 4$) or about 150° ($N = 2$) (Fig. 133A, B), see remarks below on dimorphism. Fine, openly spaced terrace lines are usually present on various parts of cranidium, notably on frontal area and laterally on frontal glabellar lobe (Fig. 133A); one small specimen have more abundant lines on glabella (Fig. 134G), and a very large specimen shows terrace lines only laterally on frontal lobe (Fig. 134D). Entire cranidial surface covered with moderately impressed, densely spaced small pits.

Librigena with flat lateral border anteriorly and anterolaterally, delimited by a wide and shallow furrow. Border tapers gently in posterior direction; border furrow shallows up level with anterior edge of posterior fixigena, and coincidentally the margin turns convex, so no lateral border is defined posterolaterally. Genal angle obtusely rounded. Eye socle narrow; a shallow paradoublural furrow extends from anterior margin of eye socle to posterior border furrow.

Paradoublural furrow and border furrow delimit a gently curved, moderately inflated paradoublural ridge. Terrace lines occur on the border, arranged parallel to outer margin with increased density towards the margin (Fig. 134F). The test surface is covered with small, densely spaced, moderately impressed pits.

Doublure rather wide (Fig. 134L), and very similar to the doublure of *N. (Niobe) tjernviki* n.sp.; 20–22 ($N = 3$) continuous, rather coarse terrace lines were counted across the doublure just anterior to eye level.

Hypostome large, length of largest specimen 28.5 mm (Fig. 135B). General outline as described for *Niobe (Niobe) tjernviki* n.sp. (*q.v.*). Hypostomal W:L ratio varies between 0.8 and 0.9 (mean 0.86; $N = 11$). Greatest width is typically across posterior border (this measure is used in the stated W:L ratio), but about 30% of the measurable specimens show a slightly greater width across anterior wings. Median body subrectangular, nearly reaching the curved anterior margin, separated only by an extremely narrow, forward sloping concave border of equal width all the way. Two specimens have a very subtle, inconspicuous median point on anterior margin. Anterior lobe of median body has a W:L ratio equal to hypostome. Premacular pits deeply impressed. Posterior lobe of median body short, divided into two gently inflated swellings by a shallow medial depression. Maculae slanting strongly forwards, with an oblique-backward strike averaging 100° (range 95°–109°, $N = 18$) to sagittal line. Anterior wings quite broad (tr.), and strongly ascend in dorsal direction. Lateral and posterior borders with furrows as in *N. tjernviki* n.sp. Posterior border wide (tr.), with a deep mesial notch, stretching for about 0.10–0.13 of maximum hypostomal length (mean 0.12; $N = 9$). Hypostomal surface, except maculae and anterior border, is covered with fine terrace lines, impressed also on internal moulds. The line configuration is apparent from Figs. 134H–I and 135A–B. The terrace lines within the furrows are very fine and generally oriented along the furrow (Fig. 134K); they are not impressed on internal moulds. A triangular band with sparse, very fine, irregular lines is seen anterior to macula. Fine, second-order terrace lines are present at the crests of the first-order lines on the median body and on the borders; these lines are not impressed on internal moulds. Density of first-order lines sagittally on frontal lobe was counted to 12 lines per 5 mm in a specimen 28.5 mm long, 19 lines per 5 mm in a specimen 16.5 mm long, and 27 lines per 5 mm in a specimen 12 mm long.

A couple of disarticulated thoracic segments must belong to *N. imparilimbata* (Fig. 135C). Axis occupies 0.3 of the segmental width (tr.), set off by shallow, but distinct axial furrows. Pleural field convex, slopes outward, only the inner one third is approximately flat. Articulating facet well-developed, but slants just gently forward; it is delimited to the rear by a crest. A deeply impressed pleural furrow extends from the axial articulating furrow to midlength of this crest. Terrace-line pattern apparently variable. A specimen with intact

Fig. 134. Niobe (Niobella) imparilimbata Bohlin, 1955. □A. Internal mould of small cranidium, $\times 5$. Long form, see also Fig. 133B. MGUH 22.570 (S 78), bed –21, Skelbro. □B. Internal mould of cranidium, $\times 4$. Short form, see also Fig. 133A. MGUH 22.571 (S 436a), bed –19, Skelbro. □C. Internal mould of small cranidium, $\times 8$. MGUH 22.572 (S 63), bed –21, Skelbro. □D. Fragmentary, partly exfoliated large cranidium, $\times 1.5$. MGUH 22.573 (GM 1884.1626), Skelbro. □E. Exfoliated librigena, $\times 2$. MGUH 22.574 (S 534), bed –18, Skelbro. □F. Partly exfoliated librigena showing cuticle terrace-line sculpture, $\times 2$. MGUH 22.575 (S 368), bed –20, Skelbro. □G. Fragment of small cranidium showing comparatively extensive glabellar terrace lines and cuticle punctation, $\times 10$. MGUH 22.576 (K 768), bed 12, Gårdlösa-4a. □H. Partly corroded hypostome showing fine terrace lines within the premacular pit (see close-up in K), $\times 3$. LO 7092 (LU 43b), Komstad. □I. Partly exfoliated hypostome, $\times 3$. MGUH 22.577 (S 341), bed –20, Skelbro. □J. Pygidium, close-up of axis showing terrace-line sculpture, $\times 8$. Same specimen as 135D. □K. Hypostome, close-up of premacular pit, showing fine cuticle terrace-line sculpture, $\times 6$. Same specimen as shown in H. □L. Internal mould of detached cephalic doublure, ventral view, $\times 3$. MGUH 22.578 (S 186), bed –21, Skelbro.

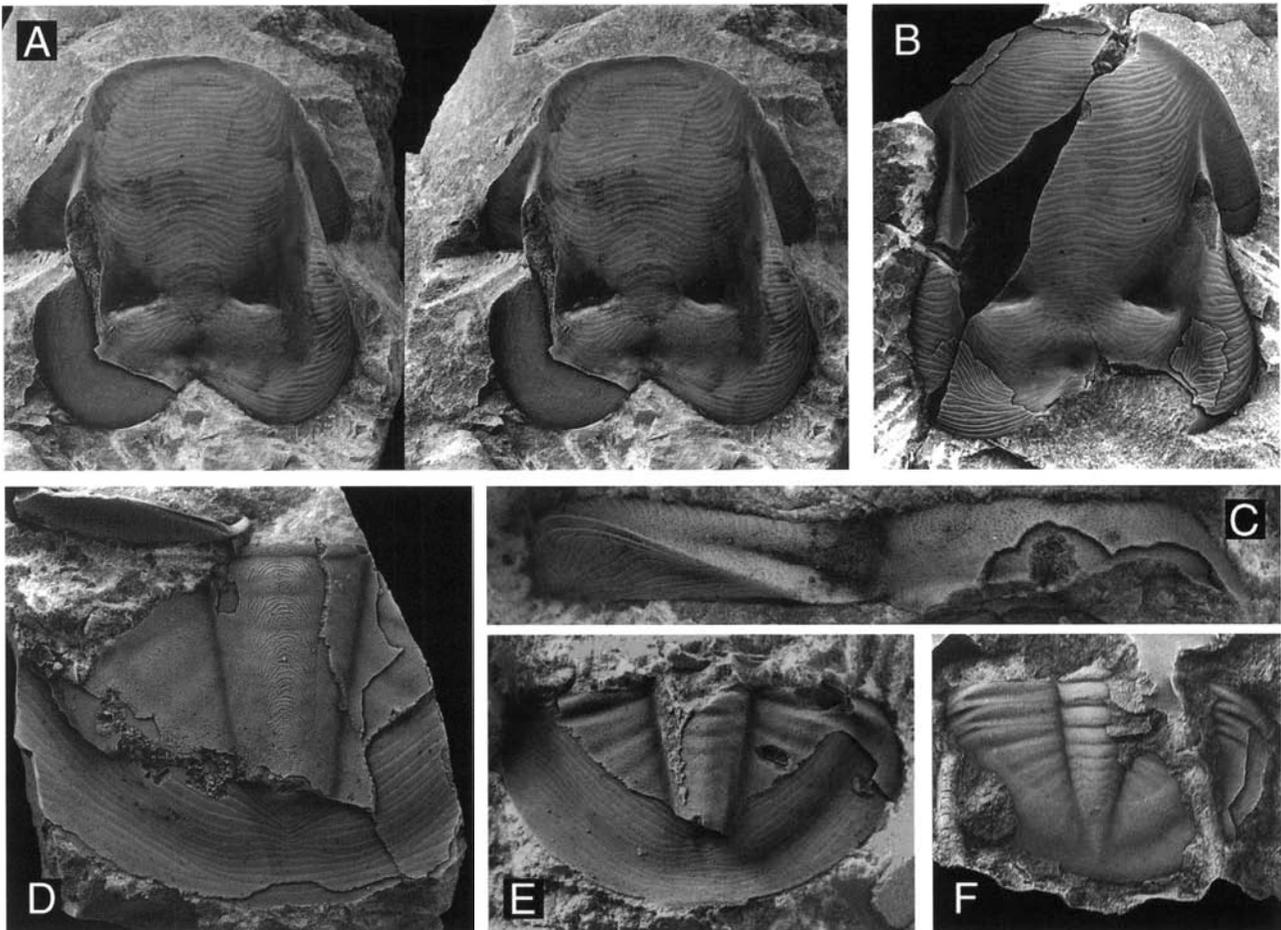


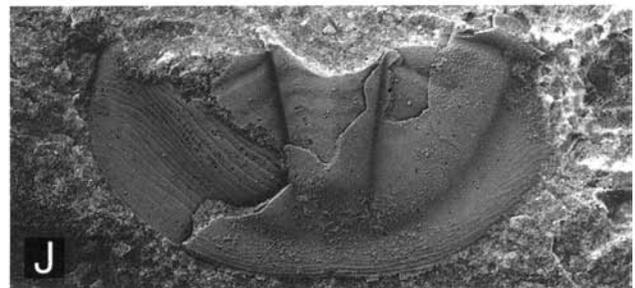
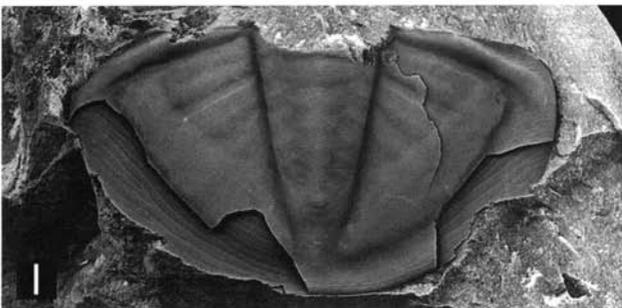
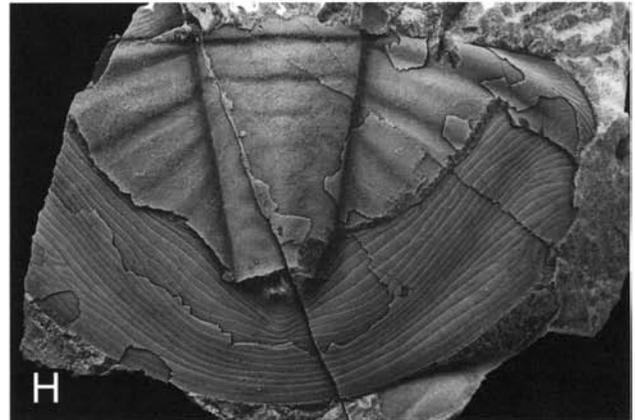
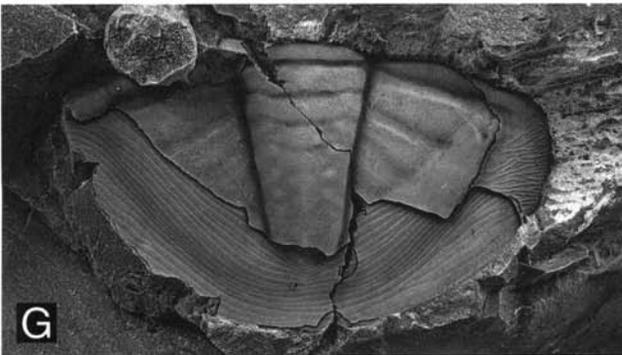
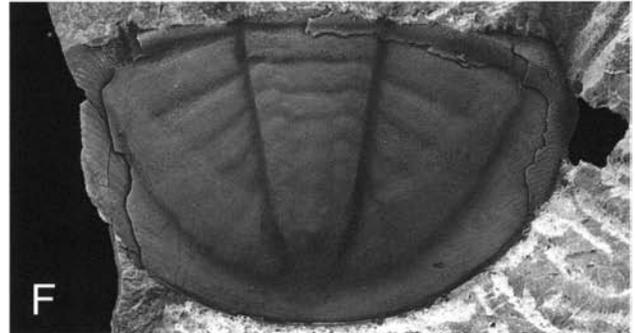
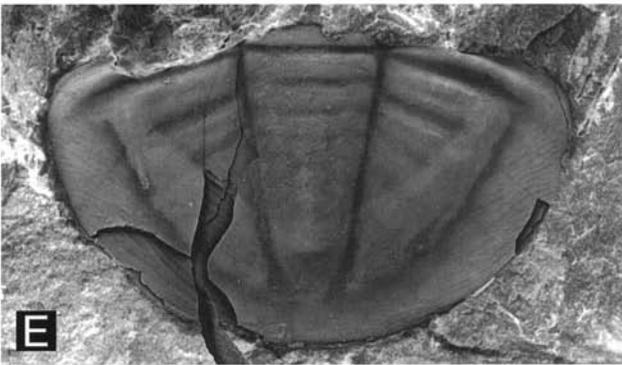
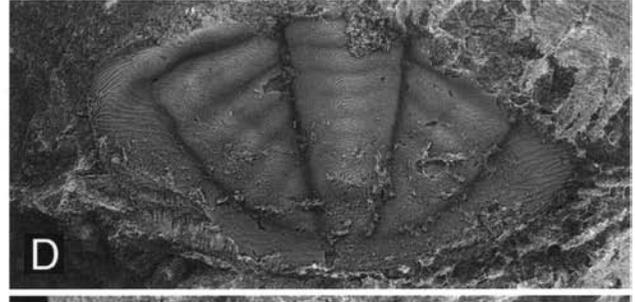
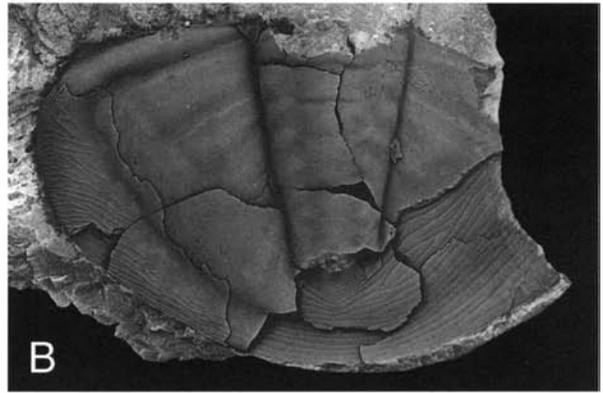
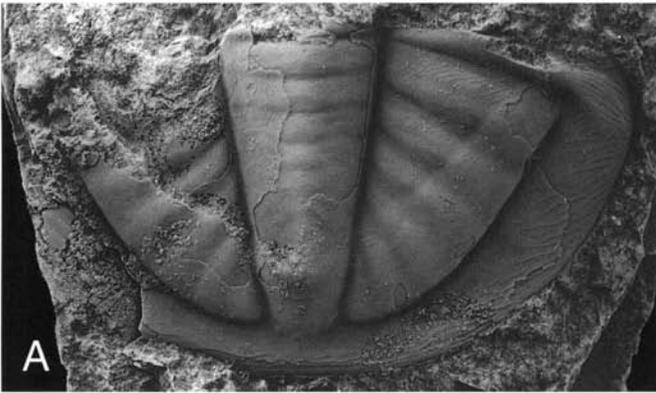
Fig. 135. *Niobe (Niobella) imparilimbata* Bohlin, 1955. □A. Internal mould of hypostome, stereo-pair, $\times 3$. MGUH 22.579 (S 195), bed -21, Skelbro. □B. Internal mould of very large hypostome, $\times 2$. MGUH 22.580 (GM 1951.41), Skelbro. □C. Fragment of thoracic pleura, $\times 7$. MGUH 22.581 (S 80), bed -21, Skelbro. □D. Partly exfoliated pygidium showing cuticle terrace-line sculpture on axis (see 134J), $\times 4$. MGUH 22.582 (S 210a), bed -21, Skelbro. □E. Internal mould of small pygidium showing double lure, $\times 6$. MGUH 23.080A, Skelbro beds, Skelbro. □F. Latex cast of transitory pygidium, $\times 8$. MGUH 22.583 (S 208b), bed -21, Skelbro.

test has a few, very short transverse lines on inner part of the pleura, in addition to the lines on articulating facet; the entire surface is densely and finely pitted. An exfoliated specimen shows imprints of fairly densely spaced terrace lines on the axis, curving around a median point at posterior margin, on inner part of the pleura, running roughly across the pleura, and on the articulating facet.

Pygidium normally semicircular in outline, but relatively broad specimens, and in particular juveniles, occasionally show a truncate posterior margin. L:W ratio varies between 0.47 and 0.65 (mean 0.56; $N = 64$; see Fig. 137A); pygidia longer than 4 mm show ratios between 0.50 and 0.63 ($N = 55$). Axis stretches for 0.60–0.74 of the pygidial length (mean 0.69; $N = 49$; Fig. 137B), and accounts for 0.23–0.29 of the width at anterior margin (mean 0.26; $N = 44$), see Fig. 137C. Axial width (tr.) at terminal piece averages 0.5 of the anterior axial width ($N = 28$). The number of axial rings is, as a rule, difficult to verify on testaceous material, as the posterior segments are effaced. Internal moulds indicate that relatively

longer pygidia generally have 8 axial rings, whereas shorter pygidia have only 7 axial rings, in addition to the terminal piece and the anterior half-ring; the variation is not stratigraphically or size controlled. In all specimens the postaxial ramp descends rapidly behind terminal piece, which is a

Fig. 136. Pygidia of *Niobe (Niobella) imparilimbata* Bohlin, 1955. □A. Long morph with six pairs of pleural ribs (cf. D), showing terrace-line sculpture on anterior pleural ribs, $\times 3$. MGUH 22.584 (GM 1874.1942), Vasegård, Bornholm. □B. Internal mould showing terrace-line sculpture of border, and part of the double lure, $\times 1.5$. MGUH 22.585 (S 133a), bed -21, Skelbro. □C. Somewhat corroded, large specimen, $\times 1$. MGUH 22.586 (S 711), bed -16, Skelbro. □D. Short morph showing five pairs of pleural ribs, $\times 3$. MGUH 22.587 (K 735), bed 10, Gårdlösa-4a. □E. Internal mould, $\times 2$. MGUH 22.588 (S 55a), bed -21, Skelbro. □F. Internal mould, $\times 2$. MGUH 22.589 (S 141), bed -21, Skelbro. □G. Internal mould showing double lure, $\times 1.5$. MGUH 22.590 (S 25), bed -21, Skelbro. □H. Internal mould showing double lure, $\times 2$. MGUH 22.591 (GM 1874.69), Vasegård, Bornholm. □I. Internal mould, $\times 2$. MGUH 22.592 (S 37), bed -21, Skelbro. □J. Partly exfoliated small pygidium, $\times 5$. MGUH 22.593 (S 175), bed -21, Skelbro.



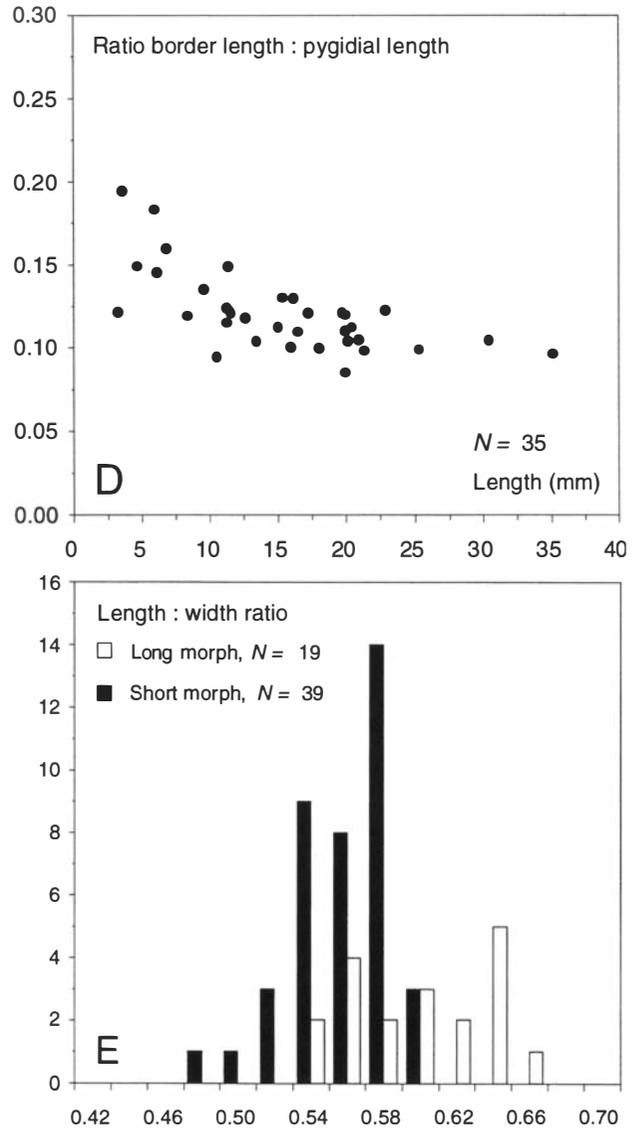
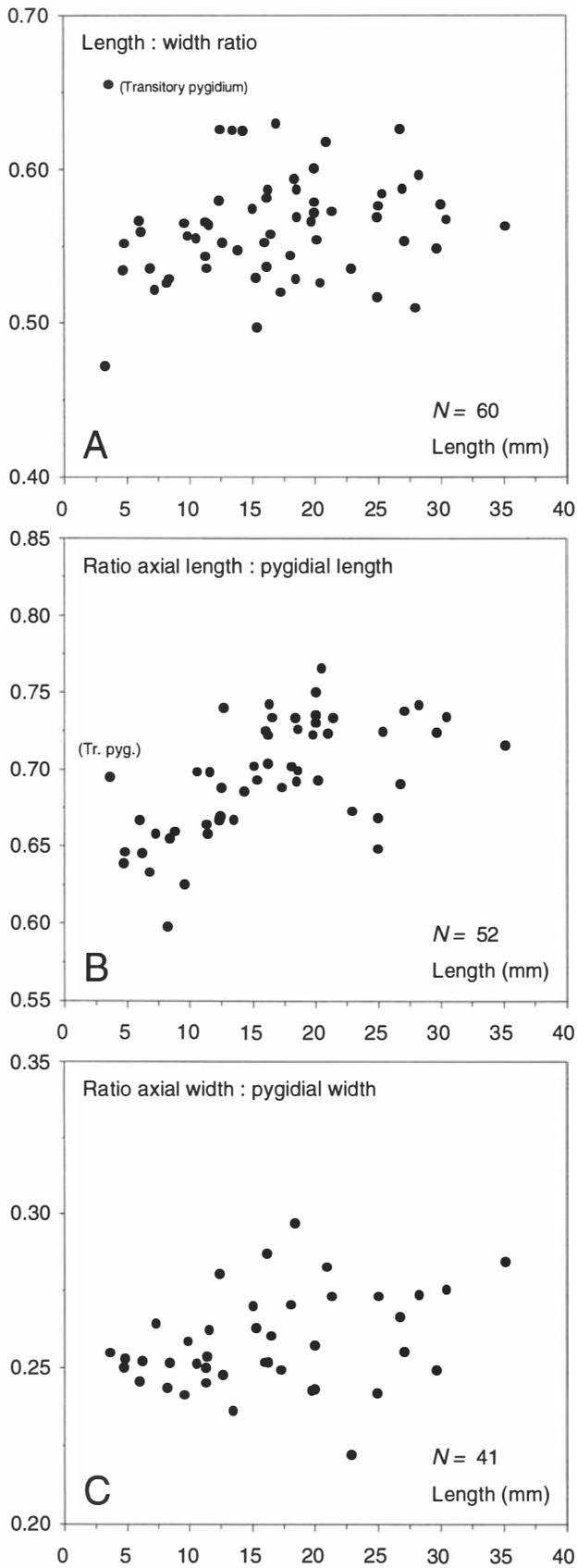


Fig. 137. Pygidia of *Niobe* (*Niobella*) *imparilimbata*. □A. Ratio between length (sag.) and maximum width plotted against pygidial length. The tiny specimen with an unusually high ratio is a transitory pygidium (MGUH 22.583). □B. Ratio between axial length and pygidial length plotted against pygidial length. The axial length is measured to the end of terminal piece. □C. Ratio between anterior axial width and maximum pygidial width plotted against pygidial length. □D. Ratio between postaxial border width and pygidial length plotted against pygidial length. □E. Length:width ratios, short and long forms.

small knob of varying prominence. The postaxial ramp is rather acuminate in some specimens and only reaches the border, whereas other specimens show a less acuminate ramp, continuing onto the inner part of border, and the termination is ill-defined. Five to six pairs of pleural ribs, which vary from being almost effaced to well defined, but are distinguishable in most specimens inside paradoublural line, also when the test is intact. The posterior one or two ribs, situated largely above the doublure, are usually rather indistinct. Later specimens tend to have more distinct ribs, but there are several exceptions. In more strongly ribbed specimens the anterior two rib pairs interfere with the border furrow, which then undulates (Fig. 136A). Internal moulds have faint to extremely faint pleural furrows on the crests of pleural ribs inside paradoublural line. There is a strong correlation between 5 pairs of ribs and 7 axial rings ($N=13$) and 6 pairs of ribs and 8 axial rings ($N=12$), but it appears, however, that two pygidia show mixed relations. Border width (sag.) 0.09–0.19 of the pygidial length (mean 0.12; $N=36$; Fig. 137D). Terrace lines are present on the pygidial border, with an increased density towards the outer margin; roughly U-shaped lines opening backwards are present on the crests of the axial rings, and terrace lines also occur on the pleural ribs. Sparse, widely spaced, and short terrace lines may be limited to the anterior edge of the rib, or the lines may be moderately densely spaced and run obliquely across the rib. All pygidia with intact test studied show terrace lines on the anterior two pairs of ribs, but lines occasionally occur on the succeeding ribs as well, and a few pygidia actually have terrace lines on all ribs. Some pygidia show terrace lines across the postaxial ramp, others do not. The described variation in line-coverage is not linked to stratigraphy. The dorsal surface of pygidium is covered with moderately impressed, densely spaced small pits, which on the border often are arranged in rows adjacent to the terrace lines.

Doublure wide, stretching for about one third of the pygidial width at anterior margin. The inner margin shows a deep mesial incision with upwards-turned edge. The doublure is covered with coarse continuous terrace lines; 22 lines, including the lines on the upturned inner edge, are present behind axis. The inner postaxial lines are somewhat disturbed, V-shaped in dorsal view.

Juveniles. – Juvenile cranidia are slightly more vaulted and have a relatively narrower glabella (Fig. 134C) compared to large specimens. The relative position of the mesial glabellar tubercle changes during growth; in a 6 mm long cranium, the tubercle is situated slightly in front of the imaginary transverse line (itl.), connecting inner posterior corners of palpebral lobes, at the itl. in a cranium 11 mm long, slightly behind the itl. in a cranium about 25 mm long, and clearly behind the itl. in a cranium 40 mm long. The relative length of palpebral lobes does not change during growth, but juveniles have much wider lobes.

Small hypostomes exhibit a slightly more inflated median body, particularly with regard to the posterior lobe, and also better impressed furrows.

Smaller pygidia tend to be relatively broader (Fig. 137A), and have a relatively shorter axis; the ratio axial:pygidial lengths usually varies between 0.60 and 0.66 in specimens shorter than 11 mm, and between 0.66 and 0.74 in pygidia longer than 11 mm long (Fig. 137B). The border tends to be relatively wider in small pygidia (Fig. 137D). Pygidia less than 5 mm long show a postaxial furrow in the doublure, stretching from the axial tip and almost to posterior margin. The external expression of this furrow, if any, is unknown (see, however, Fig. 135F). The material suggests that juvenile pygidia of the short morph possibly have a truncate posterior margin, while juvenile pygidia of the long morph are semi-circular.

Affinities. – *Niobe* (*Niobella*) *imparilimbata* is very similar to *N. (Niobella) cf. plana* (Balashova), and these taxa should probably be separated only at the subspecies level. An enumeration of the distinguishing characters can be found in the section on *N. cf. plana*.

Niobe (*Niobella*) *lindstroemi* Schmidt and *N. (Niobella) bohlini* (Tjernvik) are both markedly smaller than *N. (Niobella) imparilimbata*, with elongate, narrow (tr.) glabellas, no or only faint segmentation of the pleural fields, and a different surface sculpture with only a few terrace lines.

Niobe (*Niobella*) *laeviceps* (Dalman) has a broader glabella with a more advanced mesial tubercle, larger eyes, a distinctly narrower paradoublural ridge, and a pygidium with a less vaulted, relatively wider axis and no segmentation of the pleural fields. The pygidial border is of equal width all the way. Besides, the surface sculpture is probably different (cf. Tjernvik 1956, p. 233).

Hypostome MGUH 22.580, 28.5 mm long, has a truly remarkable size (Fig. 135B); it originates from Skelbro, probably from a level just below the *M. simon* / *M. limbata* Zonal boundary. V. Poulsen (1965, Pl. 2:5) also described an unusually large hypostome of *N. imparilimbata*, ca. 22 mm long. Such large specimens are distinguished from the equal-sized hypostomes of *Gog explanatus* by being relatively broader (tr.), by having a very narrow anterior border, by the less forward sloping maculae, which also are less obliquely backward striking, by the but slightly less inflated posterior lobe of median body, by the centrally less impressed posterior border furrow, and by the deeper notch in the posterior margin.

N. (Niobella) imparilimbata may be compared to the North American species *N. (Niobella) morrisoni* (Billings, 1865) (see Whittington 1965), from which it is distinguished by showing shorter (tr.) posterior fixigenae, a wider and more strongly inflated paradoublural ridge on librigenae, an acute genal angle (more rounded in *N. morrisoni*), a shallower but wider posterior mesial notch in hypostomes, and a

slightly narrower pygidial axis, and a much more restricted pygidial surface ornamentation.

Remarks. – The type specimen of *N. imparilimbata* is a rather transverse pygidium from the Böda Hamn core of northern Öland (Bohlin 1955, pp. 149–151, Pl. 6:12). It seems to be derived from the upper part of the *M. estonica* Zone, 0.5 m below the *M. estonica* / *M. polyphemus* Zonal boundary, and not from the ‘*Limbata* limestone’ as previously assumed (see remarks on *M. polyphemus*, p. 145).

According to Tjernvik (1956, p. 232; Pl. 5:10; see also 1980, p. 191) a species similar to the holotype, i.e. showing pygidial L:W ratios close to 1:2, is characteristic for the lower half of the *M. polyphemus* Zone of Sweden, whereas a resembling species with relatively longer pygidia occurs throughout the Billingen Stage as well as associated with *N. imparilimbata* (*s.str.*). Some of Tjernvik’s material, stored at the Uppsala University, Sweden, has been examined; it contains two species, which, however, cannot be differentiated by their pygidial L:W ratios. Pygidia of the old form (‘*aff. imparilimbata*’) have virtually no indication of pleural ribs, terrace lines are absent on the pleural fields, and occur only on the border along outer margin, the axis is strongly vaulted and with a different outline of segments, the postaxial ramp is poorly developed and does not reach the border, the axial furrows shallow up immediately behind the axis, and do not unite with the border furrow, which, therefore, continues behind the axis (see Tjernvik 1956, Pl. 5:13). Only three of the pygidia described by Tjernvik (1956: N 394, N 477, Ö1 258) were available for study, and they are all relatively long, as stated by Tjernvik; nevertheless, their W:L ratios are within the range of *N. imparilimbata*. The cranidium of the old form is more strongly vaulted, with posterior fixigenae inclined somewhat downwards, and the palpebral lobes are smaller than in *N. imparilimbata* (*s.str.*); the hypostome appears to have quite coarse terrace lines, somewhat resembling *N. cf. plana* (cf. Tjernvik 1956, Pl. 5:2). The older as yet unnamed species is characteristic of the *M. dalecarlicus* and *M. estonica* Zones, but just enters the base of the *M. polyphemus* Zone, while *N. imparilimbata* ranges from the upper part of the *M. estonica* Zone and into the lower part of the *M. limbata* Zone. *N. imparilimbata* ‘*s.l.*’, reported from the Finngrundet core (Tjernvik 1980, Textfigs. 5–6), comprises both species; note that a specimen (actually a *N. n.sp. aff. imparilimbata*) is missing in Tjernvik’s range chart at 56.54 m (I define the *M. estonica* / *M. polyphemus* boundary at 56.6 m; for details, see remarks on *M. polyphemus*, p. 145).

The material from the Komstad Limestone exclusively represents *N. imparilimbata* (*s.str.*). Transverse pygidia, like the holotype specimen, are not restricted to the *M. polyphemus* Zone (cf. Tjernvik 1956). The material furnish evidence for a distinction of a long form, characterized by L:W ratios between 0.53 and 0.63, 8 axial rings and 6 pairs of ribs, and a short form, characterized by L:W ratios between 0.50 and 0.58, 7 axial rings and 5 pairs of pleural ribs (Fig. 137E). The described variation in axial termination is not linked to

morphotype. A division of the cranidia into matching short and long forms is not obvious because of the fragmentary state of the material, but a few specimens indicate that two morphs actually can be discerned (Fig. 133A–B). The long form is characterized by a narrow glabella with rounded front and a slightly longer frontal area, as the facial sutures meet anteriorly at an angle of 150°, while the short form has a broader glabella with truncate front, a shorter (sag.) frontal area, and the facial sutures meet anteriorly at an angle of 140°. No bimodal difference are recognized for hypostomes or librigenae.

Skjeseth (1952, Pl. 2:12–13) figured a couple of pygidia from Herramb, which almost certainly belong to *N. (Niobella) imparilimbata* (the material has been examined). However, the specimens differ from the above described pygidia by lacking terrace lines on the pleural ribs, in this single aspect resembling *N. n.sp. aff. imparilimbata*.

Niobe (Niobella) cf. plana (Balashova, 1976)

Figs. 138–141

Synonymy. – □v 1882 *Niobe emarginula* Ang. [*partim*] – Brögger, pp. 68–71 (description, occurrence). □cf. 1901 *Niobe laeviceps* Dalm. [*partim*] – Schmidt, pp. 103–105, Pl. 10:5–6, non Textfigs. 59–60 (description, occurrence, illustrations of cephalon and pygidium). □cf. 1976 *Niobella plana* sp.n. – Balashova, pp. 125–126, Pls. 34:8; 38:4–7 (description, occurrence, illustrations of cranidia, hypostome, pygidia.) □1980 *Niobella* n.sp. – Tjernvik, pp. 192, 193, 202 (occurrence, short comments on morphology).

Holotype. – Pygidium 269a/9243, figured by Balashova (1976, Pl. 38:5).

Material. – Four complete specimens, 3 cephalae including 1 with hypostome, 13 cranidia, 2 librigenae, 4 hypostomata and 43 pygidia. The available material is mostly in a bad state of preservation.

List of material. – □Complete specimens A 42 (t) [MGUH 22.594], A 1019 (pim) [MGUH 22.608], A 1044 (pim) [MGUH 22.595], A 1067 (pim) [MGUH 22.598]. □Cephalae A 1054 (pim) [MGUH 22.596], A 1066 with thoracic segments (pim) [MGUH 22.597], MGUH 22.605 with hypostome (pim). □Cranidia A 82 (im), A 232 (im), A 796 (im) [MGUH 22.602], A 816-2b (t), A 874 (im), A 880 (im), A 892b (im), A 920 (pim) [MGUH 22.603], A 979 (im), A 995? (im), A 1014 (im), A 1018b (im), A 1041 (im). □Librigenae A 760 (im) [MGUH 22.604], A 878 (t). □Hypostomata A 879 (im), A 912? (em), A 952 (im), A 963 (im) [MGUH 22.599]. □Pygidia A 34 (pim), A 70 (pim), A 71? (im), A 100 (pim), A 103 (im), A 143 (im), A 172? (t), A 219 (im) [MGUH 22.609], A 286 (im) [MGUH 22.606], A 712 (im) [MGUH 22.600], A 722b (im) [MGUH 22.601], A 793 with thoracic segments (im), A 807 (im), A 808 (im), A 812 (im), A 816a (pim), A 863 (t), A 872 (im), A 875 (t), A 887 (pim), A 892a (pim), A 901 (pim), A 903 (im), A 914 (t), A 929 (im), A 942 (im), A 958 (im), A 964 (im), A 965 (im), A 967? (im), A 974 (pim), A 976a (im), A 976b? (pim), A 995 (t), A 1000 (im), A 1003a (im), A 1003b (im), A 1018a (im), A 1025 (im), A 1032 (im), A 1057 (t) [MGUH 22.607], A 1062 (t), A 1075 (im).

Occurrence. – *N. (N.) cf. plana* is fairly abundant in bed interval M-7 to A-3 at Slemmestad, which makes up the lower subzone of the *M. limbata* Zone. The species is less common in beds M-5 and M-6 of the Hukodden Limestone (*M. simon* Zone), and in beds A-6 to A-18 of the Lysaker Member (upper subzone of the *M. limbata* Zone). Very poorly preserved material from the lower part of the *M. simon* Zone, referred to as *Niobe (Niobella)* sp. (aff. *imparilimbata*), is dealt with separately below, but may represent *N. cf. plana*.

N. cf. plana or a closely similar form occurs sparsely in the *M. limbata* Zone of Sweden (*Niobella* n.sp. of Tjernvik 1980, pp. 192, 193), and the supposedly identical *N. plana* occurs in the BILY Zone of the East Baltic area (Balashova 1976).

Description. – Medium-sized to large for a *Niobella*, largest cranidium 29 mm long, largest pygidium 28 mm long. The form is very like *N. imparilimbata* Bohlin; distinguishing features are enumerated below. The material contains a short and a long morphotype, which probably represent sexual dimorphs (see introductory remarks on this issue). Short cephalae are roughly rectangular in outline with L:W ratios in the range of about 0.55–0.6 (Fig. 138C); long cephalae are semicircular and show L:W ratios around 0.7 (Fig. 138A–B). Short form has a wide glabella, emarginate at the truncate front, and the anterior branches of facial suture go directly outwards in front of the eyes for a short distance, then straight sections diverge forwards to a level roughly in line with front of glabella, where they turn sharply inward, converge strongly, and meet at a very blunt angle of about 150°. Long form has a relatively longer glabella with an evenly rounded glabellar front, and the anterior branches of facial sutures diverge outwards-forwards, but gradually turn inwards, and, in front of glabella, run obliquely towards sagittal line, meeting at a blunt, but sharper angle of about 140°. Baculae of the short form appear more prominent, wider, with an oblique-inward strike in the order of 30° to sagittal line; baculae of the long form are attenuate and strike 15–20° relative to sagittal line. Lateral margin of librigena straight to a point just in front of the eyes in the short form; lateral margin of long form curved, being straight only posterolaterally. Paradoublural ridge of short form broad, curving backwards from the eye (Fig. 138E); it is narrower and therefore appears stronger inflated in the long form, and runs more straight backward-outwards from the eye (Fig. 138D).

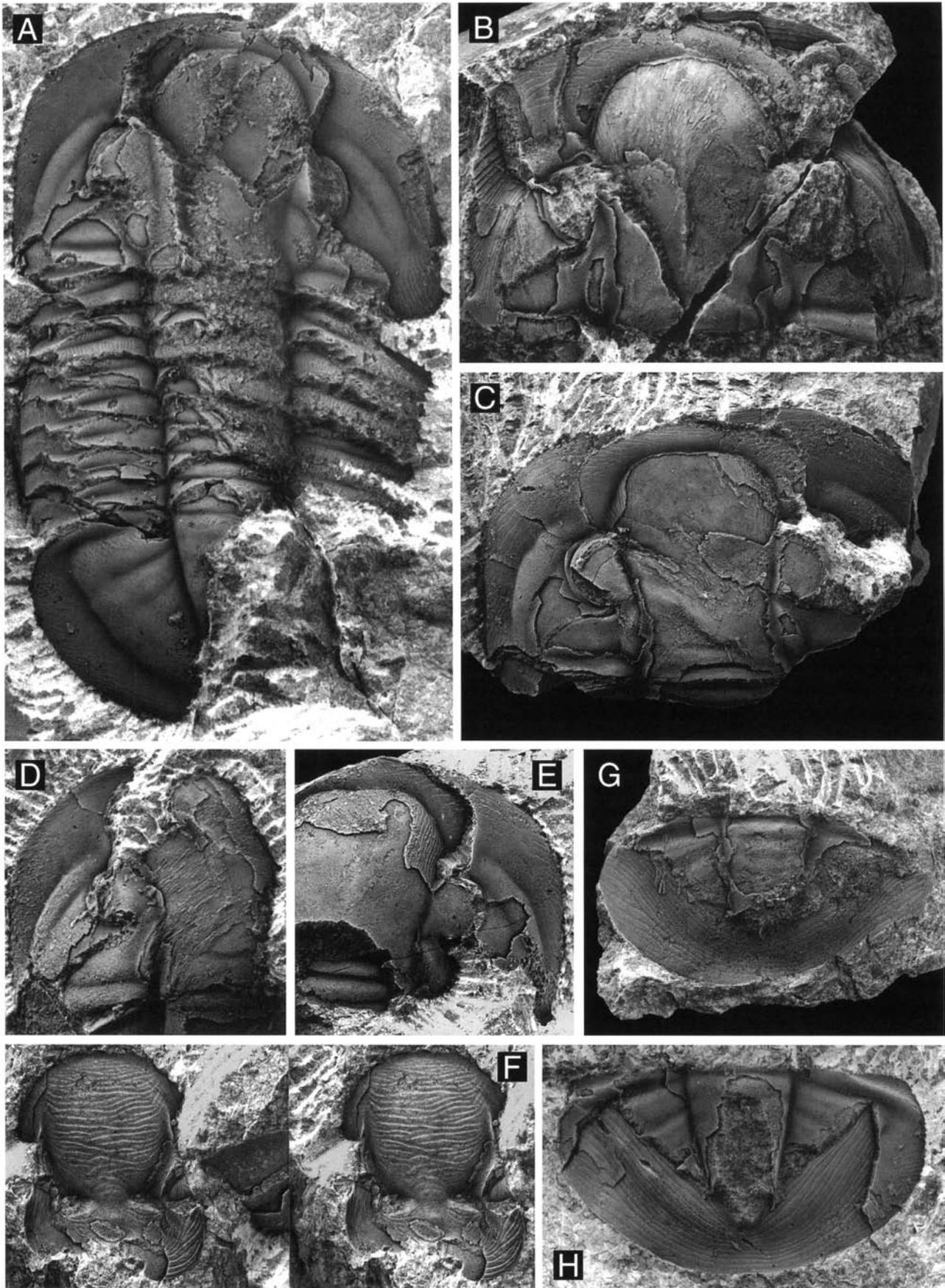
External ornamentation not fully known. Both morphs have longitudinal terrace lines laterally on frontal glabellar lobe, diverging slightly outwards (3 lines/mm were counted on the frontal glabellar lobe in a cranidium 22 mm long [short form]), and transverse lines on anterior and anterolateral border. A fairly preserved short cephalon also shows a few short terrace lines on the outer part of baculae and abundant lines on the border near genal angle; it is unknown whether the long form has similar lines. Densely spaced,

weakly impressed small pits are randomly distributed all over the patches of preserved test on glabella and inside paradoublural crest. There is at least one difference in ornamentation between the two morphotypes: the short form has coarse, densely spaced pits on the paradoublural ridge, which are not present in the long form.

No dimorphism recognized for hypostomes.

Pygidial L:W ratio varies about 20% (Fig. 141); specimens with ratios below 0.6 are referred to as short, those with ratios above 0.6 are referred to as long. Pygidium typically subsemicircular in outline, but some short specimens are transverse, and long specimens may have rather straight anterolateral margins. Short form has a shorter axis, which tends to appear more vaulted, prominent, compared to the seemingly more slender, less prominent axis of the longer type, but this impression relates to the gross outline of the respective pygidia. Short pygidia have only 6 axial rings, the longer pygidia 7, in addition to the anterior half-ring and terminal piece. Specimens from the lower half of Lysaker Member show better defined axial rings than the remaining material, but this may relate to preservational differences. Outline of postaxial ramp varies, as described for *N. imparilimbata*, but not between morphotypes. Distinctness of pleural ribs ranges from obscure to well-defined, but most specimens show fairly developed ribs; segmentation best defined on internal moulds, and tends to be more pronounced in late specimens. Posterior rib pairs, situated above the doublure, are rather indistinct, and the number of ribs may therefore occasionally be difficult to verify. It appears, however, that long pygidia possesses 5 pairs of ribs, and short specimens only 4 pairs of ribs. No differences in the dorsal surface ornamentation have been ascertained between the two morphotypes. Test surface of axis and pleural fields is covered with densely spaced small pits; they are much less abundant and less impressed on the border, being most abundant anterolaterally between the terrace lines.

Affinities. – *Niobe (Niobella) cf. plana* (Balashova) is very similar to *N. (Niobella) imparilimbata* Bohlin, and these taxa should presumably be separated only at the subspecies level; because of the strong resemblance the distinguishing characters are discussed at some length. *N. (Niobella) cf. plana* has a shorter frontal area, accounting for only about 0.12–0.10 of the cranidial length, the terrace lines on the frontal glabellar lobe are coarser and less close and diverge but slightly more outwards; moreover, terrace lines are present only on the forepart of the anterior cephalic border, and they are coarser, more continuous and more densely spaced than in *N. imparilimbata*. The paradoublural ridge of the long morph of *N. cf. plana* (Fig. 138D) is narrower and straighter than in *N. imparilimbata*, which is a useful separating character; the paradoublural ridge in the short morph of *N. cf. plana* (Fig. 138E) resembles that of *N. imparilimbata*, but the librigena of the latter is overall longer. The librigena of *N. imparilimbata* has fine terrace lines scattered on the lateral border;



N. cf. plana shows more coarse terrace lines only along margin, and the coarse punctation of the paradoublural ridge in the short form of *N. cf. plana* is not present in *N. imparilimbata*. The cephalic doublure is more strongly concave in *N. cf. plana* and the terrace lines are coarser; 15 lines were counted in front of the eye in one specimen, which compare to 20–22 in *N. imparilimbata*.

The hypostomes of the discussed species are readily separated, albeit being grossly similar. *N. cf. plana* hypostomes have an anterior margin with a vague mesial point; anterior border virtually absent, anterior wings comparatively narrower (tr.) and less steeply inclined in dorsal direction; greatest width is across posterior border; the flat maculae are less strongly slanting; premacular pits comparatively smaller, but deeper; posterior lobe of median body rather ill-defined, negligibly inflated and not raised (ventral view) above posterior border, separated from this by a wide, very shallow furrow. Terrace-line ornamentation unusually coarse and is a salient distinguishing feature; 9 lines per 5 mm were counted on anterior lobe of median body in a specimen 21 mm long.

The best distinguishing character of the pygidia is the doublure, which is more concave in *N. cf. plana* compared to *N. imparilimbata*, and with fewer (and undisturbed) post-axial terrace lines. The different number of axial rings (six to seven versus seven to eight in *N. imparilimbata*) is of limited practical value as separating character as the segments generally are indistinct, except on well-preserved internal moulds. The pleural ribs of *N. cf. plana* mostly show pleural furrows on the inner part, whereas the ribs of *N. imparilimbata* have broad, flat crests. Both species exhibit terrace lines on the axis and on the border, but *N. imparilimbata* also carries lines on the anterior two to three pairs of pleural ribs, and the lines on the border are finer and seem to be slightly more extensive.

N. cf. plana is separated from other species of *Niobella* by the same characters as stated for *N. imparilimbata* vs. these species.

Remarks. – *N. (Niobella) cf. plana*, which is quite frequent in the *M. limbata* Zone of the Hukodden Limestone at Slem-

metad, was undoubtedly included in *Niobe 'emarginula'* by Brøgger (1882); several specimens in the collection of the Paleontological Museum, Oslo, are labelled with this name. It appears, however, that Brøgger's description of *N. 'emarginula'* essentially refers to material of *Niobe (Niobe) schmidtii* Balashova.

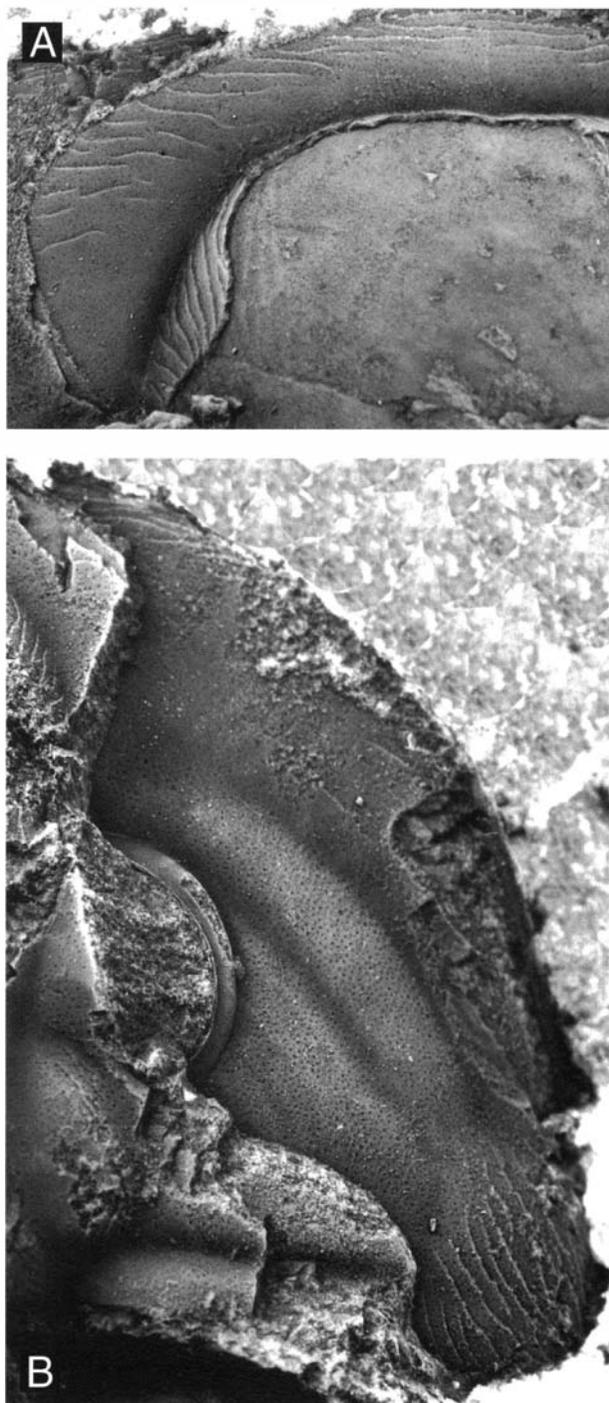


Fig. 138 (opposite page). *Niobe (Niobella) cf. plana* Balashova, 1976. □A. Slightly compacted complete specimen showing external terrace-line pattern, ×3 (close-ups shown in 139A–B). MGUH 22.594 (A 42), bed M-14, Slemmestad. □B. Internal mould of large cephalon, long morph, ×2. Complete specimen MGUH 22.595 (A 1044), bed M-11, Slemmestad. □C. Slightly compacted, partly exfoliated cephalon (short morph), showing cuticle terrace-line sculpture, ×2. MGUH 22.596 (A 1054), bed M-13, Slemmestad. □D. Fragmentary cephalothorax (long morph), showing librigena, ×2. MGUH 22.597 (A 1066), bed M-14, Slemmestad. □E. Partly exfoliated cephalon of short morph, showing librigena, ×2. Complete specimen MGUH 22.598 (A 1067), bed M-14, Slemmestad. □F. Largely exfoliated hypostome, stereo-pair, ×2. MGUH 22.599 (A 963), bed M-9, Slemmestad. □G. Internal mould of pygidium showing doublure, ×2. MGUH 22.600 (A 712), bed M-5, Slemmestad. □H. Internal mould of pygidium showing doublure, ×2. MGUH 22.601 (A 722b), bed M-5, Slemmestad.

Fig. 139. *Niobe (Niobella) cf. plana* Balashova, 1976. □A–B. Close-ups of cephalon of specimen MGUH 22.594 (A 42) (Fig. 138A), showing terrace-line sculpture of frontal area and punctate cuticle of librigena, ×6.

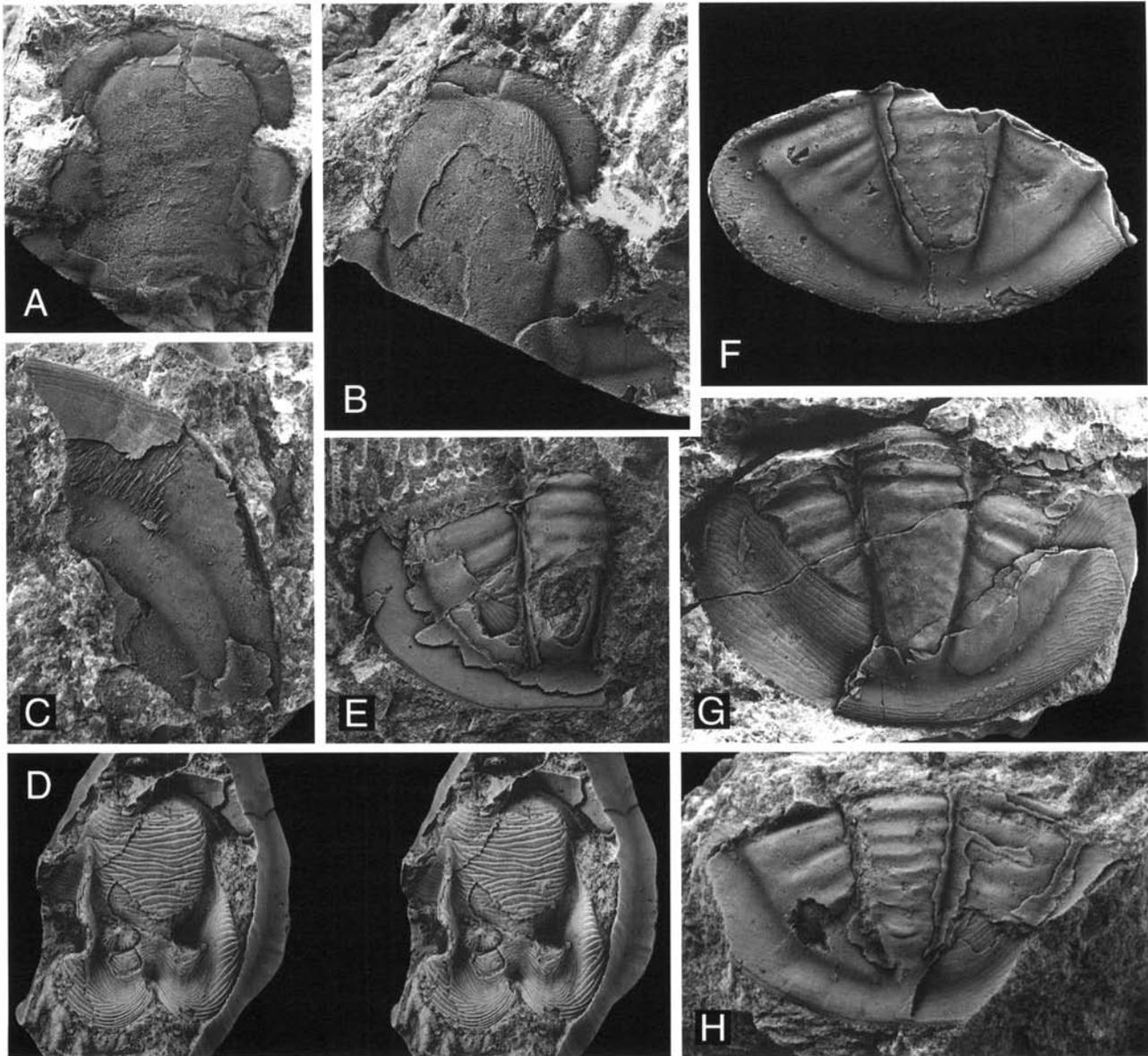


Fig. 140. *Niobe (Niobella) cf. plana* Balashova, 1976. □A. Internal mould of cranidium, $\times 2$. MGUH 22.602 (A 796), bed M-7, Slemmestad. □B. Partly exfoliated cranidium showing cuticle terrace-line sculpture of glabella and anterior border, $\times 3$. MGUH 22.603 (A 920), bed M-9, Slemmestad. □C. Largely exfoliated librigena, $\times 2.5$. MGUH 22.604 (A 760), bed M-6, Slemmestad. □D. Latex cast of fragmentary hypostome, stereo-pair, showing fine terrace-line sculpture, $\times 2$. MGUH 22.605, Lysaker Member, Slemmestad. □E. Largely exfoliated late pygidium, showing a comparatively distinct segmentation, $\times 3$. MGUH 22.606 (A 286), bed A-18, Slemmestad. □F. Pygidium showing the limited distribution of dorsal terrace lines, $\times 2$. The specimen is a typical representative of short morph. MGUH 22.607 (A 1057), bed M-13, Slemmestad. □G. Partly exfoliated large pygidium, typical representative of long morph, $\times 1.5$. Complete specimen MGUH 22.608 (A 1019), bed M-11, Slemmestad. □H. Internal mould of small, late pygidium, showing a comparatively distinct segmentation, $\times 5$. MGUH 22.609 (A 219), bed A-11, Slemmestad.

The material of *N. plana* described by Balashova (1976) is small, but it is evident from the figured specimens that the pygidial L:W ratio varies (cf. Balashova 1976, Pl. 38:5, 7). The transverse pygidium illustrated with only 6 axial rings is similar to the 'short' type of pygidia from the Oslo region, except for a slightly higher number of terrace lines on the border. The terrace-line pattern of the frontal glabellar lobe appears identical, too (cf. Balashova, 1976, Pl. 38:4b). The

undescribed hypostome figured by Balashova (1976, Pl. 38:8) is also identical to the hypostomes of *N. cf. plana* in all features; especially the coarse terrace-line pattern, the relatively small but deep premacular pits, and the insignificantly inflated posterior lobe of the median body are important points of similarity. *N. plana* has, however, terrace lines on the posterior border of cephalon and barely visible lines occur on the pleural fields of the pygidium (Balashova 1976),

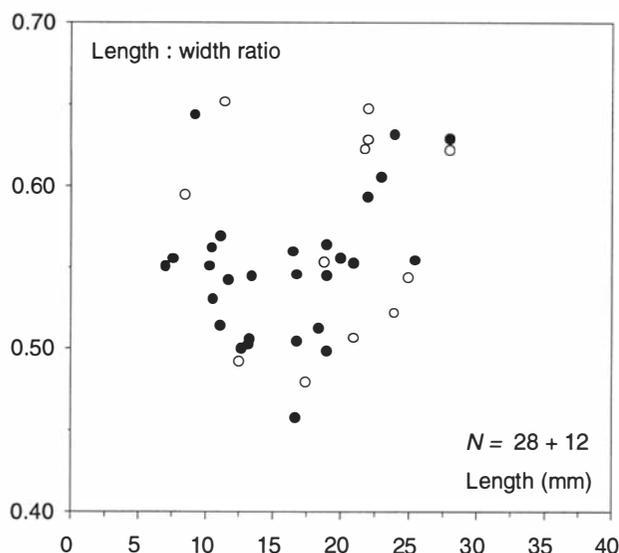


Fig. 141. Pygidia of *Niobe (Niobella)* cf. *plana*. Open symbols represent specimens in which either the length or the width could not be measured exactly. Ratio between length (sag.) and maximum width plotted against pygidial length.

in contrast to the material at hand. These differences are probably not significant for classification, but as the morphology of the posterior pygidial doublure in *N. plana* is unknown, and as the variation range of *N. plana* has not been analysed, it cannot be confidently determined whether or not *Niobe* cf. *plana* is identical to *N. plana* (*s.str.*). The two forms are believed identical, and the very minor differences are surmised to reflect variations in the environment.

Niobe (Niobella) sp. (aff. *imparilimbata*)

Material. – Three hypostomata and 4 pygidia. The material consists of fragmentary internal moulds.

List of material. – □ Hypostomata A 663 (im), A 664 (im), A 725a (im). □ Pygidia A 612 (im), A 675 (im), A 700 (im), A 725b (im).

Occurrence. – The specimens are from bed interval M-2 to M-5 of the Hukodden Limestone at Slemmestad (*M. simon* Zone).

Remarks. – The poorly preserved material undoubtedly represents a large *imparilimbata*-like *Niobe (Niobella)*. Hypostome A 664 has comparatively large premacular pits and a slightly inflated posterior lobe of the median body, as in *N. imparilimbata*, but the surface sculpture, impressed on the internal mould, is coarse and similar to *N. cf. plana* (also evident in specimens A 663 and A 725a). The pygidia are, compared to the associated *N. lindstroemi*, large and long, but the preservational state precludes further discussion. The earliest pygidia, confidently identified with *N. cf. plana*, were found in bed M-5.

Niobe (Niobella) laeviceps (Dalman, 1827)

Synonymy. – (Key papers only) □ 1827 *Asaphus laeviceps* – Dalman, pp. 58–59, Pl. 4:1a–d (description, occurrence, drawings of complete enrolled specimen). □ 1955 *Niobe laeviceps* Dalman – Bohlin, p. 150 (short discussion of species). □ 1956 *Niobella laeviceps* (Dalman, 1827) – Tjernvik, pp. 233–234, Pl. 5:15–16 [original of Angelin 1851, Pl. 11:1] (short description, occurrence, illustrations of cephalon and pygidium). □ 1976 *Niobella laeviceps* (Dalman, 1827) – Balashova, p. 124, Pl. 37:11 (designation of neotype, brief diagnosis, occurrence, illustrations of enrolled specimen [neotype]). □ 1980 *Niobella laeviceps* (Dalman) – Tjernvik & Johansson, pp. 177, 194, 202, Fig. 10G–H (occurrence, illustrations of cephalon and pygidium with thorax).

Neotype. – Complete specimen, chosen and figured by Balashova (1976, p. 124, Pl. 37:11).

Remarks. – *Niobe (Niobella) laeviceps* (Dalman) is characteristic of the *A. expansus* Zone of central Sweden but possibly occurs from just below (Tjernvik 1956); it has not been proven to occur outside that region. The classical but rather poorly known species is in need of a redescription; the majority of references to *N. laeviceps* prior to 1955 are incorrect (cf. Bohlin 1955; Tjernvik 1956). The distinguishing characters of the species are discussed by Bohlin (1955), Tjernvik (1956) and Balashova (1976). As some of the Dalman collection is preserved, it is likely that a lectotype can be designated to replace the neotype, chosen by Balashova (1976).

Gog Fortey, 1975

Type species. – (OD) *Gog catillus* Fortey, 1975.

Remarks. – *Gog* is uncommon in Scandinavia and presently known only from the *M. planilimbata* Zone of Sweden (Fortey 1975a, p. 27; Tjernvik 1980, p. 185) and the Komstad Limestone. The species occurring in the 'Latorp Limestone' is still undescribed (= *Niobe?* sp. Tjernvik (1956, p. 173); *Gog* n.sp. of Fortey (1975a, Pl. 4:3)). Pygidium no. 1 *sensu* Wiman (1905, p. 10, Pl. 2:13) is of the same age, and in all probability also belongs to *Gog*. Fortey (1975a, p. 27) suggested that 'Pygidium no. 1' may be conspecific with *Gog* n.sp., but this is not considered likely, as the specimen is characterized by a much narrower (tr.) axis.

Gog seems to be confined to marginal facies, within Scandinavia occurring only in Jämtland (Tjernvik 1980, p. 185) and Scania-Bornholm. *Gog* occurs in nileid biofacies on Spitsbergen (Fortey 1980a), and has also been reported from NW China (Zhou *in* Zhou *et al.* 1982) and Great Britain (Thomas *et al.* 1984). *Gog* is also present in the northern Urals ('*Ogygiocaris*' spp. N1–N3, '*Ogygiocaris* aff. *sarsi*' and

'*Niobe* aff. *emarginula*' sensu Burskij 1970). Despite showing a slightly different outline of the glabellar muscle insertion sites, I would also be inclined to allocate the Central Asian *Niobe tenuistriata* Chugaeva, 1958 to *Gog* (but see Fortey 1975a, p. 31; Morris 1988, p. 148).

Gog explanatus (Angelin, 1851)

Fig. 142

Synonymy. – □v 1851 *Niobe explanata* n.sp. – Angelin, p. 15; Pls. 11:4; 12:2 (brief diagnosis, illustrations of cranium, pygidium). □v 1886 *Niobe explanata* Ang. [*partim*] – Brögger, pp. 50–51, Pl. 2:36, 36a; non Pl. 2:35 [= *Niobe* (*N. tjernviki* n.sp.)] (description and illustrations of hypostome). □v 1936 *Niobe explanata* Ang. [*partim*] – C. Poulsen, pp. 49, 50 (listed). □v 1975a *Gog explanatus* (Angelin 1851) – Fortey, p. 27; Pl. 4:1, 2 (discussion of generic assignment, illustrations of lectotype cranium, pygidium).

Lectotype. – Cranium no. Ar 24085, assumed original of Angelin (1851, Pl. 11:4), designated by Fortey (1975a, Pl. 4:1). The specimen is here refigured on Fig. 142A.

Material. – Three cranidia (of which one is a tiny fragment), 5 hypostomata, and 5 pygidia.

List of material. – □Cranidia F 196 (im) fragment, Ar 24085a (pim) [lectotype], Sk 71 (im) [coll. Uppsala Univ.]. □Hypostomata F 105 (em) [MGUH 22.610], LU 62 (im) fragment, LU 122 (im/em) [LO 7118], Ar 24083 (im), Ar 24095 (im). □Pygidia GM 1885.43 (im) [MGUH 22.611], GM 1984.1804 (im) [MGUH 22.612], LU 101 (im) [LO 7110], LU 118 (is) [LO 7117], F 298 (im).

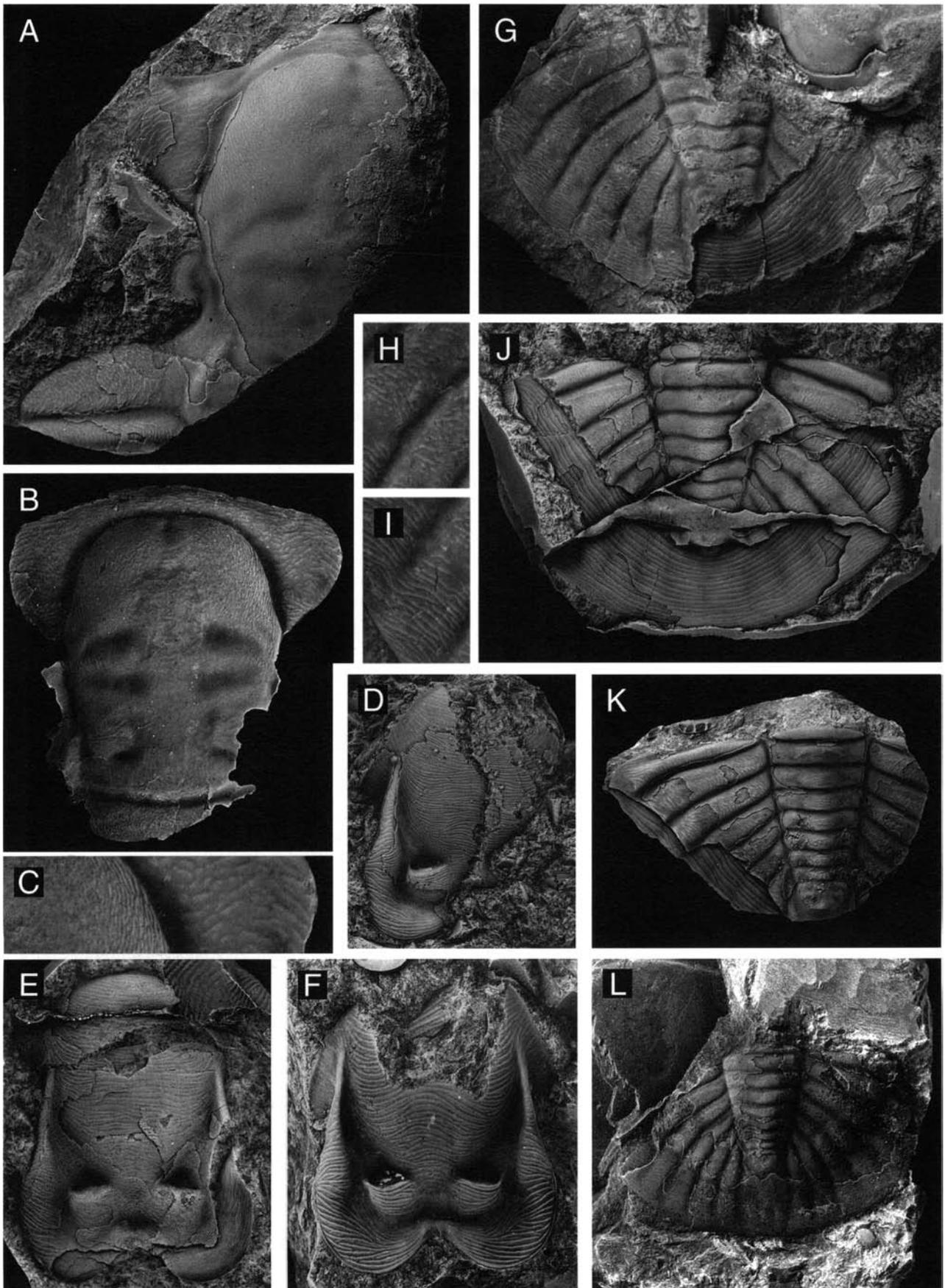
Occurrence. – Cranium F 196 and hypostome F 105 are from beds 19–20 of Fågelsång (*A. expansus* Zone). The museum specimens studied, except for the GM sample, are from the Fågelsång area, and undoubtedly originate from the basal part of the *A. expansus* Zone (bed interval 18–23). Pygidium F 298 was collected from the lowermost limestone bed intercalated within the Upper *Didymograptus* Shale at Fågelsång (*A. 'raniceps'* Zone). Pygidium GM 1984.1804 is from Vasegård, Bornholm; the sample represents the very top of bed +13, that is, base of the *A. expansus* Zone.

Diagnosis. – Glabella broad with trapezoidal anterior lobe; anterior margin of cranium truncate. Facial sutures diverge strongly in front of eyes; palpebral lobes small. Pygidium with six pairs of gently curved pleural ribs; pleural furrows continue onto border and stop short off outer margin, and are also impressed on the doublure. Dorsal surface of cranium and pygidium covered with numerous coarse, discontinuous, irregular terrace ridges. [Emended from Angelin 1851.]

Description. – Large form, largest cranium (Sk 71) 33 mm long, largest hypostome 34 mm long, largest pygidium about 55 mm long. The damaged lectotype cranium was originally 50–55 mm long; the specimen shows an original injury

in the left side of the anterior cranial margin (Fig. 142A). Cranium of low convexity, FW:L ratio ca. 2:3, PW:L ratio ca. 1:1. Glabella (including occipital ring) roughly of rectangular outline, moderately vaulted, and stretches for slightly more than 0.9 of the cranial length; glabellar W:L ratio about 2:3 (maximum width). Glabella expands gently forwards to attain maximum width immediately in front of eyes, a little more than one third of the glabella length (including occ. ring) from its front; the ratio maximum glabellar width to PW is ca. 2:3. Minimum glabellar width, shortly in front of occipital furrow, is 0.85 of the maximum glabellar width. Frontal lobe trapezoidal, delimited by well-impressed axial and preglabellar furrows, whereas the axial furrows posteriorly are ill-defined (adjacent to palpebral area) or not defined (adjacent to bacculae). Glabellar front truncate with a small mesial impression. Both specimens at hand (internal moulds) show a low mesial swelling or tubercle a short distance above this basal mesial impression; the swelling is rearwards flanked by shallow impressions of irregular outline, connected across sagittal line. Four pairs of lateral glabellar furrows (Fig. 142B), which probably are visible also on testaceous material; none of them join across glabella. F4 rather inconspicuous, short and shallow, situated adjacent to axial furrow immediately in front of F3. F3 and F2 well-impressed and quite distinctive. F3 slightly curved, running inwards, gently forwards from immediately in front of anterior corner of palpebral lobe. F2 runs inwards, gently oblique backwards from a level above the middle of the palpebral lobe. F1 is less impressed and forms a pair of U-shaped posterior impressions midway up glabella between posterior margin of palpebral lobes and mesial glabellar tubercle. F1 appears composite, formed by fusion of two muscle areas. Very small mesial tubercle situated slightly more than 0.25 of the glabellar length (including occipital ring) from posterior margin. Occipital furrow almost straight and fairly well-impressed throughout; it widens

Fig. 142. *Gog explanatus* (Angelin, 1851). □A. Largely exfoliated, fragmentary lectotype cranium, $\times 1.5$. Ar 24085, Fågelsång. Probably original of Angelin (1851, Pl. 11:3), and previously figured by Fortey (1975a, Pl. 4:1). □B–C. Internal mould of fragmentary cranium showing lateral glabellar furrows, $\times 2$; C close-up of anterior glabella and part of frontal area showing impressions of cuticle ornament, $\times 4$. SK 71, Fågelsång. □D. Latex cast of fragmentary hypostome showing cuticle terrace-line sculpture, $\times 2$. MGUH 22.610 (F 105), bed 19, Fågelsång. □E. Latex cast of partly exfoliated hypostome, $\times 2$. LO 7118 (LU 122), Fågelsång area. □F. Internal mould of large hypostome, showing impressions from cuticular terrace lines, $\times 2$. Previously figured by Brögger (1886, Pl. 2:36). Ar 24083, Fågelsång. □G–I. Internal mould of large pygidium, $\times 2$. H–I close-ups of pleural field and border, showing impressions of cuticle sculpture, $\times 4$. LO 7110 (LU 101), Fågelsång. □J. Latex cast of internal mould of pygidium showing doublure, $\times 2$. LO 7117 (LU 118), Fågelsång, loc. E21b. □K. Fragmentary internal mould of pygidium, $\times 1$. MGUH 22.611 (GM 1885.43), bed +13, Duegård, Bornholm. □L. Partly exfoliated small pygidium, $\times 2$. MGUH 22.612 (GM 1984.1804), bed +13, Vasegård, Bornholm.



slightly abaxially. Occipital ring comparatively wide (sag.), sagittally occupying about 0.15 of cranial length; it is flat and level with the rear part of glabella. Frontal area slopes gently away from sagittal line. Anterior area of fixigena tapers out in posterior direction and stops a short distance in front of eye. Palpebral lobes strongly arcuate, very small, slightly less than twice as long (exsag.) as broad (tr.), length (exsag.) equivalent to only about 0.2 of the cranial length, and posterior inner corner is situated about one third of the cranial length from posterior margin. The anterior inner corner touches the axial furrow. A rim along outer margin is flat; inner part of lobe depressed. Posterior area of fixigena slopes gently outwards; it is comparatively broad (exsag.), the exsagittal width (middle of fixigena) is by estimate equivalent to about 0.25 of the total cranial length. Posterior border convex, raised slightly above remaining part of posterior fixigena. Posterior border furrow wide, well-impressed, straight, and not confluent with occipital furrow, but join axial furrow behind the bacculae. Bacculae slender, elongate, pointing obliquely forward-inward (ca. 35° from sagittal line). Anterior sections of facial suture diverge in front of the eyes, ca. 45–50° from sagittal line, then gradually curve forwards, to turn sharply inwards and run almost straight adaxially to merge smoothly in front of glabella. Posterior section of facial suture sigmoidal (Fig. 142A). Both cranidia available are largely exfoliated, but the mould surface shows imprints of terrace lines, or rather, terrace ridges. Overall, the cranial ornamentation is extensive (Fig. 142A–C). The short, irregular terrace ridges are transverse on anterior fixigenae and frontal area, oriented largely parallel to sagittal line on posterior fixigenae, and basically follow the contour on glabella. Small patches of intact test shows that the cranial surface is also covered with small pits; this has been verified for anterior fixigena, palpebral lobes and adjacent part of glabella, bacculae and the major part of posterior fixigena. Terrace ridges are absent on the palpebral lobes and bacculae, including adjacent portion of posterior fixigena, and in axial, preglabellar, posterior border and transverse glabellar furrows; the surface of the latter is, however, irregular, reticulate.

Librigena unknown.

Apart from being larger, the hypostome is remarkably similar to that of *Niobe tjernviki* n.sp. (q.v.). *G. explanatus* differs in possessing a wider anterior lobe of median body, the W:L ratio is about 3:4; the elongate maculae are more perfectly oval in outline and strike backward at a lower angle to sagittal line (105° compared to 110°). The posterior lobe of *G. explanatus* is subdivided by a shallow mesial impression into a pair of gently inflated areas; posterior boundary of posterior lobe appears less steep, and the posterior border furrow seems to be slightly less impressed. It is also suspected that the anterior margin is less strongly curved in *G. explanatus*. No differences in surface sculpture have been ascertained.

Pygidium parabolic in outline, gently vaulted, W:L ratio about 1.8. Axis fairly prominent, moderately arched, delimit-

ed by narrow, shallow, but well-defined axial furrows. Axial width at anterior margin accounts for ca. 0.25 of the pygidial width. Axis tapers evenly backwards to just in front of terminal piece. Behind this level the axial furrows assume a slightly convex bracket-shape and run to posterior margin, thus giving the axis an infundibular appearance. Postaxial ramp descends rapidly, but has a positive relief even on the border. Eight axial rings present in addition to anterior articulating half-ring and the prominent, evenly rounded terminal piece, separated by undulating well-impressed ring furrows. Six pairs of wide pleural ribs in addition to anterior half rib, are separated by well-impressed, rather wide interpleural furrows, which continue onto the border to stop short off pygidial margin. The furrows are backward-deflected distally. Border wide, defined essentially by a change of slope, although a shallow, wide, discontinuous border furrow 'terminates' the pleural ribs. Border flat, sloping gently towards outer margin, crossed by the continuations of the pleural and axial furrows. Maximum border width attained anterolaterally at level with the second pair of ribs, minimum width, corresponding to about 2/3 of maximum border width, attained postaxially. Articulating facets not visible. Doublure rather wide, gently concave, almost flat; inner margin shows moderately deep V-shaped axial embayment. The furrows of the border region are traceable on the doublure as very wide, indistinct impressions (Fig. 142J). Inner limit of doublure gently scalloped.

Dorsal surface sculpture consists of densely spaced, rather coarse terrace ridges on the border, running subparallel to outer margin, whereas more irregular, discontinuous, crudely semi-circular terrace ridges occur on the pleural ribs (Fig. 142H–I); no ornamentation is seen in the furrows. Discontinuous, irregular, predominantly longitudinal terrace ridges are present on the axial rings, associated with small pits. The doublure is covered with coarse, continuous terrace lines. One specimen has 25–26 lines behind the axis (sag.), including the upturned inner edge of doublure.

Affinities. – *G. explanatus* is distinguished from *G. catillus* by a broader glabella, trapezoidal anterior glabellar lobe, truncate anterior margin of the cranidium, and shorter preglabellar field; the hypostome has a less curved anterior margin, less backward striking maculae, a stronger inflated posterior lobe of median body, more crest-like lateral borders stretching further forwards, a deeper posterior mesial notch and therefore a more bilobate posterior border; the pygidium possesses only six pairs of pleural ribs, the distal parts of the pleural furrows are less backward-deflected on the border area, the paradoublure line is inconspicuous, and the dorsal terrace ridges are fewer, coarser and more irregular.

The poorly known unnamed species occurring in the *M. planilimbata* Zone of the 'Latorp Limestone' (Gog n.sp. Fortey, 1975a, Pl. 4:3) seems at least to have more than six pairs of pleural ribs in the pygidium.

The pygidium figured by Wiman (1905, Pl. 2:13) differs from *G. explanatus* by having a slender axis and eight or nine

pairs of pleural ribs, besides being very broad (tr.) (which, however, may relate to compaction).

Remarks. – *Niobe explanata* was established on material from Fågelsång (Angelin 1851, p. 15), which most likely had been collected from the basal part of the *A. expansus* Zone.

Brögger (1886, p. 50; Pl. 2:35–36) figured two hypostomes from Fågelsång, attributed to '*Niobe explanata*'. One of them (Brögger 1886, Pl. 2:36; refigured on Fig. 142F) actually belongs to *G. explanatus*, while the other (Brögger 1886, Pl. 2:35; refigured on Fig. 129E) is assigned to *Niobe tjernviki* n.sp..

The posterior mesial notch of the hypostome is distinctly deeper in *G. explanatus* than in the *G. catillus*, and it appears that there is a trend within *Gog* towards a deeper hypostomal notch during evolution, just as seen in *Niobe* and *Niobella*. The hypostome of *G. explanatus* also deviates by not showing obliquely backward striking macular surfaces. In these respects the diagnosis of *Gog* should be modified (cf. Fortey 1975a, p. 22).

N. explanata, listed by C. Poulsen (1936) from Bornholm, includes *N. imparilimbata*, *Gog cf. explanatus* (see below) as well as a single specimen of *G. explanatus*.

Gog cf. explanatus

Fig. 143A–B

Synonymy. – □v 1936 *Niobe explanata* Ang. [*partim*] – C. Poulsen, pp. 49, 50 [material from '*Umbonata*' limestone = *Niobe* (*Niobella*) *imparilimbata* Bohlin] (listed). □v 1936 *Niobe* n.sp. – C. Poulsen, p. 49 (listed).

Material. – One fragmentary cranidium, 4 pygidia.

List of material. – □Cranidium F 17 (im) fragment. □Pygidia S 1299 (c) [MGUH 22.613], K 992? (c), GM 1885.43 (im), GM 1951.41 (c) [MGUH 22.614].

Occurrence. – Cranidium F 17 is from bed 1, Fågelsång, pygidium S 1299 is from bed +7, Skelbro, and pygidium K 992 is from bed +17, Killeröd; all of these beds are within the *M. limbata* Zone. Pygidium GM 1951.41 comes from Skelbro, Bornholm. The lithology is rather distinctive and leaves little doubt that the sample represents the basal part of bed –10, which belongs to the lower part of the *M. simon* Zone. Pygidium GM 1885.43 from St. Duegård, Bornholm, cannot be assigned to level.

Remarks. – The poorly preserved specimens show close resemblance to *G. explanatus*, but the pygidial axial rings are less backward-curved mesially, and the surface sculpture consists of fewer, but more regular terrace ridges. Furthermore, there seems to be an extra, very short posterior pair of pleural ribs close to the axis. Cranidium F17 is only a small fragment of the inner part of posterior fixigena. Compared to *Gog explanatus* the baccula is clearly narrower and more inflated.

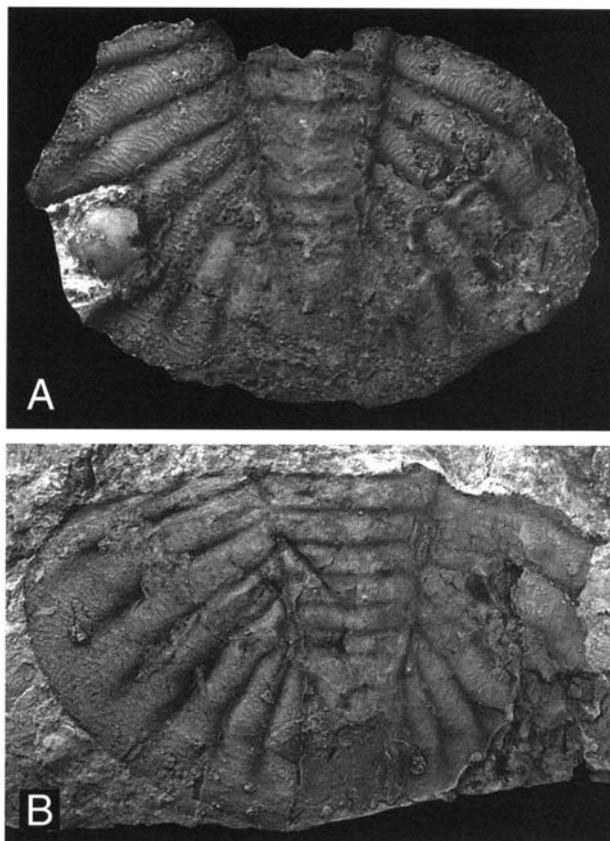


Fig. 143. *Gog cf. explanatus* (Angelin, 1851). □A. Corroded pygidium, ×2. MGUH 22.613 (S 1299), bed +7, Skelbro. □B. Corroded pygidium, ×2. MGUH 22.614 (GM 1951.41), Skelbro.

Pygidia GM 1885.43 and GM 1951.41 were listed as *Niobe* n.sp. and *Niobe explanata*, respectively, by C. Poulsen (1936)

Family Nileidae Angelin, 1854

Genus *Nileus* Dalman, 1827

Type species. – *Asaphus* (*Nileus*) *armadillo* Dalman, 1827 (SD Hawle & Corda 1847).

Material of NILEUS. – 123 complete specimens, 55 cephalae, 452 cranidia, 151 juvenile cranidia, 6 librigenae, 568 pygidia and 338 juvenile pygidia (including 187 transitory pygidia), of which 7 complete specimens, 1 cephalon, 38 cranidia, and 37 pygidia are too badly preserved to be identified at the species level. Another 11 juvenile cranidia and 20 juvenile pygidia cannot be assigned to species, because of the lack of adult characteristics. More than 100 nileid hypostomes, including *Nileus* as well as *Symphysurus*, will be the subject of future studies.

General description, including remarks on taxonomic characters. – The basic morphology of the various nileid species is very uniform. The following detailed general description serves to avoid recapitulations.

Nileus is a small to medium-sized, opisthoparian, isopygous genus; total length of adults in the range of 20–110 mm. Dorsal exoskeleton subelliptical in outline; cephalon usually occupies about or slightly less than 0.3 of the body length (dorsal projection), thorax about 0.45–0.50 and pygidium about 0.25. Skeleton tapers slightly backwards, and pygidial width is about 0.8 of the cephalic width. Enrolment sphaeroidal (*sensu* J. Bergström 1973). External side of exoskeleton rather smooth; internal side shows more ridges and furrows, produced by thickening and thinning of the test. Most features such as axial furrows, occipital furrow, pygidial axial segments etc. are more conspicuous on internal moulds and often have no external expression.

Cephalon reniform to semicircular in outline, 1.5–2 times as wide as long, and fairly convex (both ways). Frontal area extremely narrow, consisting of the narrow border only, defined by a change of slope and typically formed by the librigenae alone; no border furrows or preglabellar furrow developed. In a few species a narrow, flattened anterior fringe of cranidium is less sloping and joins anterior border. Glabella very wide, gently arched (tr.) with a varying sagittal convexity between species. Glabella usually longer than broad, slightly tapering in forward direction to front of eyes, then expands to a more or less rounded front parallel to anterior cephalic margin. Central part of glabella, between palpebral areas, may be roughly rectangular, subquadratic, or slightly rounded; the outline is a useful taxonomic character. Axial furrows, delimiting glabella from palpebral lobes, typically wide and shallow on testaceous material, if not effaced, more distinct on internal moulds, but may rarely be absent there as well. The furrows are, however, typically augmented by a change of slope between glabella and palpebral areas. They run downwards inside eye anteriorly and posteriorly to connect with furrow at base of eye socle. A small mesial tubercle, situated posteriorly on glabella, is present on internal moulds; the tubercle is difficult to recognize on testaceous material if not indicated by colour differences. Lateral glabellar furrows absent; three to five pairs of faint impressions, representing muscle insertion sites, are occasionally defined on internal moulds. Internal moulds normally show an indistinct sagittal keel, running from tubercle to stop about 0.15–0.20 of the cranial length from anterior margin. Occipital furrow usually effaced on testaceous material; internal moulds show a mesial expansion flanked by a pair of muscle insertion sites. Occipital ring is in most species defined exclusively on internal moulds; it is very short (sag.), consisting only of the raised posterior margin, and, in fact, rather represents an articulating half-ring than a true occipital ring. Anterior area of fixigena not defined, as axial furrow does not continue forwards. In a few species the facial suture runs very shortly anteriorly-inwards from the

palpebral lobe, before joining the axial furrow, and a diminutive triangular area may thus be present immediately in front of palpebral lobe, i.e. an ‘anterior fixigena’. Palpebral area flat, or, usually, gently convex (tr.); palpebral lobe pronouncedly arcuate. Maximum cranial width is across palpebral lobes. Short (tr.), narrow (exsag.) posterior area of fixigena confluent with glabella; length (exsag.) equivalent to about 0.15 of the cranial length; it is more or less inclined downwards and the distal tip points slightly backwards. Posterior border very narrow, vaguely defined only by a slightly different slope, and the term posterior border is generally not used. Posterior margin of occipital region straight, but an indistinct axial socket, moderately incised in a few species, is situated level with posterior corner of palpebral lobe; the margin turns slightly obliquely backwards abaxially to socket. Anterior branches of facial suture run from palpebral lobes, inside the eye-lenses, diverging more or less strongly in front of eyes to turn adaxially close to anterior margin, and then run adjacent to anterior cephalic margin. Anterior branches merge smoothly or meet more or less angularly; the outline is a useful taxonomic character. In *N. armadillo* and *N. orbiculatoide* the anterior margin shows a characteristic small mesial protuberance, referred to as the anterior mesial boss. Posterior branches of facial suture run from palpebral lobes and obliquely backwards-outwards; they may be straight or gently sigmoidal.

Holochroal eye comparatively very large, semicircular, with well-developed eye socle. Slender anterior continuation of librigena forms, sometimes together with flattened anterior cranial margin, a very narrow concave anterior border. Lateral border widest at anterolateral part of eye, thence tapers rearwards and does not reach genal angle. Librigena is therefore convex posteriorly, but the degree of convexity varies between species. Posterior border not defined. Genal angle normally spineless, rounded, but genal spines have been reported in juveniles of some species (e.g., Tjernvik 1956).

Surface sculpture of cephalon variable. The test is mostly smooth or provided with more or less indistinct minute pits, which may be present all over or only cover parts of cephalon, and then predominantly the palpebral lobes and posterior portions of librigenae. This appears not to be a useful taxonomic character. Only a few species carries terrace lines on cephalon. Well-preserved cephalons of most species show a ‘wrinkled’ pattern along sagittal line, produced by an uneven test surface; rarely other areas, corresponding to muscle insertion sites, are ‘wrinkled’ as well. The wrinkling probably formed by muscle action while the test was still soft during and immediately after exuviation.

Cephalic doublure strongly concave, except mesially, where inner margin is down-flexed, forming a socket for hypostome, and posteriorly, along posterior margin of librigena, where the doublure is flattened and ‘pleura-shaped’, forming a stopping device for the first thoracic segment; the posterior flattened part stretches inwards almost to the inter-

section of facial suture with posterior margin, and is separated by a marked, transverse crest from the concave anterior part (Fig. 149B). Maximum doublural width is sagittally, where it stretches below about one third of the cephalic length; minimum doublural width is close to posterior margin in front of flattened part, there extending inwards for about 0.2 times the cephalic width in total (tr., both sides). Laterally the doublure touches outer eye-level. It is covered with coarse, continuous terrace lines, running largely parallel with outer margin.

Hypostome not yet studied; see Brögger (1886), Lindström (1901) and Schrank (1972).

Thorax almost parallel-sided, slightly tapering backwards, consisting of eight segments; some North American species, however, possess only seven segments (see, e.g., Whittington 1963). W:W (tr.) and L:L (sag.) ratios of posterior vs. anterior thoracic segment are about 0.8–0.9 and 0.6–0.7, respectively. Moderately convex axis set off by flanking articulating processes and sockets, and by a 'pseudo' axial furrow, produced by short pleural furrows on each segment, running obliquely outwards-backwards from axial articulating furrow to stop about 0.25 of pleural width (tr.) from axis. Axis very wide, occupying about or slightly more than half of thoracic width; it is typically widest on the third segment and tapers very slightly in both directions, most so backwards. Pleurae gently convex with truncate extremities and well-developed articulating facets. Thoracic skeleton shows several ridges and furrows on ventral side, particularly in the axial region, produced by thickening and thinning of test; axis is smooth on external side. Each segment has, when exfoliated, a pair of transversely elongate crescentic swellings laterally on axis, whose inner parts undoubtedly were sites of muscle insertion. Deep articulating furrow developed anterior to swellings, delimiting a very narrow (sag.) articulating half-ring. Articulating furrows continue laterally into deep pleural furrows, running outwards-obliquely backwards, to stop at paradoublural line. These furrows are usually visible also on testaceous material, although less deep than on internal moulds.

Thoracic test surface mostly smooth with only a few, well-impressed transverse terrace lines on axis and pleurae; articulating facets always provided with numerous, fine terrace lines, running obliquely downwards-outwards.

Thoracic doublure wide, stretching inwards for about 0.75 of the pleural width (tr., in dorsal projection); a low crest (panderian protuberance *sensu* Hupé 1954) crosses doublure diagonally from anterior margin and obliquely backwards, forming a stopping device for the succeeding thoracic segment. Doublure covered with terrace lines, arranged in an outwards directed herringbone pattern along the crest; no panderian openings.

Spineless pygidium semicircular to semielliptical in outline, almost twice as wide as long, L:W ratio normally about 0.55–0.60. Pygidium gently to moderately convex (both ways) with rounded anterolateral corners. Axis mostly

poorly outlined on testaceous material, sometimes indistinguishable, internal moulds normally show a fairly defined axis, but a few species have a nebulous axis even on internal moulds. Axis stretches for about 0.6 of the pygidial length and is strongly tapering, hence the outline is more or less triangular. Axial furrows effaced externally, or nearly so, internal moulds commonly show wide and shallow, rather indistinct furrows. There are three to five axial rings in addition to terminal piece; segmentation typically outlined by lateral swellings, while sagittal part of axis is smooth. Deep anterior transverse axial furrow always defined on internal moulds (effaced or nearly so on testaceous specimens), delimiting very short (sag.) articulating half-ring, which consists only of the raised anterior margin. Transverse furrow continues laterally into pleural furrow, running outwards to stop at paradoublural line, that is, close to inner termination of articulating facets; furrow occasionally faintly defined also on testaceous material. Apart from this furrow, the pleural fields are without ribs or furrows. Articulating facets elongate triangular, well-developed, adaxially flanked by a pair of inconspicuous articulating processes, best seen on internal moulds. A concave border, less inclined than pleural fields, is often present. It is defined only by a change of slope and is not delimited by a border furrow. Width and degree of convexity are varying, and some species lack a border, which, though, should not be given much weight in taxonomy, as the condition border/no border occasionally varies even within a species (e.g., *Nileus latifrons* n.sp.).

Pygidial doublure very wide, absent only below axial region and anterior pleural furrow; it is typically strongly concave, with a gently upturned inner margin around tip of axis, and slightly downflexed anterolateral corners below articulating facets. Doublure covered with coarse, continuous terrace lines, roughly following the doublural contour, turning outwards along anterior margin. Most species have 14–22 lines, but a few show a different number.

Pygidia may or may not carry external terrace lines, this is a feature of prime taxonomic importance. Some species also exhibit a delicate pitting of test. Three basic types of pygidial terrace-line patterns are distinguished:

- 1 'exarmatus-type': test surface almost smooth with only a few terrace lines situated along anterior margin and on anterolateral part of border
- 2 'orbiculatoides-type': like 'exarmatus-type', but widely spaced terrace lines are present also on pleural fields and at times on the entire border
- 3 'depressus-type': densely spaced terrace lines cover entire pygidium, \pm the axial area. The latter condition apparently related to environment and is of no importance for classification.

Juveniles. – Cranidia less than 4 mm long are usually of low convexity (sag.), slightly longer than wide, with a comparatively strongly rounded anterior margin; glabella 15–20%

longer than in adults; no axial furrows defined. The cephalic elongation affects all ratios measured relative to the sagittal length. Cranidia about 4–5 mm long are less elongate, but still more so than adults; the smallest fully adult cranidia are typically about 5–7 mm long.

In a few species, notably *N. armadillo*, cranidia less than 3 mm long are quite strongly convex both ways, highest at glabellar tubercle, assuming a 'humpbacked' appearance. No axial furrows developed, anterior margin rounded and posterior fixigenae pointed downwards, so these small specimens are grossly spherical.

Tiny pygidia, 1.1–1.5 mm long, are quite convex (sag.) and lack a concave border; axis is narrow, long, and anteriorly provided with a well-defined articulating half-ring, projecting in front of pygidial margin. These transitory pygidia, referred to as growth stage A, appear to have only one unreleased segment. Doublure much narrower than in adults.

Transitory pygidia, 1.6–2.0 mm long, resemble group A pygidia, but have a well-defined concave border, presumably two unreleased anterior segments, and no forward-protruding half-ring. Doublure wider than in preceding stage. This growth stage is termed B.

A suite of similar-looking transitory pygidia with three, two, and one unreleased anterior segment(s), is termed stages C, D, and E, respectively. Group C pygidia are usually about 2–2.5 mm long, and have a concave, wide border, a less conspicuous, but still slightly raised axis, without a well-marked articulating half-ring. Dorsal surface smooth except for a few transverse terrace lines outlining the unreleased segments. Group D and E transitory pygidia with two and one unreleased segments are generally about 2.5–3.5 and 3–4 mm long, respectively, and fairly closely resembles the transitory pygidia of stage C. In all transitory pygidia, except for stage A, the unreleased segments are best seen on internal moulds, where they are outlined by well-defined axial rings, pleural furrows (proximally, inside doublure) and faint interpleural furrows (distally, above doublure).

Some unusually large representatives of stages C, D and E appear to represent specimens in which the anterior segment did not detach during moulting, which applies to 16 or 17 out of 187 transitory pygidia. These specimens are important, as they suggest that only one segment was released during each meraspid molting.

Small holaspid pygidia, 3.5–5 mm long, may differ from larger adults by the lack of a fully developed terrace-line pattern and by having a more or less well-defined concave border, which eventually may disappear in the fully adult specimens.

In species with a 'depressus-type' terrace-line pattern in the adult stage, terrace lines occasionally appear on the pleural fields of stage E transitory pygidia, and then typically arranged in a 'orbiculatoides-type' terrace-line pattern. However, the 'depressus-type' and 'orbiculatoides-type' terrace-line patterns mostly do not appear before in the first or

second holaspid instar, and it is generally impossible to refer isolated juvenile pygidia to species.

Remarks on Baltoscandian species. – The vertical distribution of Baltoscandian species is shown in Fig. 144.

Nileus armadillo was previously a collective label for most Baltoscandian representatives of *Nileus* (cf. Angelin 1851; Volborth 1863; Törnquist 1884; Moberg 1890; Schmidt 1904; Wiman 1904; Moberg & Segerberg 1906; C. Poulsen 1936; Skjeseth 1952, and others); Tjernvik's (1956) brief description heralded a more restrictive interpretation of the species. Besides *N. armadillo* only a few other Baltoscandian species and so-called variants were defined before the turn of the century, namely *Nileus chiton* Pander, 1830, *Nileus armadillo* var. *depressus* (Boeck, 1838), *Nileus armadillo* var. *oblongatus* (Boeck, 1838) (here synonymized with *N. armadillo*), *Nileus limbatus* Brögger, 1882, and *Nileus armadillo* var. *cornutus* Moberg, 1892. *Nileus?* *lineatus* Angelin, 1854 was transferred to *Diaphanometopus* Schmidt by Wiman (1906b), and *Asaphus* (*Nileus*) *palpebrosus* Dalman, 1827 was relocated to *Symphysurus* by Barrande (1852).

N. armadillo var. *depressus* was described in some detail by Brögger (1882), but has since then been mentioned only cursorily (Schrank 1972; Fortey 1975a), distinguished solely by size difference (e.g., Tullberg 1882) or synonymized with *N. armadillo* (e.g., Törnquist 1884; Schmidt 1904; Moberg & Segerberg 1906). *N. depressus* is here redescribed, based on material collected at Slemmestad, and it is concluded that *N. depressus* (s.l.) lately has been referred to as *N. glazialis* (Fortey 1975a; Tjernvik 1980). Three new subspecies are described, *N. depressus schranki* n.subsp., *N. d. serotinus* n.subsp. and *N. d. parvus* n.subsp.

N. chiton has usually been cited as a synonym of *N. armadillo* (see Schmidt 1904; Balashova 1976), but this interpretation is unlikely, as that species apparently does not occur in the eastern Baltic area. However, the definition of *N. chiton* is vague (restricted to conditions regarding the thoracic articulation and the outline of librigena), and cannot serve as basis for identification of new material, and the original illustrations are poor (Pander 1830, pp. 132–133, Pls. 4–C:12; 5:1a–c). The steep librigena may point to an identification with *N. depressus*, but the pygidium is stated to be smooth (Pander 1830, p. 132), and the transverse cephalic convexity is high according to the figures (Pander 1830, Pl. 5:1a). The name *Nileus chiton* Pander, 1830 must therefore be declared a *nomen dubium*. According to Vogdes (1925) the Pander fossil collection was lost in a fire.

N. armadillo var. *cornutus* Moberg, 1892, characterized by the presence of genal spines (Moberg 1892b, p. 3, footnote), is a *nomen nudum*. Funkquist (1919, p. 39) listed this so-called variant from the Komstad Limestone (? *lapsus calami*) as well as from the overlying beds at Tommarp (of Llandeilo age). It is suspected that the peculiar cranidium figured by Funkquist (1919, Pl. 2:4), identified as *N. armadillo*, may represent *N. cornutus*. It appears possible that the species

belongs to a new genus. No resembling material has been met with during the present study.

Nileus limbatus is fairly well-known from the descriptions published by Brögger (1882), Tjernvik (1956, 1980), and Schrank (1972); the latter author designated a lectotype.

N. orbiculatus is a rare small species, described by Tjernvik (1956) and Schrank (1972); it is known only from the basal Billingenian 'Transition beds'. *N. orbiculatus sensu* Balashova (1976), reported from a somewhat higher level, appears wrongly identified.

Schrank (1972) described *N. platys* and *N. globicephalus* from stratigraphic levels well above the Komstad Limestone; the former of these was divided into two subspecies, *N. p. platys* and *N. p. stigmatus*.

For the most recent review of non-Scandinavian nileids, see Fortey (1975a). To his list of species should be added *N. armadillo expansus* Gortani, 1934, *N. elegans* Xiang & Ji, 1988, *N. exarmatus obsoletus* Chang & Fan, 1960, *N. fenxiangensis* Xiang & Zhou, 1987 [however, hardly a *Nileus!*], *N. huanghuachangensis* Xia, 1978, *N. huanxianensis* Zhou

in Zhou *et al.*, 1982, *N. kasachstanicus* Koroleva, 1982, *N. klimoliensis* Lu in Lu *et al.*, 1976 *N. liangshanensis* Lu, 1975, *N.? luoxuensis* Li & Xiao, 1984, *N. malayensis* Kobayashi & Hamada, 1978, *N. petilus* Xia, 1978, *N. rugosus* Xia, 1978, *N. sanduensis* Yin in Yin & Li, 1978 [hardly a *Nileus!* ?*Poronileus*], *N. shibingensis* Yin in Yin & Li, 1978, *N. symphysoides* Lu, 1975, *N. teres* Tripp, 1976, *N. transversis* Koroleva, 1982, *N. transversus* Lu, 1975, *N. xilingxiaensis* Xiang & Zhou, 1987, *N. walcotti* Endo, 1932 and *N. yichangensis* Xiang & Zhou, 1987; the list is probably not complete.

Remarks on the phylogenetic relations of Scandinavian species of NILEUS

The phylogeny of *Nileus* has been briefly discussed by Schrank (1972, pp. 352–354) and Tjernvik (1980; personal communication, 1983, see Fig. 146), and the issue is of utmost relevance in a stratigraphical context. The present sketchy interpretation is summarized in Fig. 145.

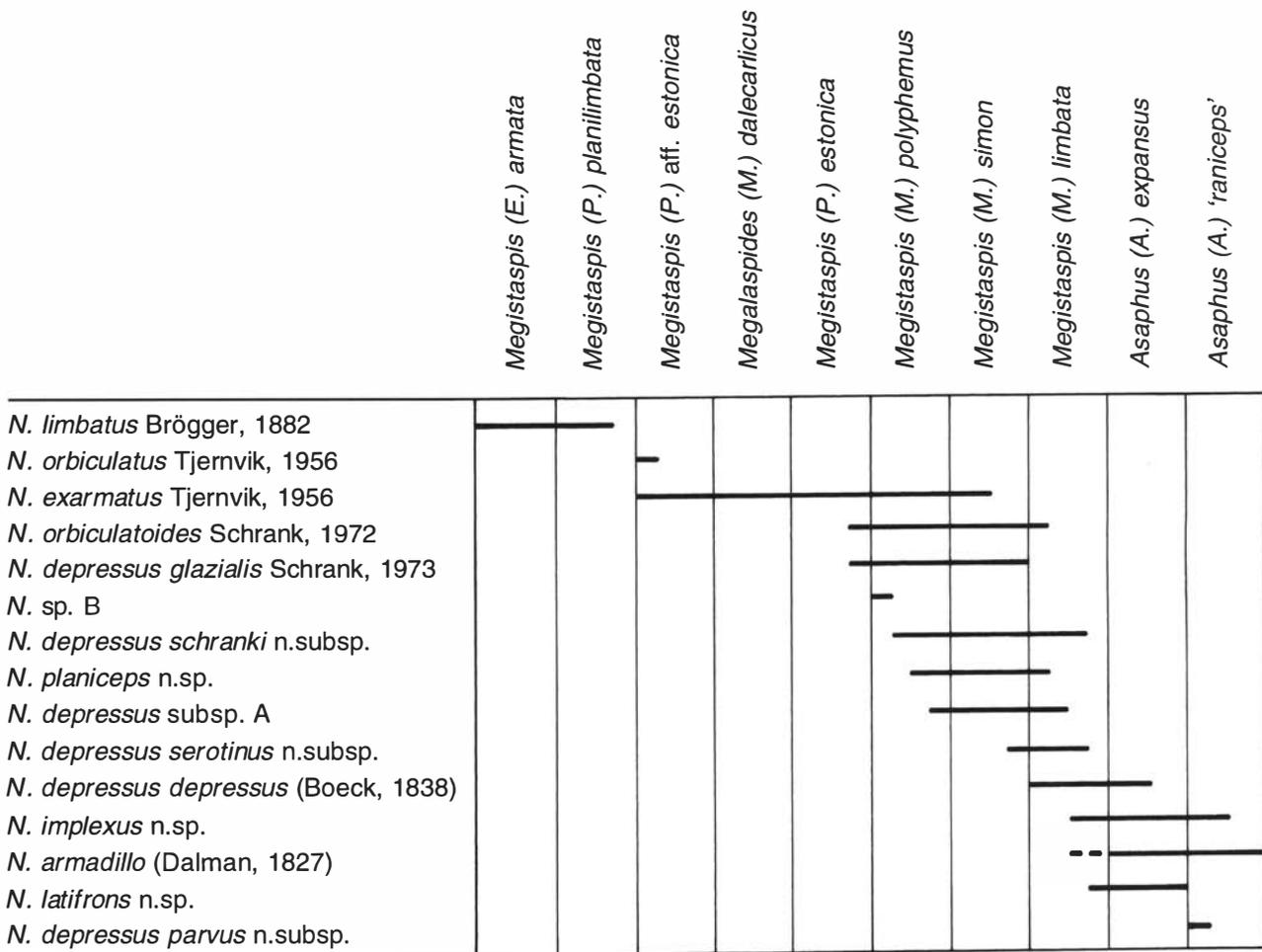


Fig. 144. Stratigraphical distribution of Baltoscandian species of *Nileus* (includes data from Tjernvik 1956, 1980; Schrank 1972).

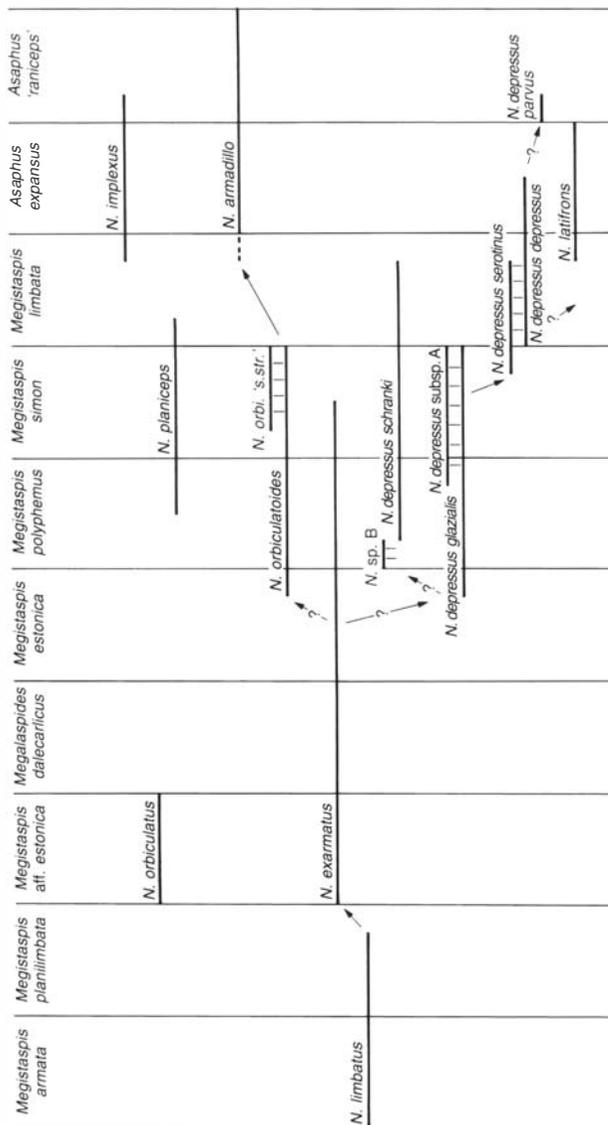


Fig. 145. Hypothesis of phylogenetic relations between Baltoscandian species of *Nileus* (includes data from Tjernvik 1956, 1980; Schrank 1972).

I am confident that the inferred lineages *N. limbatus* – *N. exarmatus* and *N. orbiculatooides* – *N. armadillo* are correct, as the respective couplets of species are very similar. It is likely that the *armadillo* line was continued by the comparatively large-sized *N. platys* and *N. globicephalus*, as suggested by Schrank (1972). The plexus of *N. depressus* subspecies is also believed closely related, but details are obscured by the interplay between evolution and environmental influence (ecophenotypes), which needs clarification. This is also the case for *N. orbiculatooides*. The remaining relationships indicated in Fig. 146 are uncertain (and based mainly on stratigraphic reasoning), including whether *N. orbiculatooides* and/or *N. depressus* originated from *N. exarmatus*, as inferred by Tjern-

vik (1980, p. 203; Fig. 145). The process of drawing inferences is much hampered by the lack of detailed knowledge of Baltoscandian nileids in general, but a parochial 'Scandinavian approach' is also hazardous since *Nileus* is a widespread genus. A large scale revision is, however, beyond the scope of the present paper.

Schrank (1972, pp. 352–354) mentioned *N. orbiculatus* in conjunction with the later *N. orbiculatooides* and *N. 'lineatus'* [= *glazialis*, Schrank, 1973] as a branch of *Nileus* characterized by an increasing terrace-line coverage of the pygidium and with an occasionally poorly defined or absent pygidial border. This interpretation was rejected by Tjernvik (1980, p. 203). The holotype of *N. orbiculatus* (see Tjernvik 1956, Pl. 2:22), which is an internal mould, show shallow imprints of terrace lines, and a major portion, or all, of the cephalic surface appears to have been terrace-line covered (the specimen has been examined). This condition may in fact point to a relationship to *N. depressus* [= '*lineatus*' Schrank].

Tjernvik (1980, p. 203) distinguished two forms of *N. orbiculatooides*, an early, called *N. exarmatus orbiculatooides* n.sp. or subsp. and a late, referred to just as *N. orbiculatooides*. It appears, however, that *N. 'exarmatus orbiculatooides'* occurs throughout the *M. polyphemus* and *M. simon* Zones of the Komstad Limestone, hence it is more likely that the apparent gradual evolution within *N. orbiculatooides* of central Sweden reflects environmental changes, and *N. 'exarmatus orbiculatooides'* and *N. orbiculatooides sensu* Tjernvik are here interpreted as ecophenotypes.

As remarked above *Nileus armadillo* is most likely a descendant of *N. orbiculatooides*, an inference based on their grossly identical basic morphology, the rather similar external terrace-line patterns, and especially the shared presence of a mesial cranidial boss. Tjernvik (1980, p. 202) suggested *N. armadillo* to be derived from a form called *Nileus* n. subsp. (aff. *N. armadillo*) [= *Nileus exarmatus* n. subsp. Tjernvik 1980, p. 192], characterized by a broad, almost quadratic glabella and smaller size than *N. armadillo*. In the absence of a more detailed description the form cannot be evaluated.

Another lineage of *Nileus* is represented by the *N. depressus* subspecies (attributed to *N. glazialis* by Tjernvik 1980). The earliest Scandinavian representatives of the *N. depressus* group appear just below the *M. estonica* / *M. polyphemus* Zonal boundary; various subspecies then range upward into the *A. expansus* Zone. *N. depressus* reappears at higher levels (Wandås 1984; see also discussion herein of *N. depressus depressus*). It is possible that *N. depressus* originated from *N. exarmatus*, as believed by Tjernvik (personal communication, 1983; see also Tjernvik 1980, p. 203), but if the species group is pandemic, a larger scale analysis is needed. Tjernvik (1980) discerned three subspecies of *N. glazialis* [here assigned to *N. depressus*], assumed to represent an evolutionary lineage, and considered useful for stratigraphy (cf. Fig. 146). However, the ranges within the Slemmestad section of *N. depressus glazialis* [= *N. glazialis* subsp. 1 *sensu* Tjernvik]

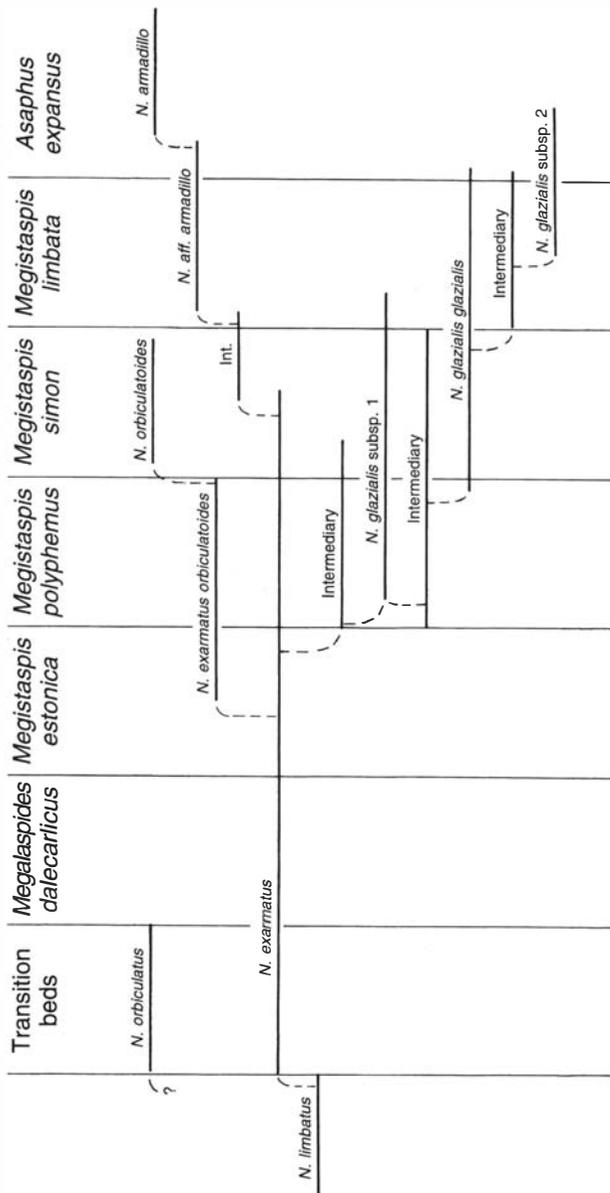


Fig. 146. Hypothesis of phylogenetic relations of Baltoscandian species of *Nileus* according to Tjernvik (personal communication, 1983). Redrawn from unpublished figure made by Tjernvik, slightly modified according to Tjernvik (1980). *N. glazialis* subsp. 1 was reported only from the *M. polyphemus* Zone by Tjernvik (1980), which, however, is a matter of subspecies definition.

and *N. depressus* subsp. A [= *N. glazialis glazialis sensu* Tjernvik] differ from those seen in central Sweden (Figs. 145 vs. 146), hence *N. depressus glazialis* and *N. depressus* subsp. A more likely represent ecophenotypes rather than chronosubspecies. This deduction is further supported by unpublished information on a complex intermingling between the two subspecies in the Lanna section (Tjernvik, personal communication, 1983, see discussion of *N. depressus glazialis* for details). *N. depressus depressus* [= *N. glazialis* subsp. 2

sensu Tjernvik], which turns up at the base of the *M. limbata* Zone at Slemmestad, is treated as a chronosubspecies of *N. depressus glazialis*, but may, in fact, merely represent another ecophenotype.

The suite of *N. depressus* subspecies occurring in mainland Sweden is not present in the Komstad Limestone. Here *N. d. serotinus* n.subsp. appears in the upper part of the *M. simon* Zone, but has its main occurrence in the middle part of the *M. limbata* Zone. The new subspecies is very similar to *N. depressus depressus*, and is almost certainly a closely related Scanian counterpart (ecophenotype?). *N. depressus schranki* n.subsp. is common in the Komstad Limestone and occurs from the lower part of the *M. polyphemus* Zone and well into the *M. limbata* Zone. It is regarded as a sister group to the *N. depressus glazialis / depressus* line, and *N. d. depressus*, *N. d. glazialis*, *N. d. serotinus* n.subsp. and *N. d. subsp. A* are probably mutually closer related than to *N. d. schranki* n.subsp. A third new subspecies, *Nileus depressus parvus* n.subsp., has been found only in one bed near the base of the *A. 'raniceps'* Zone at Killeröd. It is almost certainly related to the somewhat younger *Nileus* sp. *sensu* Wandås (1984).

A problematic nileid, referred to as *Nileus* sp. B, occurs solely at the very base of the *M. polyphemus* Zone at Skelbro. The cranidium of sp. B is extremely similar to the early representatives of *N. d. schranki* n.subsp., while the thorax and pygidium resemble *N. orbiculatoides*. This early 'hybrid' superficially looks like a 'missing link' between *N. orbiculatoides* and *N. depressus*, which, though, is hardly the case. *Nileus* sp. B is believed to represent a shallow-water ecophenotype of *N. d. schranki* n.subsp. (for details, see discussion of sp. B).

A corollary of the *N. depressus* phylogeny outlined above is that presence or absence of pitting on the cranidium are of no phylogenetic significance. Thus *N. depressus schranki* n.subsp. and *N. depressus depressus* both have pitted test; neither *N. depressus glazialis*, supposed ancestor of *N. depressus depressus*, nor *N. depressus serotinus* n.subsp., assumed closely related to *N. d. depressus*, show pitted cranidial test. It is also obvious that the presence or absence of terrace lines on the axial area of *N. depressus* pygidia is a character subjected to infrasubspecific variation (see description of *N. d. glazialis* and *N. d. depressus*), and most of the apparent gradual evolution, seen in the *N. depressus* group of central Sweden, is believed to reflect environmental changes rather than evolution.

N. latifrons n.sp. has a cephalon resembling *N. depressus* in gross outline, but the characteristic pygidial 'depressus-type' terrace-line pattern is not developed. Despite this, it appears reasonable to infer that *N. latifrons* n.sp. is related to the *N. depressus* group, and the relationship may be a case analogous to that between *N. depressus schranki* n.subsp. and *Nileus* sp. B.

The relationships of *N. implexus* n.sp. and *Nileus planiceps* n.sp., both having a terrace line covered pygidium, are obscure.

Nileus armadillo (Dalman, 1827)

Figs. 147–151

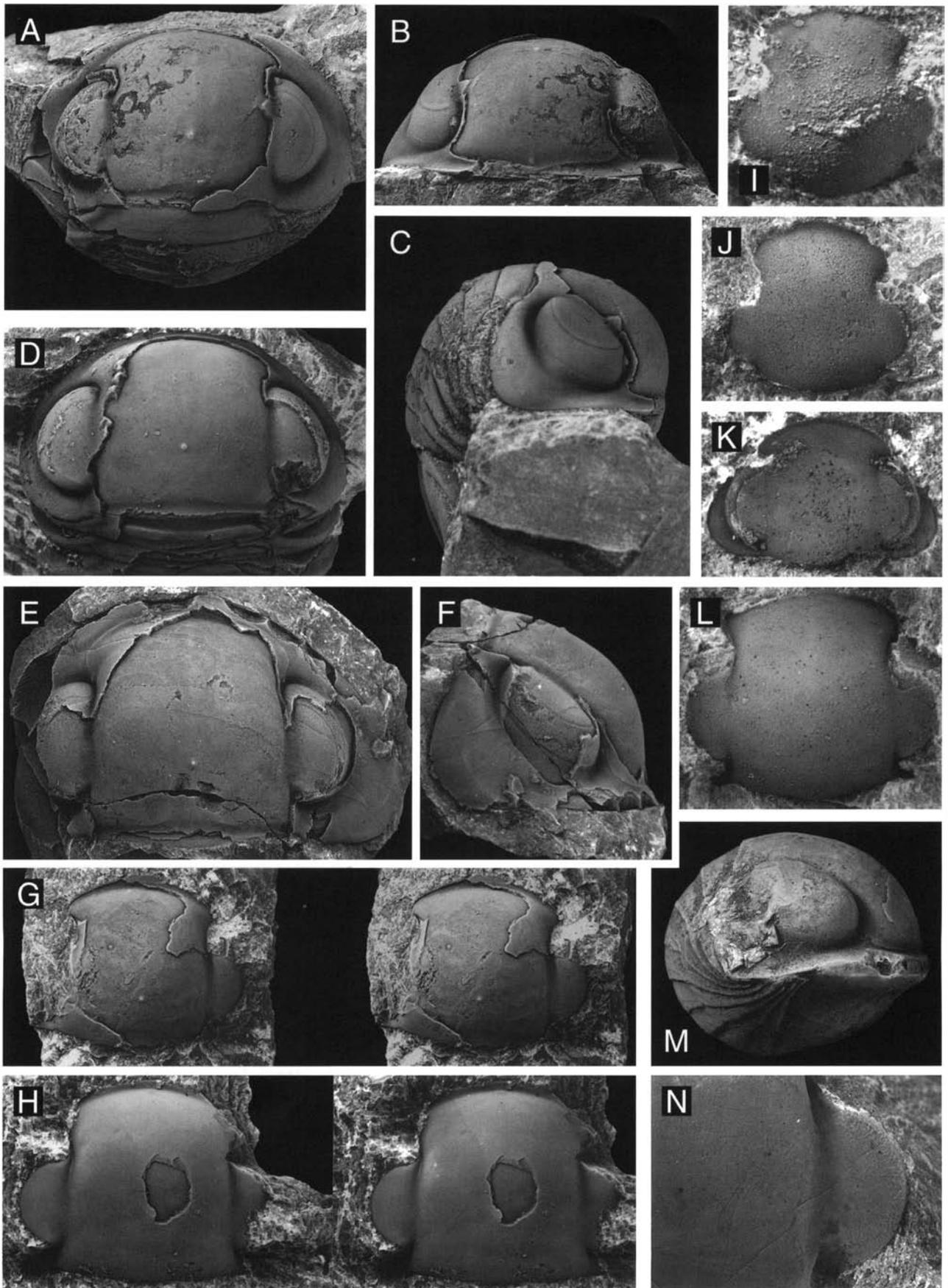
Synonymy. – (Additional references in Brögger 1882, Schmidt 1904 and Schrank 1972) □v 1827 *Asaphus* (*Nileus*) *Armadillo* – Dalman, pp. 61–63, Pl. 4:3a–e (short definition, description, illustrations of complete specimens, cephalon, pygidium). □1838 *Trilobites oblongatus* – Boeck, p. 142 (brief statement of diagnostic characters). □1851 *Nileus Armadillo*. Dalm. [*partim*] – Angelin, p. 19, Pl. 16:5, 5b–c, non Fig. 5a (brief diagnosis, illustrations of complete specimen, cephalic side-view and hypostome). □v 1882 *Nileus Armadillo*, Dalman – Brögger, pp. 62–64 [main description in discussion of var. *depressa*] (short description, occurrence). □v 1882 *Nileus Armadillo* var. *oblongata*, Boeck – Brögger, pp. 64–65; Pl. 12:8 (description, occurrence, illustration of cephalon). □1902 *Nileus armadillo* Dalman – Moberg, pp. 296–299; Textfig. 1; Pl. 3:1–5 (description of muscle scar impressions on cranidium, illustrations of cranidium test surface and cranidium [dorsal, frontal, side view]). □1904 *Nileus Armadillo*, Dalman [*partim*] – Schmidt, pp. 64–68; Pl. 8:15; non Pl. 8:12–14, 16–18 (description, occurrence, illustrations of complete specimens, cephalon, pygidium). □v 1904 *Nileus armadillo* Dalm. – Wiman, pp. 87–90, Textfigs. 2–5 (description of muscle scars and markings on cephalon and a pygidium). □non 1906 *Nileus armadillo* Dalman – Moberg & Segerberg, p. 93, Pl. 6:1–5 [= *N. limbatus* Brögger]. □v 1919 *Nileus Armadillo* Dalm. [*partim*] – Funkquist, pp. 8–46 (occasionally listed), non Pl. 2:1–4. □v 1936 *Nileus armadillo* Dalm. [*partim*] – C. Poulsen, pp. 48, 50 (listed). □1941 *Nileus armadillo*, var. *oblongata* (Boeck) – Størmer, p. 143 (review of previous information, designation of lectotype). □v non 1952 *Nileus armadillo* (Dalman, 1827) – Skjeseth, p. 170; Pl. 2:7, 8, 11 [= *N. exarmatus* & *N. depressus*]. □1956 *Nileus armadillo* (Dalman, 1827) – Tjernvik, p. 208; Textfig. 33D (short description, illustrations of cranidia including a redrawing of holotype). □non 1960 *Nileus armadillo* Dalman – Balashova, Pl. 6:1 [? = *N. depressus*]. □1968 *Nileus armadillo* (Dalman) – Bednarczyk, pp. 715, 724; Pl. 2:2, 7 (occurrence, illustrations of complete specimen). □v 1972 *Nileus armadillo* (Dalman, 1827) – Schrank, pp. 365–367; Textfig. p. 353; Pl. 6:1–3, 5–6 (short description, occurrence, illustrations of cephalon, cranidium, pygidium). □1973 *Nileus armadillo* Dalman, 1827 – Modliński, p. 51; Pl. 3:2, 3 (illustrations of cranidium and pygidium). □1976 *Nileus armadillo* Dalman, 1827 [*partim*] – Balashova, pp. 138–139; Pl. 40:3a–b, non Pl. 40:1a–b, 2, 9, 10; non Pl. 29:6 (description, occurrence, illustration of entire specimen from Oslo region, illustration of thoracic doublure). □1976 *Nileus armadillo* (Dalman) – Fortey & Clarkson, pp. 101–105, Fig. 1A–D (discussion of glabellar tubercle, illustrations of enrolled specimen). □v 1980 *Nileus armadillo* Dalman – Reyment, Fig. 3A–D (designation of lectotype, illustrations of the enrolled specimen original of Dalman 1827, Pl. 4:3b). □1984 *Nileus armadillo*? (Dalman, 1827) – Wandås, Pl. 11C (illustrations of cephalon).

Lectotype. – Specimen figured by Dalman (1827, Pl. 4:3b), designated and refigured by Reyment (1980, Fig. 3A–D).

Material. – Seventy-five complete specimens, 20 cephalon, 54 cranidia, 20 juvenile cranidia, 3 librigenae, 74 pygidia and 35 juvenile pygidia. The majority of the complete specimens and the cephalon are rather poorly preserved. Additional juvenile specimens are described separately as ‘juvenile specimens of *Nileus armadillo* / *Nileus latifrons*’.

List of material. – □Complete specimens K 298 (t), K 299 (c), K 300 (c), K 303 (c), K 304? (c), K 305 (c), K 306 (c), K 307 (c), K 308 (pc), K 309 (c), K 310a (c), K 316 (c), K 317 (pc), K 318 (c), K 319 (pc), K 320 (t), K 321 (c), K 322 (c), K 323 (c), K 324 (c), K 327 (c), K 329a (t), K 329b (c), K 330 (c), K 340a (c), K 340b (c), K 340c (c), K 341b (c), K 341c (c), K 343 (pc), K 345 (c), K 349? (c), K 353 (pim), K 383a (c), K 383b (c), K 394 (t), K 891b (c), K 892a (c), K 892b (c), K 898 (c), K 900 (c), K 901 (im), K 902 (pc), K 903 (c), K 905a (c), K 905b (c), K 1324 (c), K 1325 (c), K 1326 (pc), K 1327 (c), K 1329 (pc), K 1330 (c), K 1332 (pc), K 1333 (pc), K 1334 (pc), K 1335 (pc), K 1337 (pim), LU 7a (c), LU 7b (pim) [LO 7066], LU 7e? (t), LU 7f (pim), LU 8 (im), LU 12a (t) [LO 7068], LU 12b (im) [LO 7069], LU 12c (t), LU 14a (pim), LU 14b (pim), LU 17a (pim) [LO 7072], LU 17b (c), LU 17c (t) [LO 7073], LU 72b (t), A 568 (pim) [MGUH 22.615], GM 1869.878 (pim), GM 1869.885 (c), GM 1995.11 (t). □Cephalon K 301 (c), K 314 (c), K 315 (c), K 326 (pc), K 332 (c), K 333 (t), K 335 (pim), K 337 with thoracic segments (pc), K 341a (c), K 346 (c), K 891a (pc), K 896 (c), K 897 with thoracic segments (c), K 899 (c), K 905c (c), K 1114 with thoracic segments (pim), LU 6e (is), LU 19b (t), A 490 with thoracic segments (pim) [MGUH 22.616], GM 1995.10 (im). □Librigenae S 1594b (pim), K 1129? (pim), LU 7d (t). □Cranidia S 1465 (pim), S 1500b (pim), S 1520a (im) [MGUH 22.624], S 1520d (im), S 1525 (t), S 1537 (im), S 1538a (im), S 1538b (im), S 1554? (im), S 1561 (im), S 1581a (im), S 1581b (im), S 1606 (im), S 1685c (im), S 1700 (im), S 1706 (t) [MGUH 22.618], S 1707a (im), S 1728a (pim), S 1738 (t) [MGUH 22.630], S 1749 (im) [MGUH 22.617], K 359 (pim), K 375b (im), K 395a? (c), K 875 (pim), K 1043 (pim), K 1079 (t), K 1093 (t), K 1095 (t), K 1128 (pim), K 1133a (pim), K 1133b (pim), K 1136 (t) [MGUH 22.626], K 1137a? (t), K 1137b (t), K 1151 (t), K 1171 (pim), K 1191 (t), K 1196 (im), K 1290 (t), F 30 (im), F 99 (t), F 119 (t), F 132 (pim), F 193 (im), LU 1a (im), LU 2b (t), LU 4 (im), LU 6a (im), LU 6d (im) [LO 7065], LU 10 (t), LU 18a (im), LU 87a (t), GM 1984.1804b (im) [MGUH 22.623], GM 1988.14 (t) [MGUH 22.625]. □Juvenile cranidia S 1708a (t), S 1624? (im), K 347b (t), K 351 (t), K 845 (im), K 1110 (t), K 1133c (t), K 1137d? (t), K 1139 (t) [MGUH 22.620], K 1174c (c), K 1182b (t), K 1197?

Fig. 147. *Nileus armadillo* (Dalman, 1827). □A–C. Largely exfoliated cephalothorax, showing comparatively wide lateral border, anterior mesial boss of cranidium, and no flattened anterior cranial fringe; dorsal, frontal and side views, ×2. A close-up of the cephalic doublure is shown on Fig. 149B, and the pygidium is shown on Fig. 150C. Complete specimen MGUH 22.615 (A 568), Lysaker Member, Slemmestad. □D. Largely exfoliated cephalon, showing comparatively narrow lateral border, ×2. MGUH 22.616 (A 490), bed A-40, Slemmestad. □E–F. Largely exfoliated large cephalon, dorsal and side views, ×1.5. Ar 24 234, Fågelsång. □G. Internal mould of cranidium, showing paired muscle impressions on glabella and centrally flattened anterior fringe, stereo-pair, ×2. MGUH 22.617 (S 1749), bed +13, Skelbro. □H. Well-preserved small cranidium showing flattened fringe all the way along anterior margin, stereo-pair, ×2. MGUH 22.618 (S 1706), bed +13, Skelbro. □I. Corroded juvenile cranidium, ×9. MGUH 22.619 (GM 1984.1804b), bed +13, Vasegård, Bornholm. □J. Juvenile cranidium, ×6. MGUH 22.620 (K 1139), bed 7, Killerød site b. □K. Juvenile cephalon, ×6. MGUH 22.621 (K 1298), bed 15, Killerød b. □L. Juvenile cranidium, ×6. MGUH 22.622 (GM 1984.1804c), bed +13, Vasegård, Bornholm. □M. Enrolled specimen, side view, ×3. LO 7068 (LU 12a), Komstad. □N. Close-up of internal mould of cranidium showing caecate pattern on palpebral lobe, ×3. LO 7065 (LU 6d), Fågelsång.



(im), K 1209b? (t), K 1211a? (t), K 1292? (c), K 1298 (t) [MGUH 22.621], F 106 (t), F 107b? (pim), GM 1984.1804b (t) [MGUH 22.619], GM 1984.1804c (t) [MGUH 22.622]. □ Pygidia S 1464 (im), S 1484 (d), S 1489 (d), S 1506 (im), S 1520b (im), S 1520e (im), S 1545a (im), S 1545b? (im), S 1568a (pim), S 1586 (im), S 1589b (d) [MGUH 22.641], S 1595b (pim), S 1596 (im) [MGUH 22.633], S 1615 (d), S 1616a (pim) [MGUH 22.639], S 1638 (pim), S 1692 (t) [MGUH 22.635], S 1714 (pim) [MGUH 22.632], S 1715 (pim), S 1717 (pim), S 1724 (im), S 1740 (pim), S 1754 (d), S 1757 (im), K 302? (t), K 311 with thoracic segments (pc), K 324 (t) [MGUH 22.631], K 325 with thoracic segments (c), K 334 (t), K 355 (c), K 357 (pim), K 816b (pim), K 828? (im), K 872 (im), K 877 (im), K 878 (im), K 882 (d), K 894 (pim), K 1029 (pim), K 1041 (d), K 1072 (t), K 1087 (im) [MGUH 22.637], K 1088 (d), K 1097 (t), K 1107 (pim), K 1108 (pim), K 1118 (pim), K 1131? (t), K 1132? (d), K 1133d (im), K 1135 (im), K 1137c (t), K 1138a (t) [MGUH 22.636], K 1139a (pim), K 1140 (im), K 1141 (t), K 1154 (t) [MGUH 22.634], K 1161 (t), K 1162? (im), K 1202a (pim), K 1209c (im), K 1262? (t), K 1323 (c), K 1328 (c), K 1336 (t), K 1341 with thoracic segments (pc), F 34 (im) [MGUH 22.640], F 54 (d) [MGUH 22.638], F 173? (im), LU 6f (d), LU 19a (t) [LO 7074], LU 61? (is), LU 66 (im) [matches LU 74], GM 1984.1804d (im). □ Juvenile pygidia S 1500a (t), S 1511a (t), S 1750? (t), S 1751? (t), S 1752? (t) [MGUH 22.627], K 807 (pim), K 816a (em), K 820 (t) [MGUH 22.628], K 824 (t) [MGUH 22.643], K 830 (t), K 834 (pim) [MGUH 22.648], K 835 (pim), K 844 (t), K 862 (t), K 892c (pim), K 1017 (t), K 1018 (t), K 1020 (t) [MGUH 22.642], K 1031 (t), K 1038a (t), K 1038b (t), K 1052 (t) [MGUH 22.644], K 1071 (t), K 1109 (t), K 1130 (pim), K 1138b (t) [MGUH 22.647], K 1159 (t), K 1177b? (t), K 1187? (im), K 1192 (pim), K 1201a (t), K 1207 (t), K 1296 (t) [MGUH 22.645], K 1306 (t) [MGUH 22.629], F 33? (t) [MGUH 22.646].

Occurrence. – *Nileus armadillo* is common in the *A. expansus* and *A. 'raniceps'* Zones of the Komstad Limestone, but locally occurs even in the upper subzone of the *M. limbata* Zone. At Skelbro the species has been found in the uppermost part of bed +13 and in bed +14 (Zone of *A. expansus*); at Killeröd it is very abundant from bed +22 and upwards (Zone of *A. expansus*); at Killeröd site b *N. armadillo* occurs throughout the exposed interval (Zones of *A. expansus* and *A. 'raniceps'*); at Fågelsång the species has been found in beds 7 and 9, corresponding to the upper part of the *M. limbata* Zone and in beds 19 and 20, corresponding to the base of the *A. expansus* Zone. The early, albeit sparse occurrence of *N. armadillo* (*s.str.*) in the *M. limbata* Zone is currently not known from any other locality within Scandinavia.

The museum material studied originates from Fågelsång, Komstad and Vasegård. A large share of it can be assigned fairly precisely to level; in all cases the specimens originate from levels with known occurrence of *N. armadillo*. Specimens GM nos. 1869.878, 1869.885, 1995.10 and 1995.11 from Fågelsång were most likely collected from bed interval 18–20. Specimens LU 66, LU 72 and LU 74 were sampled by Ekström from bed Ik [= bed 7] at Fågelsång (see Ekström 1937, p. 15), belonging to the *M. limbata* Zone. Specimens LU 14a, b from Komstad are labelled 'Undre ljustare delen' [= lower lighter part], which evidently are incorrect, as that interval corresponds to the *M. simon* Zone, and sample LU 14 most likely originates from a level corresponding to the upper part of bed +22. Specimen LU 10, also from Komstad, is according to the label collected from the uppermost part of the limestone, which is in agreement with the lithology.

A single specimen was found in bed A-40 at Slemmestad (Lysaker Member), upper part of the *A. expansus* Zone.

Another specimen comes from an unknown level of the Lysaker Member.

N. armadillo is a widespread species in Scandinavia, characteristic of the *A. expansus* Zone and younger levels (Tjernvik 1956; Tjernvik & Johansson 1980). Wandås (1984, Pl. 11C) figured a cephalon from the *Ogygiocaris* Shale of the Oslo Region, tentatively assigned to *N. armadillo*. Although younger than the presently investigated material, the specimen appears similar in all visible details to the cephalon of *N. armadillo* from the Komstad Limestone. If the identification is correct, it extends the range of *N. armadillo* to the top of the Kunda Stage.

Diagnosis. – Large species; cephalon semielliptical in outline, twice as wide as long in dorsal projection, and strongly convex (both ways, but most pronounced sag.). Cephalic axial furrows almost straight, gently forwards converging; anterior cranial margin may show a mesial boss and a flattened rim. Pygidium with concave border of variable width; scattered terrace lines present anterolaterally and may enter pleural fields, particularly in larger specimens; pygidial doublure typically covered with about 19 terrace lines. [Emended from Dalman 1827 and Schrank 1972.]

Description. – Very large for a *Nileus*, largest cranium 28 mm long, largest pygidium 30 mm long (Fig. 151A). Total length of an individual carrying the 30 mm long pygidium is about 105–110 mm. Length ratios between cephalon, thorax and pygidium are about 28:46:26 in adult specimens ($N = 2$, dorsal projection). The length of pygidium averages 0.83 ($N = 23$) of the cranial length and the width of pygidium averages 0.92 ($N = 20$) of the cephalic width in complete specimens; these ratios change during growth (Fig. 151B). The stated cranium:pygidium length ratio is based on maximum length measures, which are not identical to dorsal projection.

Fig. 148. Nileus armadillo (Dalman, 1827). □A–C. Exfoliated cephalothorax, dorsal, frontal and side views, $\times 2.5$. Complete specimen LO 7069 (LU 12b), Komstad. □D. Internal mould of large cranium, $\times 1.5$. The small cranium in upper right corner is shown on Fig. 147L. MGUH 22.623 (GM 1984.1804a), bed +13, Skelbro. □E. Exfoliated cranium showing indistinct paired muscle impressions on glabella, and well-defined flattened anterior fringe, $\times 3$. MGUH 22.624 (S 1520a), bed +13, Skelbro. □F–G. Cephalon distorted by compaction, lectotype of *N. oblongatus* (Boeck, 1838), dorsal and frontal views, $\times 1$. Previously figured by Brögger (1882, Pl. 13:8). PMO 20 187, unknown locality, Oslo region. □H. Cranium showing narrow anterior flattened fringe, $\times 4$. MGUH 22.625 (GM 1988.14), Vasegård, Bornholm. □I. Large cranium, $\times 2$. MGUH 22.626 (K 1136), bed 7, Killeröd site b. □J–K. Large complete specimen, dorsal view of cephalon and pygidium, the latter showing doublure, $\times 1.5$. Side view shown on Fig. 149A. LO 7066 (LU 7b), Fågelsång area. □L. Close-up of exfoliated thorax showing doublure, side view (edge of cephalon to the right), $\times 3$. LO 7072 (LU 17a), Fågelsång. □M. Transitory pygidium, stage D, $\times 6$. MGUH 22.627 (S 1752), bed +13, Skelbro. □N. Transitory pygidium, stage E, $\times 6$. MGUH 22.628 (K 820), bed 1, Killeröd site b. □O. Transitory pygidium, stage E, $\times 9$. MGUH 22.629 (K 1306), bed 13, Killeröd site b.

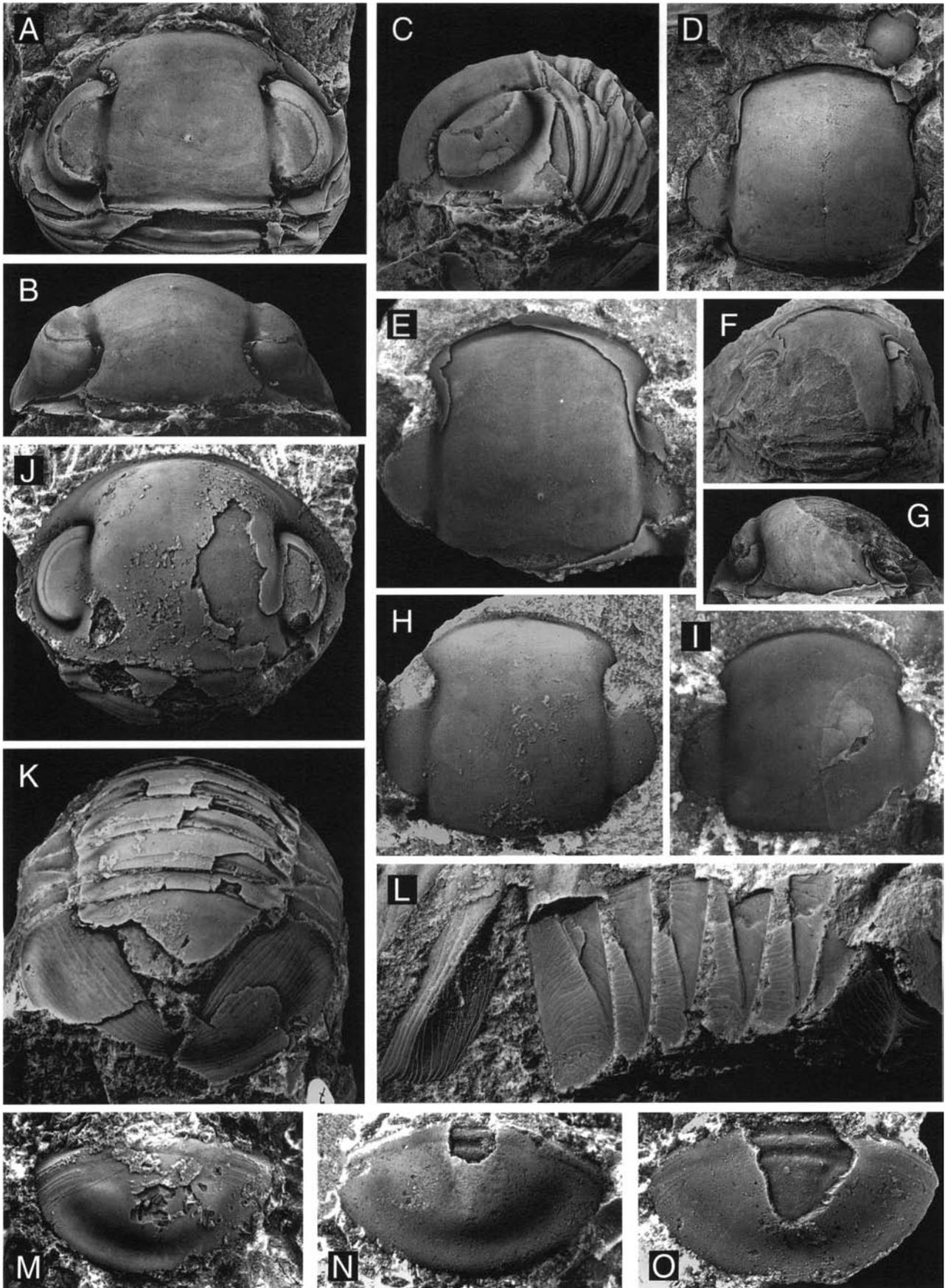


Table 11. *Nileus armadillo*. Ranges for variation of cranidia, expressed as ratios of cranial length.

Size (mm)	Maximum width of cranidium			Glabella width			Palpebral lobe length (exsag.)			Glabellar tubercle, distance to post. margin		
	Range	Mean	N	Range	Mean	N	Range	Mean	N	Range	Mean	N
3.2–5.2*	1.00–1.05	1.02	5	0.66–0.70	0.67	5	0.38–0.43	0.41	5	–	–	0
4.4–5.1	1.10–1.16	1.13	3	0.73–0.78	0.75	3	0.43–0.47	0.44	3	–	–	0
5.6–6.6	1.18–1.24	1.21	6	0.76–0.85	0.81	6	0.42–0.46	0.44	7	0.33–0.38	0.35	5
>7	1.15–1.37	1.26	62	0.75–0.92	0.85	62	0.35–0.46	0.42	60	0.31–0.40	0.35	48

* Same narrow growth stage

Cephalon semielliptical in outline and strongly convex (both ways); L:W ratio averages 0.64 ($N = 30$). Glabella elongate, although it widens with increasing size (Fig. 151D; Table 11). Axial furrows subparallel, wide and shallow, but augmented by the change of slope between glabella and palpebral lobes; furrows best defined on internal moulds. Anterior margin of cranidium rounded (dorsal view), but of somewhat varying appearance. Of 83 investigated specimens with intact anterior margin, 75 show a more or less flattened margin and a weakly to well-developed mesial boss, 4 specimens have a mesial boss, but no flattened fringe (including the two specimens from Slemmestad), and 4 specimens have an evenly rounded, unflattened margin without mesial boss. The degree of flattening is varying; some specimens, mainly from Skelbro and some from Fågelsång, show a flattened rim along almost the entire cranial margin (e.g., Fig. 147H), but usually only the central part or only the mesial boss is flattened. Flattened 'preglabellar area', including mesial boss, occupies 0.02–0.06 of the cranial length (mean 0.04; $N = 49$; Fig. 151G) (cranidia without flattened margin not taken into account). Outwards sloping palpebral lobes moderately short (Table 11). A radiating caecate pattern is occasionally seen on the lobes of internal moulds (Fig. 147N). Mesial glabellar tubercle (Table 11; Fig. 151F) small to medium-sized on internal moulds, and often indicated by a coloured spot on testaceous material. Sagittal keel, as seen on internal moulds, stops about 0.15 of cranial length from anterior margin. Low, rounded sagittal swelling present on internal moulds immediately above the flattened cranial margin. Occipital furrow defined only on internal moulds; it is wide, deepest laterally, and the mesial expansion, usually seen in Nileids, is indicated by a lowering of the anterior edge of occipital furrow, so the furrow, in effect, becomes ill-defined mesially. Paired muscle insertion sites, flanking the mesial expansion, very faint. Posterior fixigena broad-based and appears comparatively prominent, but the average length (exsag.) is equivalent to most other species, averaging 0.14 times the cranial length ($N = 54$). Gena triangular, pointed slightly backwards, with a rather distinctly incised articulating socket. Anterior branch of facial suture runs shortly forwards-inwards from inner corner of palpebral lobe, descends along the rounded upper margin of eye-lens, then turn outwards at an angle of about 30–35° to sagittal

line. Facial sutures meet anteriorly in a more or less blunt angle; only about 5% of the specimens at hand exhibit a smooth anterior cranial margin (see above). Posterior branch of facial suture gently sigmoidal, running obliquely backwards-outwards from palpebral lobe at an angle of about 35° to sagittal line. Inner part of suture very closely follows the lower margin of the eye-lens, and consequently, the posterior fixigena assumes a broad-based appearance.

Librigena comparatively wide; anterior border wider than in most other species studied. Lateral border comparatively very broad and almost flat, tapers out at about midlevel of eye. The width of the lateral border is variable, though, best exemplified by the equal-sized specimens A 568 and A 490 from Slemmestad, both about 18 mm long, and which appear to represent extremes in a continuous variation spectrum (Figs. 147A vs. D). Cephalon A 490 has a prominent, wide glabella, a very narrow anterior border and a rather narrow lateral border, whereas cephalon A 568 has a narrower glabella, a clearly wider anterior cephalic border and a comparatively very wide lateral border. Posterior part of librigena slopes fairly strongly outwards. Outer margin occasionally thickened.

Fig. 149. *Nileus armadillo* (Dalman, 1827). □A. Internal mould of large specimen showing doublure of thorax and pygidium, side view, ×2. Dorsal views of cephalon and pygidium shown on Fig. 148J–K. LO 7065 (LU 7b), Fågelsång area. □B. Internal mould of cephalothorax showing part of doublure, ×3. Dorsal view shown in Fig. 147A–C. MGUH 22.615 (A 568), Lysaker Member, Slemmestad. □C. Well-preserved cranidium showing sagittal 'wrinkling' of cuticula, ×5. MGUH 22.630 (S 1738), bed +13, Skelbro. □D. Non-whitened pygidium with transparent cuticle showing light-coloured muscle insertion sites on axial area, ×2. LO 7073 (LU 17c), Fågelsång. □E. Pygidium, ×3. MGUH 22.631 (Complete specimen K 324), bed +22, Killeröd. □F. Partly exfoliated pygidium showing axis, ×2. MGUH 22.632 (S 1714), bed +13, Skelbro. □G. Internal mould of pygidium showing anterior pleural furrows, ×2. MGUH 22.633 (S 1596), bed +13, Skelbro. □H–I. Small pygidium, dorsal and side views, ×3. MGUH 22.634 (K 1154), bed 7, Killeröd b. □J. Pygidium showing the typical external adult terrace-line sculpture, ×3. MGUH 22.635 (S 1692), bed +13, Skelbro. □K. Very large pygidium, ×1.5. MGUH 22.636 (K 1138a), bed 7, Killeröd site b. □L. Internal mould of very large pygidium showing doublure, ×1.5. MGUH 22.637 (K 1087), bed 6, Killeröd site b. □M. Internal mould of early pygidium showing the doublure, ×2. MGUH 22.638 (F 54), bed 9, Fågelsång.

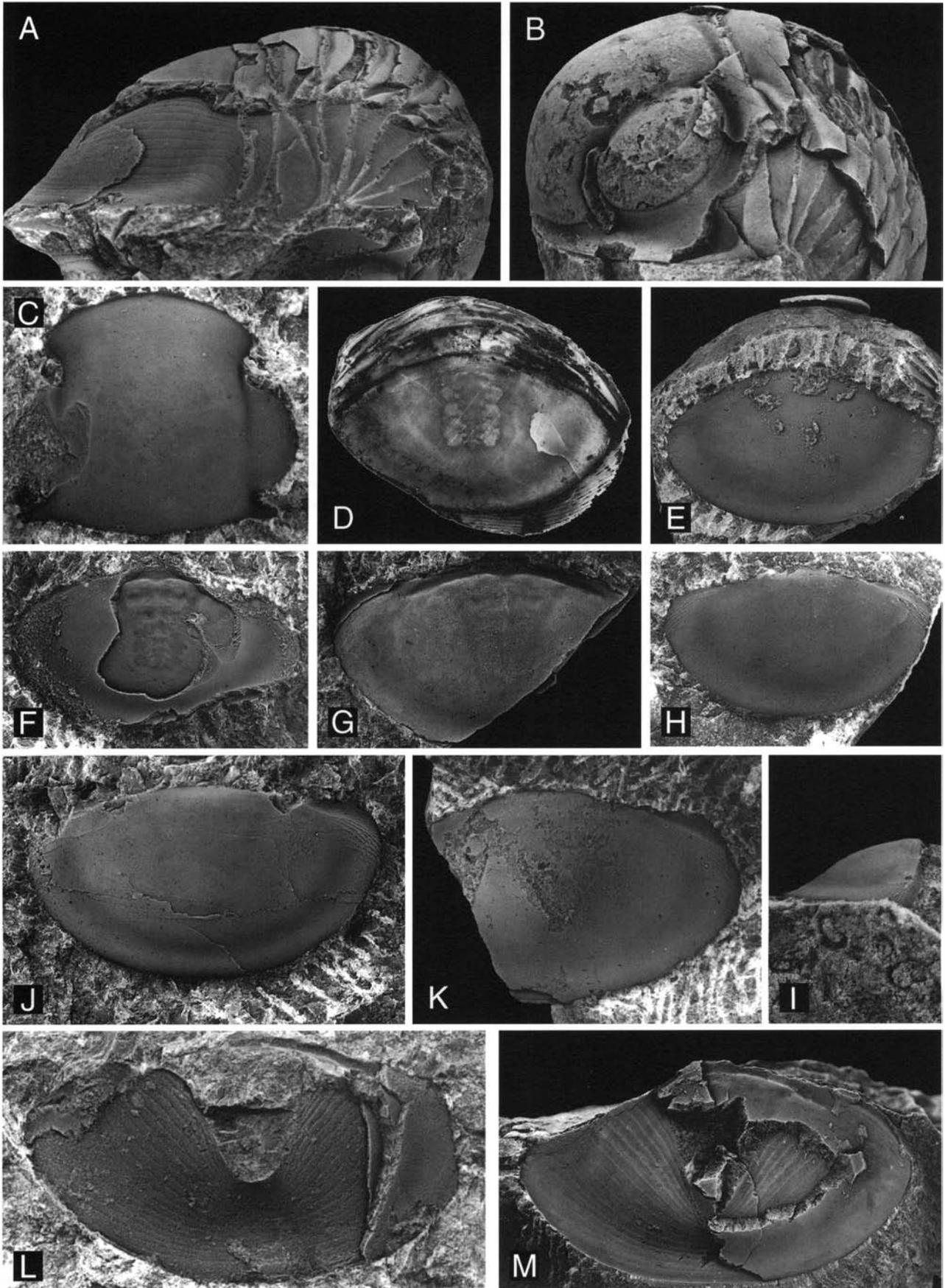


Table 12. *Nileus armadillo*. Ranges for variation of pygidia, expressed as ratios.

Size (mm)	Pygidial L:W ratio			Axial width : pygidial width			Axial length : pygidial length			Border length (sag.) : pyg. length		
	Range	Mean	N	Range	Mean	N	Range	Mean	N	Range	Mean	N
2.4–4.6 [Stage D]	0.59–0.68	0.65	7	0.38–0.42	0.40	5	0.50–0.62	0.57	7	0.21–0.20	0.24	9
3.2–4.6 [Stage E]	0.54–0.64	0.60	10	0.35–0.40	0.37	5	0.51–0.63	0.58	5	0.19–0.26	0.24	10
4.0 and 5.2–5.6 [Hol.]	0.51–0.60	0.55	9	0.33–0.35	0.34	3	0.51–0.60	0.56	4	0.18–0.28	0.23	8
>6 [Hol.]	0.52–0.63	0.58	64	0.30–0.50*	0.37	24	0.54–0.78*	0.64	24	0.13–0.25	0.17	49

* The wide range of variation reflects the difficulties of making exact measurements of the axis.

Test surface of palpebral lobes and posterior part of librigenae punctate; remaining cephalic surface smooth, except for a 'wrinkled pattern' along sagittal line (Fig. 147H).

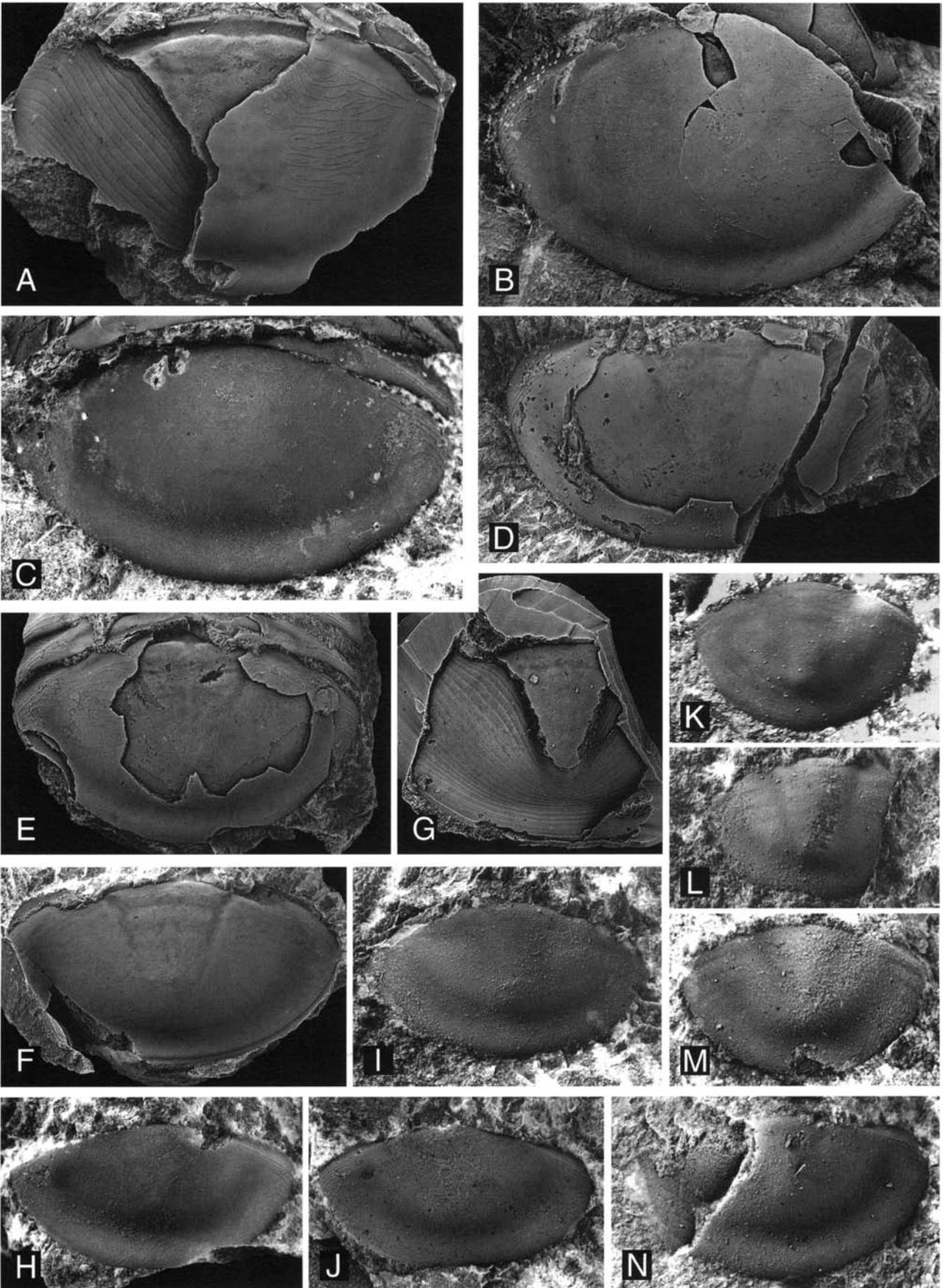
Cephalic doublure of usual nileid outline. Anterior part provided with 11–12 coarse, continuous terrace lines; a small central part of hypostomal socket is devoid of lines, and the posterior, flattened part of doublure shows numerous short terrace lines running obliquely backwards-inwards (Fig. 149B).

Thorax basically as described for *N. latifrons* n.sp. (*q.v.*). Posterior segment 10% narrower (tr.) and about 30% (in the largest specimens) to 40% (in the smallest specimens) shorter (sag.) than anterior segment. Axis occupies about half of the thoracic width on anterior segment; on internal moulds the area posterior to the axial crescentic elongate swellings appears slightly better impressed, and in smaller specimens the adaxial part of the swellings are more clearly developed as a pair of muscle insertion sites. Pleural furrows, running obliquely outward-backwards on the pleura to stop at paradoublural line, are slightly better impressed in *N. armadillo*, compared to *N. latifrons* n.sp., and therefore better defined on testaceous material, also on the posterior segments. A single, distinct terrace line typically crosses (tr.) the axis of each segment; it runs immediately behind the position of the axial swellings seen on internal moulds. The terrace line stops shortly above base of axis. One Norwegian specimen, A 568, shows a weakly impressed terrace line, stopping well above base of axis, and which apparently is effaced also mesially; the posterior two segments of this specimen are smooth. Pleura show two to three long, coarse terrace lines. Doublure basically as described for *N. latifrons* n.sp., with only subtle differences in the terrace-line pattern. Thus the distal terrace lines anterior to doublural crest are less oblique in the available material (see, however, discussion below), and consists typically of only 5–7 lines, a single smaller specimen appears to have 8–9 lines. The terrace lines posterior to crest appear but slightly coarser in *N. armadillo* and without marked change of direction in the distal, outer part (Figs. 148L, 149A). The posterior segment shows a curved doublural crest, and more prolific terrace lines.

Pygidium moderately vaulted and semielliptical in outline. An elongate triangular axis may have a faint relief, and/or shallow, indistinct axial furrows may be present, but the axis is mostly not delimited from or raised above the pleural

fields. A nebulous axial region is usually crudely outlined by uneven muscle scars on internal moulds or, more rarely, by colour differences of the test. Exact dimensions of axial area are, in consequence, difficult to obtain (Table 12). A deep transverse furrow delimits articulating half-ring, but is visible only on internal moulds; apart from that at least four, but presumably five axial rings are present in addition to the terminal piece, as faintly indicated in a few specimens about 10 mm long. Contrary to most nileids, in which axial segments are indicated by lateral swellings, the axis of smaller pygidia of *N. armadillo* shows lateral swellings connected across the sagittal area, i.e. 'true' rings; exfoliated larger pygidia sometimes show a very low sagittal keel, stretching for the entire length of axis. Specimen LU 17c shows light colour muscle markings in the axial region (Fig. 149D) in a configuration identical to the pattern displayed by better preserved specimens of *N. latifrons* n.sp. (Fig. 157A). Articulating facets of relatively moderate size, elongate triangular in outline, and forward-slanting at an angle of about 45°; inner portion may be slightly concave. Each facet provided with 20–25 fine, densely spaced terrace lines, running obliquely downwards-outwards. Border concave, fairly wide; maximum width attained anterolaterally, although no border is defined immediately behind articulating facets; minimum

Fig. 150. *Nileus armadillo* (Dalman, 1827). □A. Large pygidium showing terrace lines on pleural fields, ×2. Ar 24 343, Fågelsång. □B. Partly exfoliated large pygidium showing terrace lines on pleural fields, ×2. LO 7074 (LU 19a), Fågelsång. □C. Pygidium showing an almost smooth cuticular surface, ×3. Cephalon shown on Fig. 147A–C. Complete specimen MGUH 22.615 (A 568), Lysaker Member, Slemmestad. □D. Largely exfoliated large pygidium, ×1.5. MGUH 22.639 (S 1616a), bed +13, Skelbro. □E. Partly exfoliated large pygidium showing terrace lines on pleural fields, ×1.5. LO 7072 (LU 17a), Fågelsång. □F. Internal mould of early pygidium showing impressions from unusually widely distributed dorsal terrace lines, ×2. MGUH 22.640 (F 34), bed 7, Fågelsång. □G. Latex cast of internal mould of pygidium showing doublure, ×2. MGUH 22.641 (S 1589b), bed +13, Skelbro. □H. Small holaspid pygidium, ×5. MGUH 22.642 (K 1020), bed 0, Killeröd site b. □I. Pygidium representing smallest holaspid stage, ×8. MGUH 22.643 (K 824), bed 1, Killeröd site b. □J. Small holaspid pygidium, ×5. MGUH 22.644 (K 1052), bed 0, Killeröd site b. □K. Transitory pygidium, stage E, ×12. MGUH 22.645 (K 1296), bed 13, Killeröd site b. □L. Transitory pygidium, stage D, ×10. MGUH 22.646 (F 33), bed 7, Fågelsång. □M. Transitory pygidium, stage D, ×10. MGUH 22.647 (K 1138b), bed 7, Killeröd site b. □N. Pygidium representing smallest holaspid stage, ×8. MGUH 22.648 (K 834), bed 2, Killeröd site b.



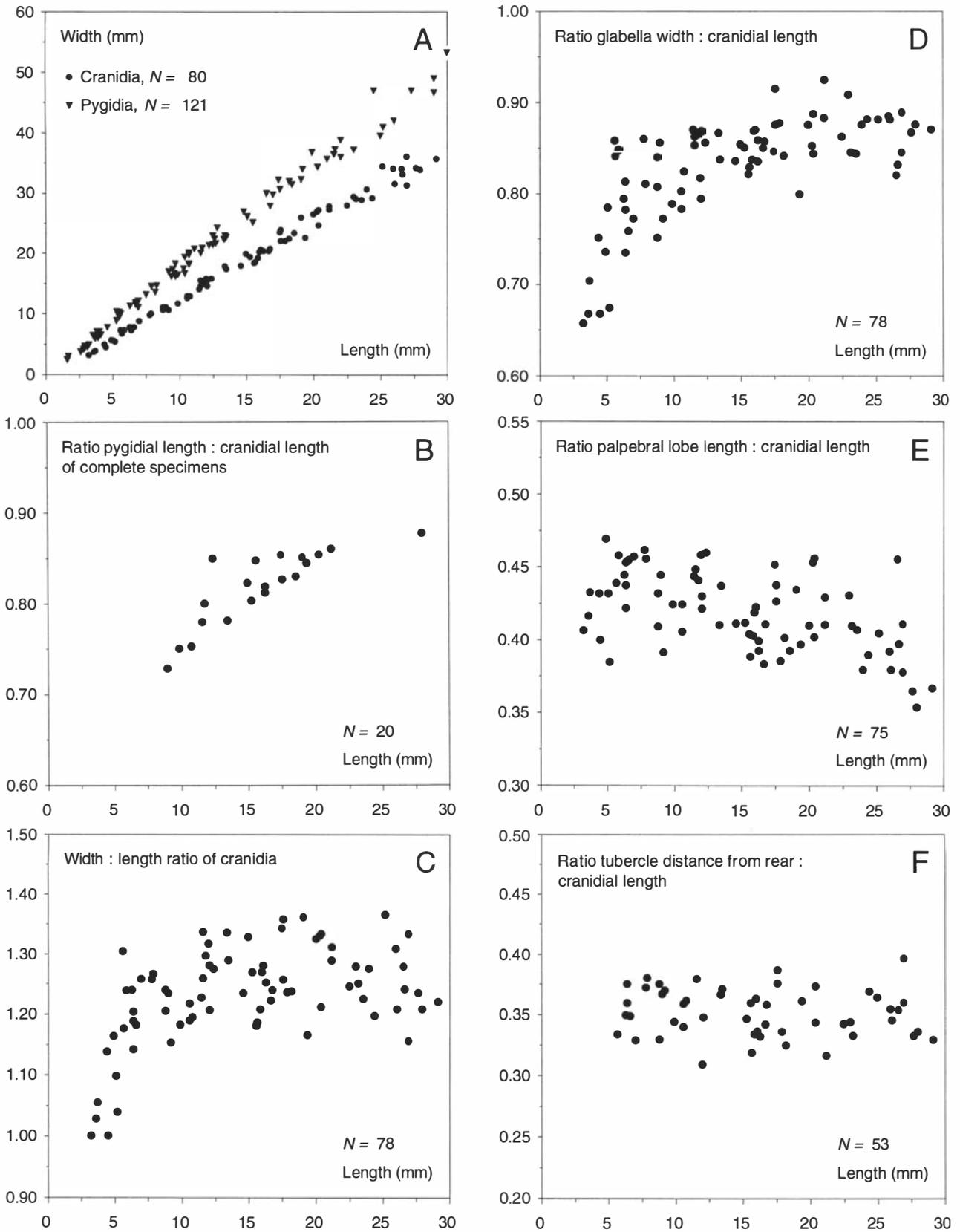


Fig. 151. *Nileus armadillo*. □A. Maximum width plotted against sagittal length, crania and pygidia. □B. Ratio between pygidial length and cranial length of entire specimens plotted against cranial length. □C. Ratio between maximum cranial width and cranial length plotted against cranial length. □D. Ratio between glabella width and cranial length plotted against cranial length. □E. Ratio between palpebral lobe length (exsag.) and cranial length plotted against cranial length. □F. Relative distance of glabella tubercle plotted against cranial length.

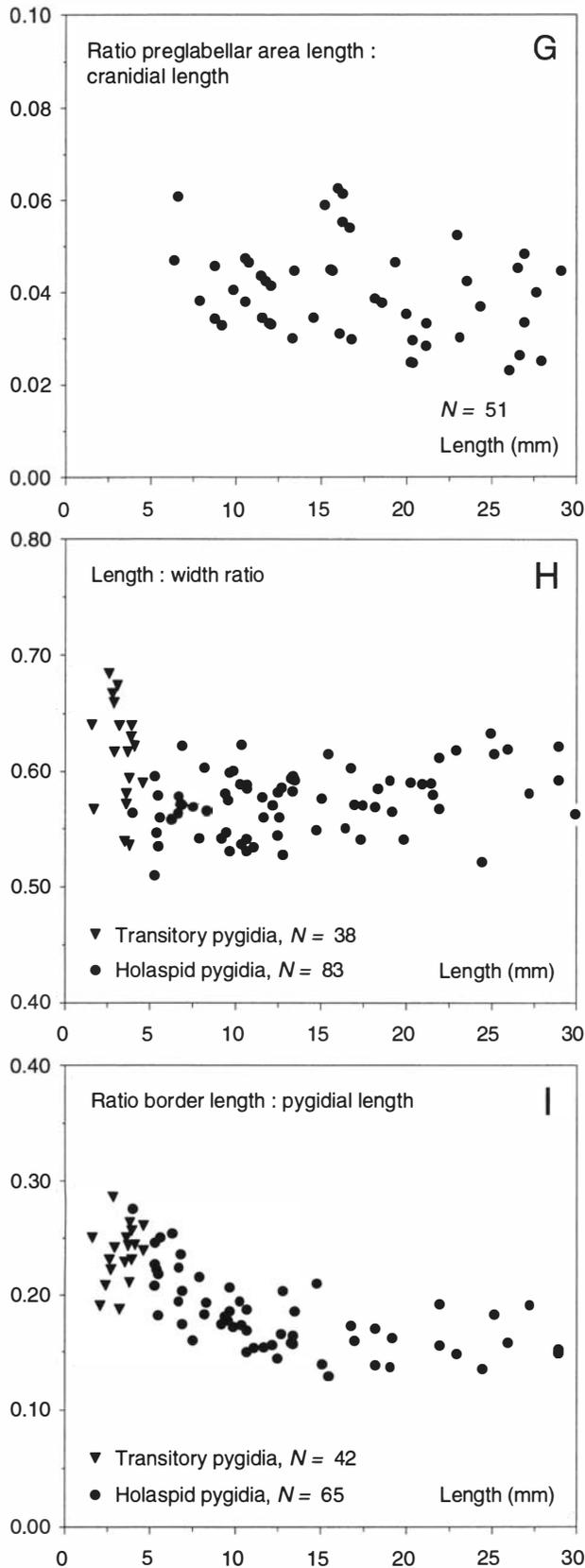


Fig. 151 (cont.). □G. Ratio between length of preglabellar area (sag.) and cranial length. □H. Ratio between sagittal length and maximum width of pygidia plotted against pygidial length. □I. Ratio between sagittal length of pygidial border and pygidial length plotted against pygidial length.

width, equivalent to about 0.75 of the maximum border width, is behind axis (Table 12). Relative width of postaxial border decreases with size (Fig. 151I).

External pygidial terrace-line pattern variable, with, broadly speaking, more abundant terrace lines in the larger specimens. All specimens studied have 2–4 transverse terrace lines situated along distal half of anterolateral margin, and this is perhaps the typical condition for *N. armadillo* (cf. Schrank 1972, p. 366). In the material at hand this pattern is seen in pygidia from Killeröd site b and from Slemmestad. Most specimens studied, however, also show 1–4 transverse lines along adaxial part of the anterior margin, and short, backwards curving lines anteriorly on the border. A few, mainly larger specimens, exhibit scattered lines on the pleural fields as well, and three large pygidia from Fågelsång show an openly spaced ‘orbiculatoides-type’ terrace-line pattern on the pleural fields (Fig. 150A–B, E). Only two specimens carries scattered terrace lines in the flexure between pleural fields and border. Pitting of the pygidial test has been seen with certainty only in a single specimen from Fågelsång.

Pygidial doublure very wide. Inner margin shows a minor, but characteristic outwards flare close to anterior margin, below the pleural furrow (Fig. 149A); this outline is different from the other nileid species described here. Doublure only little upturned around axial tip and is strongly concave, so outer part is almost flat. It is provided with 19–21 continuous, coarse terrace lines; a single early pygidium from the *M. limbata* Zone seems to have only 16–17 lines.

Juveniles. – The majority of juvenile cranidia are positively identified by the presence of an anterior mesial boss, while the bulk of the small pygidia show a general juvenile morphology (they are predominantly from beds containing only *N. armadillo*). See also ‘Undifferentiated juveniles of *Nileus armadillo* and *Nileus latifrons* n.sp.’.

The cranidium of *N. armadillo* appears to develop from a small, 2–3 mm long, fairly strongly convex (sag.), ‘hump-backed’ stage (see description of ‘Undifferentiated juveniles etc.’), through an only moderately convex (sag.), elongate stage, about 3–4 mm long, often with the mesial boss developed as the salient distinguishing feature, to a subadult stage, about 4–7 mm long, still more elongate than adults and, in the larger juveniles, with beginning development of axial furrows.

In the small growth stages no axial furrows are defined and glabella is confluent with palpebral area; faint axial furrows are developed in specimens >5.5 mm long. Four out of five specimens, 3.2–5.2 mm long, with intact anterior margin show a distinct mesial boss, whereas the fifth has an even, unflattened anterior margin. One of three cranidia, 4.4–5.1 mm long, and four of seven cranidia, 5.7–6.6 mm long, almost lacks a mesial boss, but has a flattened rim along anterior margin. The other specimens have a mesial boss.

Two stage B pygidia are each 1.6 mm long; a 2.1 mm long transitory pygidium probably belongs to stage C, but owing to poor preservation no further details are revealed. Ten

transitory pygidia, 2.4–4.6 mm long, belong to size group D, and ten transitory pygidia, 3.2–4.6 mm long, represent stage E. These specimens match the description of equivalent material (pp. 244–245), but attain larger sizes, are relatively wider and the D-stage pygidia has a proportionally slightly shorter axis (Tables 12 vs. 21). Nine pygidia, 4.0 and 5.2–5.6 mm long, are holaspides, but differ from larger specimens by showing a wider border. Terrace-line ornamentation limited to 2–4 transverse lines, running anterolaterally along anterior margin.

Affinities. – *Nileus armadillo* is most likely a descendant of the closely similar *N. orbiculatoides*. Nearly all of the biometric ratios obtained are similar between these species and the presence of a mesial boss on the anterior cranial margin is, so far, reported only from *N. orbiculatoides* and *N. armadillo*. The cephalon of *N. armadillo* is distinguished from *N. orbiculatoides* by showing pitting of the test surface (absent in *N. orbiculatoides*), by the occasional presence of a more or less flattened rim along the anterior cranial margin, by the slightly stronger convexity (sag.), by the more semielliptical outline, and the lateral border tapers out slightly further from the genal angle. The pygidium of *N. armadillo* generally carries fewer terrace lines, has a slightly better defined border (may be equally concave in *N. orbiculatoides*, but the central Swedish types of *N. orbiculatoides* often show a steeper, poorly defined border), and the inner margin of the doublure exhibits a distinctive outwards flare below the pleural furrow.

N. armadillo is probably the ancestor of *Nileus platys*, but is separated from this species by never showing terrace lines on the librigenae, the cephalic border is generally wider, the cephalon has a more elliptical outline, and the pygidial terrace-line pattern is usually more limited, and punctuation of the pygidial surface is usually effaced.

Nileus platys stigmatus has, compared to *N. armadillo*, a significantly lower cranial convexity (sag.), hence the cephalic outline is semicircular, not elliptical as in *N. armadillo*. Besides, the test surface of librigenae, palpebral lobes and pygidium is punctate in *N. p. stigmatus*.

The large *N. globicephalus* is separated from *N. armadillo* by possessing terrace lines on the librigenae, in showing fine terrace lines on the hypostomal socket of the doublure, by the distinct punctuation of test (cephalon and pygidium), by the more strongly vaulted pygidium, also showing a narrower postaxial border, and, typically, terrace lines along the pygidial margin.

Remarks. – *Trilobites oblongatus* Boeck, 1838 was described in some detail by Brögger (1882, pp. 64–65; Pl. 12:8), who ranked it as a variant of *N. armadillo*. Størmer (1941, p. 143) designated a lectotype. The poorly preserved material available to Brögger, a cephalon and a cranidium, inclusive of the specimen on which Boeck based his diagnosis, has been reexamined. The right side of the lectotype is distorted by

compaction (Fig. 148F–G), and the eye and genal region figured by Brögger (1882, Pl. 12:8) are not well-drawn. Brögger (1882) also emphasized the non-divergent course of the facial suture of *N. oblongatus*, but the anterior branches do actually diverge slightly in front of the eyes in the lectotype cephalon, although less so than usual for *N. armadillo*. The sutures clearly diverge in the second specimen, and both specimens undoubtedly belong to *N. armadillo*. *Nileus oblongatus* (Boeck, 1838) is, accordingly, a subjective junior synonym of *N. armadillo* (Dalman, 1827).

Schmidt (1904) figured and described several specimens assigned to *N. armadillo*, of which only the complete specimen from the Oslo Region seems to belong to *N. armadillo* (*s.str.*) (cf. Schmidt 1904, Pl. 8:15). The enrolled specimen (Schmidt 1904, Pl. 8:12) presumably belongs to the *N. depressus* group (see also Balashova 1960, Pl. 6:1), and a similar assignment is likely for the pygidium (Schmidt 1904, Pl. 8:17; see *N. depressus depressus* for discussion). The entire specimen from Hunneberg (Sweden), of which only the pygidium is shown (Schmidt 1904, Pl. 8:16), belongs to *N. exarmatus* (cf. Balashova 1976, p. 139; Pl. 40:8, figuring the cephalon of the specimen).

Balashova (1976, Pl. 40:3a–b) figured an entire specimen from the Oslo Region, which appears to be a true *N. armadillo*; it has more numerous terrace lines on the thoracic doublure (Balashova 1976, Pl. 40:9) than seen in any specimen at hand, suggesting a rather large variability of this feature. The figured doublure shows a distinctly curved crest, which is characteristic for the last segment of *N. armadillo*, but the illustrated segment is, according to the plate explanation (Balashova 1976, p. 166), the seventh, left segment, which is puzzling. All other specimens assigned to *N. armadillo* by Balashova (1976) belong to different species. The pygidium (Balashova 1976, Pl. 40:2) may be a *Nileus orbiculatoides*. A second pygidium (Balashova 1976, Pl. 40:10) has a surface ornamentation much different from that of *N. armadillo* and must belong to *N. depressus* (see discussion of *N. depressus depressus*). The cephalic doublure (Balashova 1976, Pl. 29:6) is not from a *N. armadillo*, and it is suspected that the fragment is not from a *Nileus* at all.

It appears that *N. armadillo* (*s.str.*) does not occur in the eastern Baltic area (Schmidt 1904, pp. 67–68; Lamansky 1905, p. 169). This is relevant for *N. chiton* Pander, 1830, which by Schmidt (1904) and Balashova (1976) was listed as a junior synonym of *N. armadillo*. *N. chiton* is, however, inadequately characterized, and the figures are too poor to permit a safe assignment of new material, hence the name must be regarded a *nomen dubium* (cf. Pander 1830, pp. 132–133; Pls. 4–C:12; 5:1a–c). The comparatively steep librigenae of *N. chiton* point to a relationship to the *N. depressus* group.

Hupé (1954, Fig. 1B) figured the doublure of the 8th thoracic pleura of a nileid, assigned to *N. armadillo*, later refigured by Harrington (1959, Fig. 79H). Since the thoracic doublure of *N. armadillo* possibly is rather variable (see

above remarks on Balashova 1976), it cannot be excluded that Hupé's identification is correct, but the discussed doublure does not resemble any specimen in the material at hand. The differences concern for instance the doublural crest, which appears to be present only proximally, whereas it more or less crosses the doublure in the available material. The terrace-line pattern is also denser in Hupé's specimen. It is therefore believed that the discussed doublure is from some other (unknown) nileid, and not from *N. armadillo*.

Wiman (1904, Figs. 2–5) figured three specimens assigned to *N. armadillo*. All cephalae, showing muscle scars and muscle markings, are figured as having wide librigenae, and the cephalic outline is almost subtrapezoidal; besides, the anterolateral glabellar expansion of one of the specimens (Wiman 1904, Fig. 3) is apparently minimal. The figures are, however, poorly drawn, and the specimens do belong to *N. armadillo* (the material has been examined).

Tjernvik (1956, p. 208) briefly described specimens of *N. armadillo* from Östergötland and Närke (Sweden). The anterior cranial margin was described as evenly rounded; this is unusual in the present material, but is expected to be more common for specimens from central and southern Sweden (see Moberg 1902, Fig. 2 and Schrank 1972, Pl. 6:1–3, 6). The flattened rim and the mesial boss may turn out to be characteristic of *N. armadillo* from the marginal facies, represented by the Komstad Limestone and the Huk Formation, perhaps linked with a slightly higher number of terrace lines on the pygidium (compare descriptions of *N. armadillo* by Brögger 1882, p. 63, Wandås 1984, Pl. 11C, Schmidt 1904, p. 65, and Balashova 1976, p. 138).

Strandmark (1902) listed *N. armadillo* from the limestone beds at site E22 of Fågelsång, later referred to by Cooper and Lindholm (1985, p. 284). It has not been possible to retrieve the material, but it is unlikely that Strandmark's identification is correct.

Funkquist (1919) listed *N. armadillo* from the Komstad Limestone of SE Scania. His material, most of which has been restudied, includes *N. orbiculatooides*, *N. depressus schranki* n. subsp. as well as *N. armadillo* (s. str.) None of the specimens figured by Funkquist (1919, Pl. 2:1–4) can positively be identified with *N. armadillo*, although the pygidium Fig. 2 presumably belongs to that species. The cranidium Fig. 1 in all probability represents *N. depressus schranki* n. subsp., and the cranidium Fig. 4 does not belong to any of the species described here, and may represent the unknown *N. cornutus* Moberg, 1892 [*nomen nudum*] (see introductory discussion of *Nileus*). *N. cornutus* was also listed from the Komstad Limestone (Funkquist 1919, p. 39); no specimens resembling the figured cranidium (Funkquist 1919, Pl. 2:4) have been found during the present investigation.

C. Poulsen (1936) listed *N. armadillo* from the 'Orthoceras' limestone of Bornholm. The material includes *N. armadillo* (s. str.) as well as *N. exarmatus*, *N. orbiculatooides* and *N. latifrons* n. sp.

Nileus latifrons n. sp.

Figs. 152–160

Synonymy. – □v 1936 *Nileus armadillo* Dalm. [*partim*] – C. Poulsen, pp. 48, 50 (listed). □v aff.? 1972 *Nileus depressus* (Sars & Boeck, 1838) [*partim*] – Schrank, p. 367; Pl. 7:2, 2a; non Pl. 7:1–1c (illustrations of cephalon). □v aff.? 1972 *Nileus globicephalus* sp. n. [*partim*] – Schrank, p. 372; Pl. 11:5–5a (illustrations of small cephalon).

Derivation of name. – Latin *latifrons* = broad forehead, alluding to the wide glabella of the new species.

Holotype. – Cephalon MGUH 22.651 (S 1556) (Fig. 153C–E) from 11 cm below top of bed +13, Skelbro. Top of the *M. limbata* Zone.

Paratypes. – Complete specimen MGUH 22.649 (Figs. 153A, 156A–B, 158B) from the uppermost part of bed +13, Duegård (very top of *M. limbata* Zone); pygidium MGUH 22.672 (S 1624a) (Fig. 157K, L) from the base of bed +14 (*A. expansus* Zone), Skelbro.

Additional material. – One complete specimen (damaged), 57 cranidia (including 10 juvenile specimens), 39 pygidia (including 1 specimen with articulated thorax) and 33 juvenile pygidia.

List of additional material. – □ Complete specimen GM 1884.1620b (t) [MGUH 22.650]. □ Cranidia S 1459 (t) [MGUH 22.652], S 1460b? (t), S 1490 (t), S 1503 (pim), S 1511 (t), S 1522 (im), S 1524a (t) [MGUH 22.653], S 1534 (im) [MGUH 22.659], S 1546 (im), S 1550 (pim), S 1553b (pim) [MGUH 22.655], S 1560? (t), S 1566b (pim), S 1568b (im), S 1594a (im), S 1595a (pim), S 1598a (im), S 1607 (t) [MGUH 22.654], S 1616b (im), S 1617 (t), S 1693 (im), S 1694 (im), S 1695 (pim), S 1698 (im), S 1705 (im), S 1707 (im), S 1708b (im), S 1728b (im) [MGUH 22.660], S 1731 (im), S

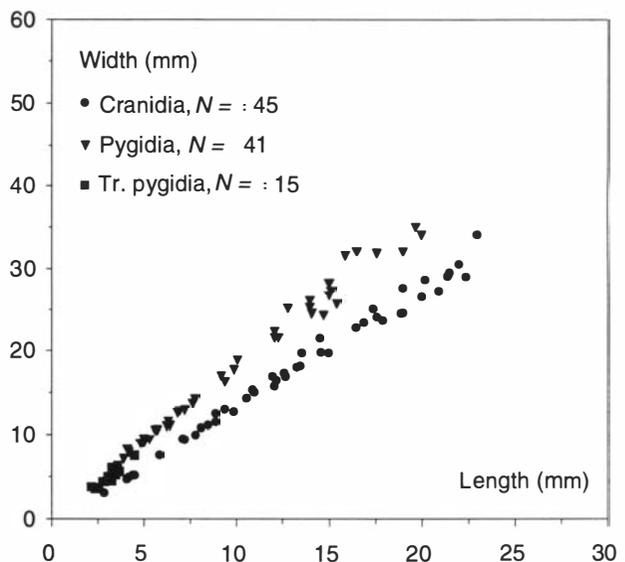


Fig. 152. Cranidia and pygidia of *Nileus latifrons* n. sp. Maximum width plotted against sagittal length.

Table 13. *Nileus latifrons* n.sp. Ranges for variation of cranidia, expressed as ratios of cranial length.

Size (mm)	Maximum width of cranidium			Glabella width			Palpebral lobe length (exsag.)			Glabellar tubercle, distance to post. margin		
	Range	Mean	N	Range	Mean	N	Range	Mean	N	Range	Mean	N
2.9	—	1.07	1	—	0.69	1	—	0.45	1	—	0.31	1
4.1–4.5	1.15–1.18	1.16	4	0.75–0.80	0.78	4	0.48–0.51	0.49	4	0.29–0.34	0.32	3
5.8	—	1.29	1	—	0.83	1	—	0.47	1	—	0.38	1
>6	1.26–1.48	1.37	39	0.81–1.01	0.92	39	0.40–0.52	0.46	37	0.36–0.42	0.39	46

1734 (im), S 1737 (t), S 1739 (im) [MGUH 22.658], S 1741 (im), S 1742 (im), K 375a (im), K 1224? (pim), K 1258 (im), K 1263a (pim), F 90 (im), F 94 (im), F 100 (t), F 123 (im), F 126 (pim), F 138 (im), F 150a (im) [MGUH 22.657], F 159 (im), F 167 (im), F 169a (t), F 172 (t), F 184 (t) [MGUH 22.656], LU 1b (is), LU 2a (im), LU 3a (im) [LO 7063], LU 6b (im) [LO 7064], LU 6c (im), LU 12d (im), LU 98 (im). □Pygidia S 1449 (pim), S 1500c (im), S 1517 (im), S 1520c (pim), S 1524b? (im), S 1526 (im), S 1527 (im), S 1553a (t), S 1553c (im), S 1563 (im), S 1569 (t), S 1570 (im), S 1584 (pim), S 1589a (pim) [MGUH 22.675], S 1592 (pim) [MGUH 22.678], S 1603a (im), S 1699 (im), S 1716 (pim) [MGUH 22.666], S 1723? (im), S 1725 (im) [MGUH 22.677], S 1726 (im), S 1748 (im), S 1749b (pim), S 1753 (pim), S 1756 (im), GM 1884.1620a with thoracic segments (t) [MGUH 22.663], K 347a (t), K 376a? (t), K 1249? (t), K 1257 (pim), K 1261 (d) [MGUH 22.679], K 1273 (t), F 71 (t), F 77 (im), F 80 (im), F 141? (im), F 144 (pim) [MGUH 22.676], LU 13a? (im), LU 13b (im). □Juvenile pygidia S 1447 (t) [MGUH 22.669], S 1452 (t), S 1457 (pim), S 1458 (t) [MGUH 22.665], S 1460a (t) [MGUH 22.668], S 1466 (t), S 1473 (t), S 1480 (t), S 1481 (t) [MGUH 22.667], S 1487a (t) [MGUH 22.671], S 1487b (t), S 1502 (t), S 1526 (t), S 1549 (t) [MGUH 22.674], S 1553c (im), S 1564 (t) [MGUH 22.670], S 1566a (t), S 1578 (im), S 1579a (t), S 1579b (pim), S 1588 (t), S 1618 (t) [MGUH 22.673], S 1685a (im), S 1751 (t) [MGUH 22.664], F 68 (pim) [MGUH 22.661], F 72 (im), F 83 (pim), F 104 (im), F 107a (t), F 163 (im) [MGUH 22.662], K 1223a (t), K 1231a (im), K 1234a (im).

Occurrence. – *Nileus latifrons* n.sp. ranges from the uppermost part of the *M. limbata* Zone and through most of the *A. expansus* Zone of the Komstad Limestone. The new species is presently not known from outside the Komstad Limestone area.

N. latifrons n.sp. is common in beds +13 and +14 at Skelbro, representing the very top of the *M. limbata* Zone and the base of the *A. expansus* Zone. The excellent museum specimen MGUH 22.649 is from Duegård, Bornholm; the sample represents the upper part of bed +13, 5–7 cm below the top of bed. Specimens GM 1884.1620a, b are labelled 'Bornholm'. The lithology of 1620a unmistakably corresponds to bed +13 (below the blackish top), whereas the lithology of the smallish sample 1620b is less diagnostic, but may represent the lower part of bed +13 as well. All museum specimens from Bornholm appear to originate from the very top of the *M. limbata* Zone.

N. latifrons n.sp. has also been found at Fågelsång in beds 18–20, which constitute the lowermost part of the *A. expansus* Zone. Museum material from the Fågelsång area (LU nos.), appears, as far as can be established, to originate from the same interval.

N. latifrons n.sp. is infrequent in SE Scania, and has been found only in beds +23 and +35 at Killeröd, and in beds 10, 11 and 12 at Killeröd site b. This interval represents the *A.*

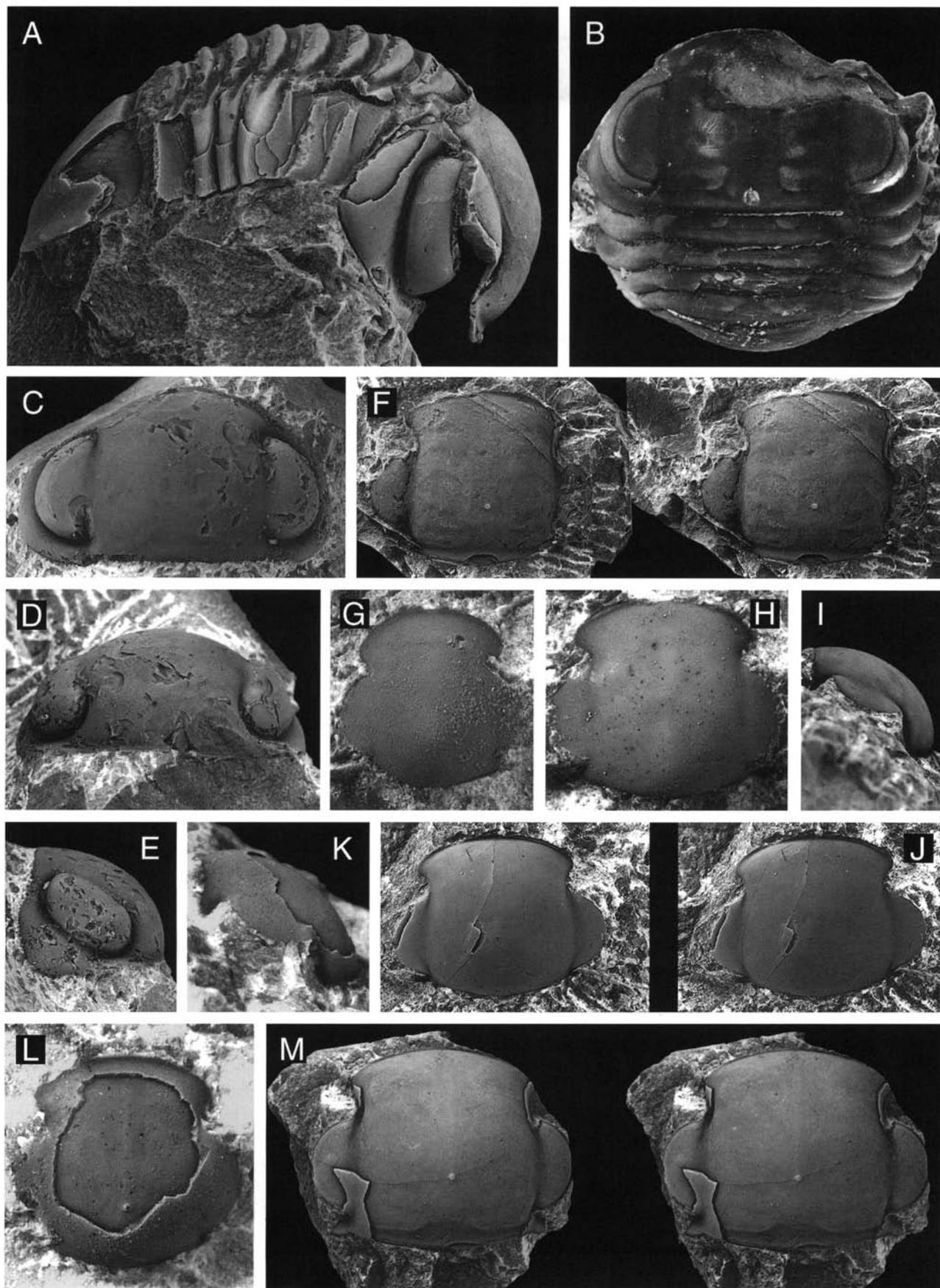
expansus Zone. Specimen LU 12d is from an unknown level at Komstad.

Diagnosis. – Fairly large species; cephalon reniform, strongly convex (both ways); glabella almost as wide as long, and gently rounded between palpebral lobes; anterior margin of cranidium truncate, typically with an extremely narrow flattened rim along margin; glabellar tubercle in a relatively forward position. Pygidium proportionally short, no axial relief at all, border normally ill-defined or absent; pygidial dorsal terrace lines few, but well-impressed, limited to anterolateral parts of pygidium; test surface punctate; pygidial doublure only gently concave and very slightly upturned around tip of axis.

Description. – Large species; largest specimen is complete specimen MGUH 22.649 possessing a cranidium 23.0 mm long and a pygidium 18.1 mm long (Fig. 152). Outstretched length approximately 75 mm; ratio between cephalon, thorax and pygidium 31:47:22 (dorsal projection). Maximum width of cephalon 38.0 mm; pygidium 34.7 mm wide (for further comments on this specimen, see remarks). The fragmentary pygidium S 1449 was presumably about 20 mm long, and, thus, is the largest pygidium found.

Cephalon reniform in outline, and strongly convex (both ways); W:L ratio 0.6 ($N = 2$). Cranidia from Fågelsång are consistently slightly less convex (sag.), compared to the

Fig. 153. *Nileus latifrons* n.sp. □A. Paratype. Internal mould of entire specimen, probably representing failed exuviation, lateral view, $\times 2$. The specimen was preserved lying on its back with open facial suture. See also Figs. 156A–B, 158B. MGUH 22.649 (GM 1984.1617), Duegård, Bornholm. □B. Damaged, non-whitened cephalon with transparent cuticle showing light coloured muscle insertion sites, $\times 3$. MGUH 22.650 (GM 1884.1620b), locality unknown, Bornholm. □C–E. Holotype. Cephalon, dorsal, frontal and side views, $\times 2$. MGUH 22.651 (S 1556), bed +13, Skelbro. □F. Internal mould of cranidium showing paired glabellar muscle impressions, stereo-pair, $\times 1.5$. The specimen exhibits a comparatively low sagittal convexity. LO 7063 (LU 3a), Fågelsång area. □G. Juvenile cranidium showing narrow flattened rim along anterior margin, $\times 10$. MGUH 22.652 (S 1459), bed +13, Skelbro. □H. Juvenile cranidium, $\times 8$. MGUH 22.653 (S 1524a), bed +13, Skelbro. □I–J. Well-preserved small cranidium showing sagittally 'wrinkled' cuticle, side and dorsal (stereo-pair) views, $\times 3$. MGUH 22.654 (S 1607), bed +13, Skelbro. □K–L. Partly exfoliated juvenile cranidium, side and dorsal views, $\times 9$. MGUH 22.655 (S 1553b), bed +13, Skelbro. □M. Exfoliated cranidium, stereo-pair, $\times 2$. LO 7064 (LU 6b), Fågelsång.



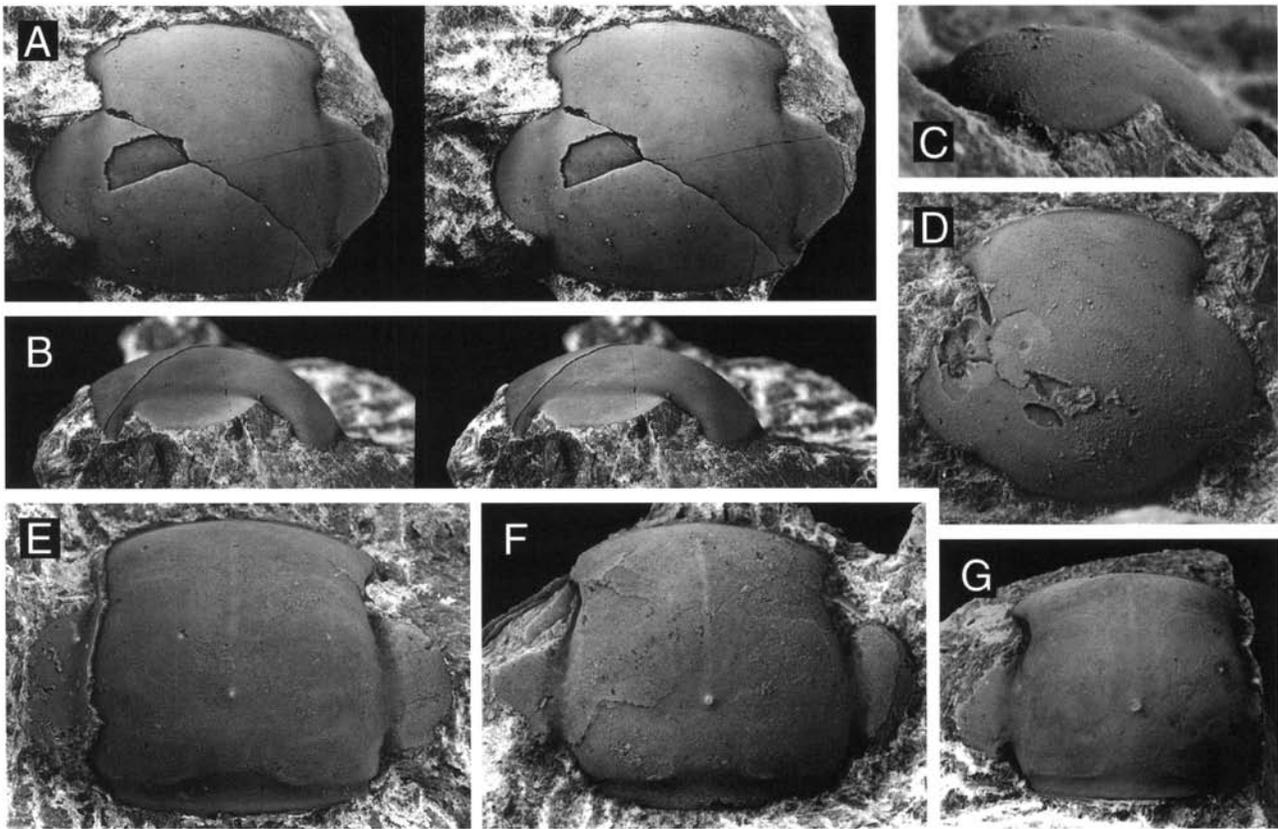


Fig. 154. *Nileus latifrons* n.sp. □A–B. Well-preserved cranidium, stereo-pairs of dorsal and side views, $\times 3$. MGUH 22.656 (F 184), bed 20, Fågelsång. □C–D. Juvenile cranidium, side and dorsal views, $\times 10$. MGUH 22.657 (F 150a), bed 19, Fågelsång. □E. Internal mould of cranidium, $\times 2$. MGUH 22.658 (S 1739), bed +13, Skelbro. □F. Internal mould of cranidium, $\times 2$. MGUH 22.659 (S 1534), bed +13, Skelbro. □G. Internal mould of cranidium, $\times 2$. MGUH 22.660 (S 1728b), bed +13, Skelbro.

specimens from Skelbro (e.g., Fig. 153J vs. F). The small difference influences biometric ratios such as cranidial W:L ratio, glabellar W:L ratio etc., which consequently are lower in the Fågelsång material. Cranidium relatively short (sag.), wide (tr.) (Table 13); material from Fågelsång has a mean cranidial W:L ratio of 1.32 ($N = 12$), whereas the slightly more convex (sag.) cranidia from Skelbro and Killeröd show a mean of 1.39 ($N = 27$) (Fig. 155A). Glabella almost as wide as long in adults (Table 13; Fig. 155B); specimens from Fågelsång tend to have a relatively narrower glabella, showing W:L ratios varying between 0.81 and 0.96 (mean 0.89; $N = 12$), while specimens from Skelbro and Killeröd exhibit glabellar W:L ratios between 0.85 and 1.01 (mean 0.93; $N = 27$; Fig. 155B). Axial furrows gently arcuate between palpebral lobes and do not converge forwards; furrows wide, but comparatively well-impressed, and visible also on testaceous material. Anterior margin of cranidium rather straight, producing a truncate appearance. Extremely narrow, flattened anterior rim present in most specimens (Fig. 153A, J), accounting for half of the very narrow anterior cephalic border. Palpebral lobes gently convex (tr.), sloping rather strongly in

outward direction. A radiating caecate pattern is occasionally present on the lobes of internal moulds, particularly distinct along the palpebral suture. Mesial glabellar tubercle small on internal moulds, and often difficult to recognize on testaceous material, but may be indicated by a change of colour or by an interruption of the 'wrinkled' test surface. Tubercle in a relatively advanced position (Table 13), partly as a consequence of the high sagittal convexity of cranidium. Sagittal keel on internal moulds as in *N. armadillo*. Wide and shallow occipital furrow defined on internal moulds, with a mesial expansion to twice the lateral width; it is almost effaced on testaceous material, but may be very gently impressed mesially. Shallow lateral glabellar impressions not uncommon on internal moulds (Figs. 153F); a single specimen with intact test exhibits coloured muscle insertion sites (Fig. 153B). Posterior fixigena slender, pointed triangular, bent slightly down; length (exsag.) averages 0.14 of the cranidial length ($N = 27$). Anterior branch of facial suture turn gently outwards in front of eyes at an angle of about 25° to sagittal line, later turning inwards to merge smoothly mesially. Posterior branch of facial suture almost straight, but in detail

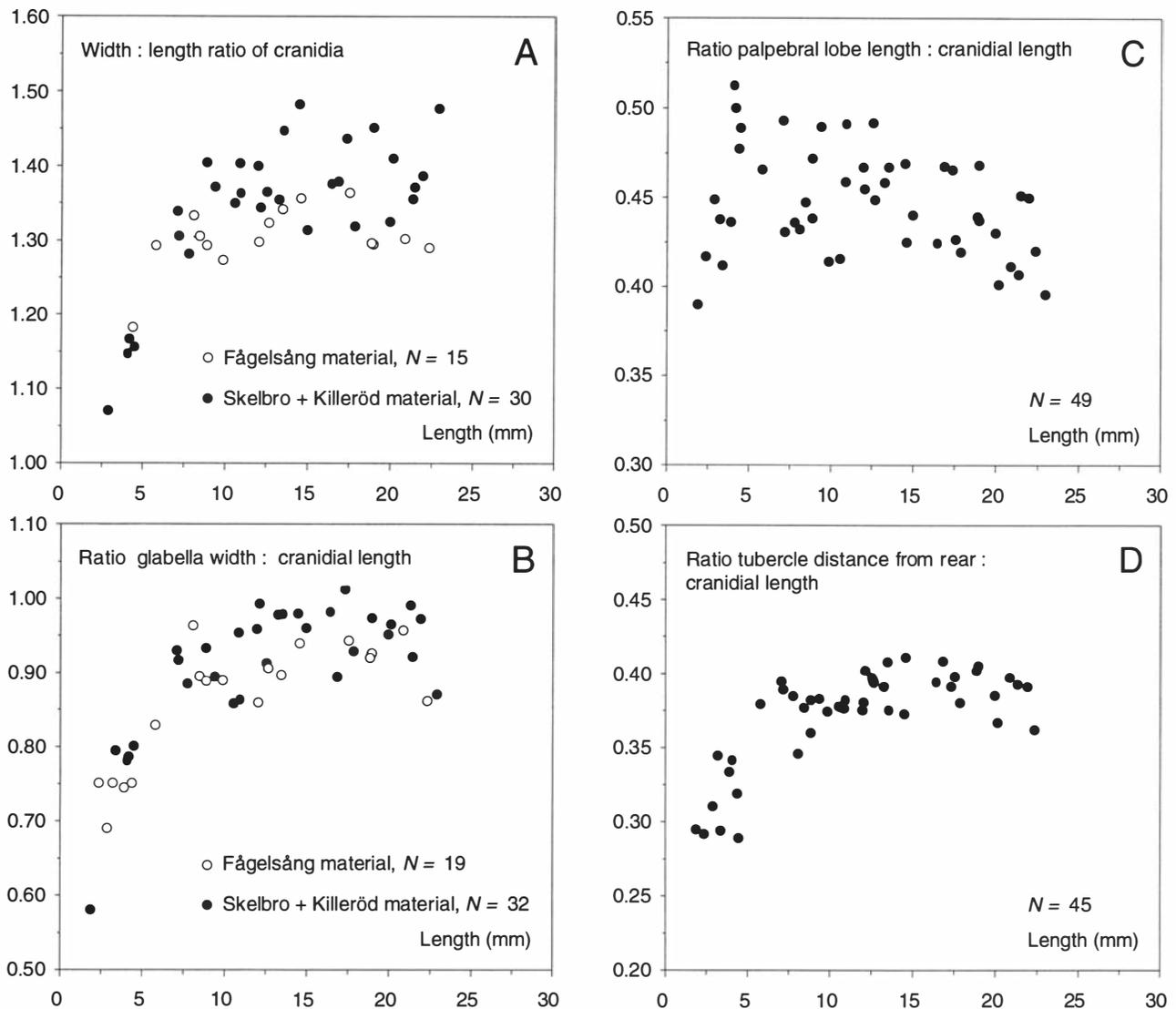


Fig. 155. Crania of *Nileus latifrons* n.sp. Distinction is made between specimens from Fågelsång and Skelbro–Killeröd only when differences between the materials are evident. The material from Fågelsång includes the tiny crania described separately as ‘Undifferentiated juvenile specimens of *Nileus armadillo* and *N. latifrons* n.sp.’. □A. Width:length ratio (measured across the palpebral lobe) plotted against cranial length. □B. Ratio between glabella width (measured between posterior corners of palpebral lobes) and cranial length plotted against cranial length. □C. Ratio between palpebral lobe length (exsag.) and cranial length plotted against cranial length. □D. Relative position of glabellar tubercle plotted against cranial length.

consists of two straight parts, an inner section with a direction of about 45° from sagittal line, and an outer section with a direction of about 25° from sagittal line, equalised angle from lobe to intersection with posterior margin about 35° to sagittal line. Librigena slender; lateral border stops shortly before midlevel of eye, and the convex (tr.) posterolateral part of librigena slopes strongly outwards.

Cephalic test surface shows minute pits, which are particularly distinct on the palpebral lobes and on posterolateral portion of librigena. It is possible that pitting genuinely is absent on glabella in some specimens, but the fine ornament

is obliterated by even the slightest corrosion. Well-preserved specimens often show a ‘wrinkled’ surface pattern on muscle insertion sites.

Hypostome unknown.

Thorax with eight segments, decreasing gently in size backwards; posterior segment 10% narrower (tr.) and almost 40% shorter (sag.) than anterior segment. Axis of equal width on the anterior three segments, then tapers slightly rearwards; it occupies 0.55 of the thoracic width on the anterior segment and 0.50 of the width on the posterior. Axis not raised above pleurae, except for the relief inherent from

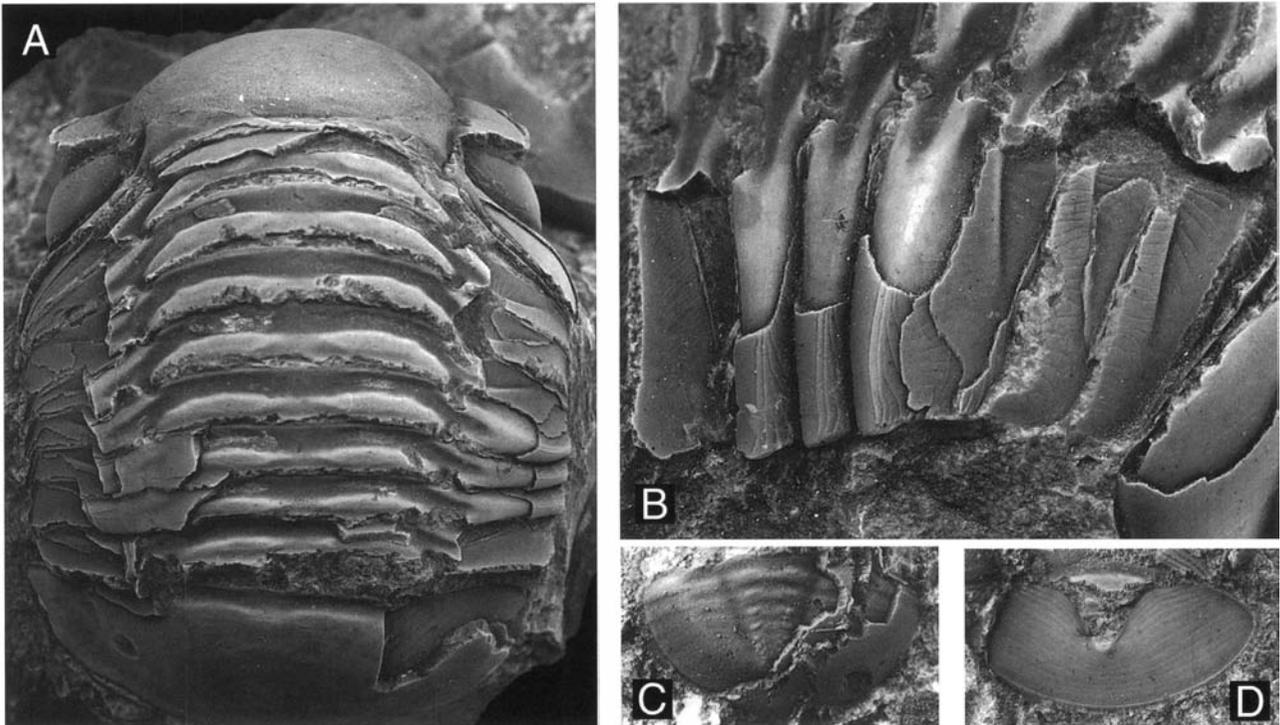
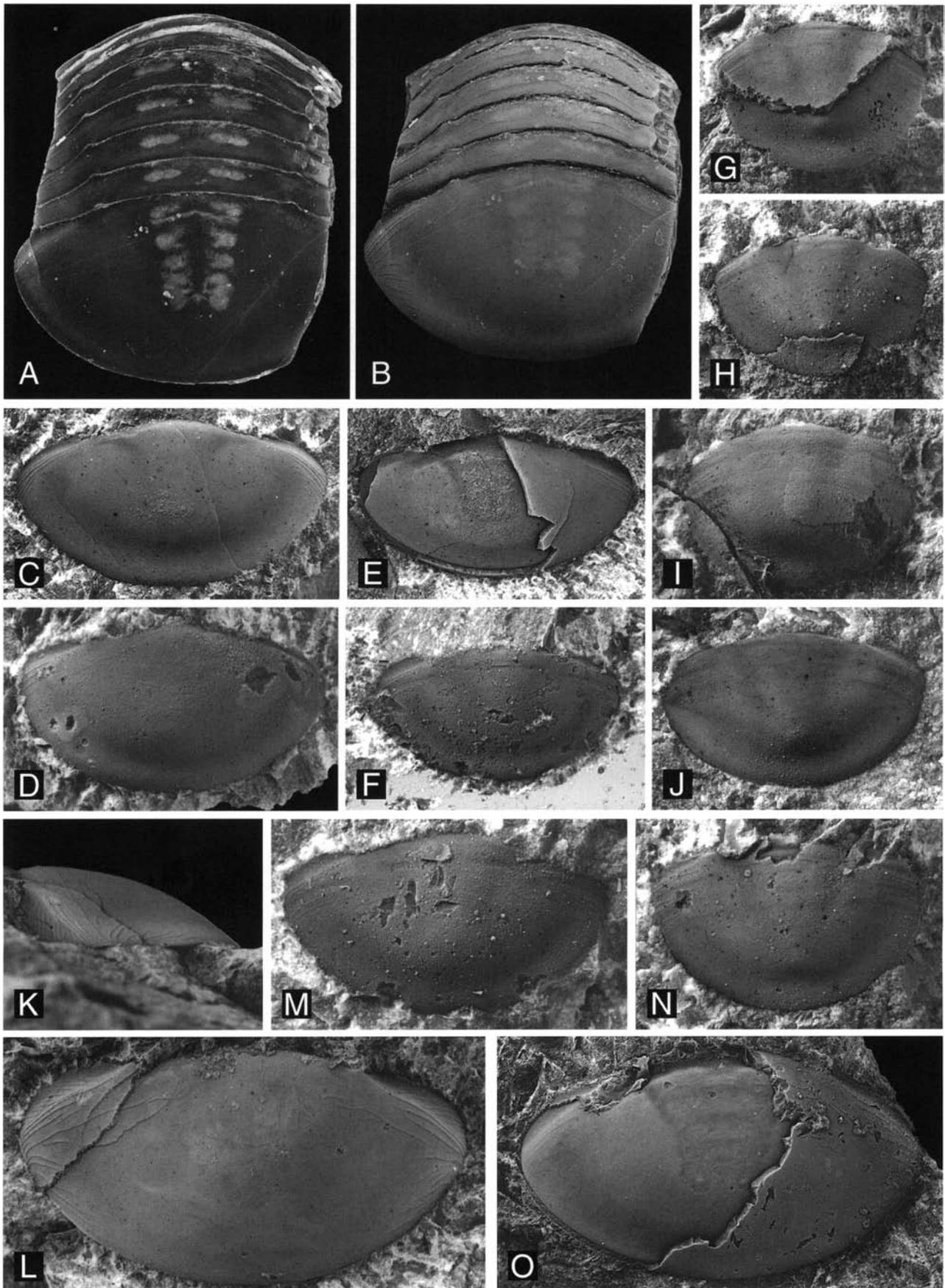


Fig. 156. *Nileus latifrons* n.sp. □A. Paratype. Internal mould of thorax showing axial muscle insertion sites, dorsal view, $\times 2$. MGUH 22.649 (GM 1984.1617), Duegård, Bornholm. □B. As A, close-up of anterior thoracic segments (edge of cephalon to the right) showing doublure and pleural furrows, side view, $\times 4$. □C. Exfoliated transitory pygidium, stage C, $\times 10$. MGUH 22.661 (F 68), bed 18, Fågelsång. □D. Internal mould of small holaspid pygidium showing doublure, $\times 5$. MGUH 22.662 (F 163), bed 19, Fågelsång.

skeletal convexity (tr.), and it is defined mainly by the position of articulating processes/sockets. On internal moulds the axis of each segment has a pair of elongate, crescentic, lateral swellings, connected across sagittal area by a narrow low ridge (Fig. 156A). Paired, light coloured muscle markings, corresponding to the position of the axial swellings, are seen in one well-preserved specimen with intact test (Fig. 157A); apart from that, there is no indication of the swellings on the smooth outside. Obviously, the swellings are reflecting a thinning of the test, and correspond in all probability to muscle insertion sites. Articulating half-ring, as seen on internal moulds, short (tr.), consisting only of the raised anterior edge of the segment. It is delimited by a deep transverse furrow, likewise defined only on internal moulds, which turns backwards laterally, and continues into short pleural furrows running behind articulating processes to stop at paradoublural line on the middle of the segment (Fig. 156A). Pleural furrows shallow on testaceous material, most deeply impressed on the anterior segments, almost effaced on posterior segments; together they form an indistinct 'pseudo' axial furrow. Articulating facets well-developed, occupying main part of the segments (exsag.) distally. Fairly prominent articulating processes situated on anterior margin, flanking the axis, and corresponding articulating sockets are present in posterior margin; these articulating features are most prominent on internal moulds.

Test surface is covered with minute pits; a faint 'wrinkled' pattern may be indicated laterally on axis, running parallel to sagittal line. A single terrace line crosses the axis of each segment; it is effaced mesially on the posterior two segments. The terrace line runs immediately behind the position of the

Fig. 157. *Nileus latifrons* n.sp. □A. Non-whitened, well-preserved thorax and pygidium with transparent cuticle showing light coloured muscle insertion sites, $\times 3$. MGUH 22.663 (GM 1884.1620a), Bornholm. □B. As A, whitened, showing typically developed adult terrace-line pattern, $\times 3$. □C. Small pygidium showing comparatively broad concave border, $\times 6$. MGUH 22.664 (S 1751), bed +13, Skelbro. □D. Small pygidium showing almost complete lack of exterior terrace lines, $\times 6$. MGUH 22.665 (S 1458), bed +13, Skelbro. □E. Partly exfoliated small pygidium showing comparatively well-developed border, $\times 4$. MGUH 22.666 (S 1716), bed +13, Skelbro. □F. Transitory pygidium, stage E; $\times 6$. MGUH 22.667 (S 1481), bed +13, Skelbro. □G. Transitory pygidium, stage C; $\times 10$. MGUH 22.668 (S 1460a), bed +13, Skelbro. □H. Transitory pygidium, stage C; $\times 9$. MGUH 22.669 (S 1447), bed +13, Skelbro. □I. Transitory pygidium, stage C, $\times 9$. MGUH 22.670 (S 1564), bed +13, Skelbro. □J. Transitory pygidium, stage D, $\times 9$. MGUH 22.671 (S 1487a), bed +13, Skelbro. □K-L. Paratype. Well-preserved pygidium showing typical dorsal terrace-line pattern, radiating 'wrinkled' pattern around axis, and ill-defined border, side and dorsal views, $\times 3$. MGUH 22.672 (S 1624a), bed +14, Skelbro. □M. Transitory pygidium, stage E, $\times 9$. MGUH 22.673 (S 1618), bed +13, Skelbro. □N. Transitory pygidium, stage D, $\times 9$. MGUH 22.674 (S 1549), bed +13, Skelbro. □O. Partly exfoliated pygidium showing axial outline on internal mould, $\times 3$. MGUH 22.675 (S 1589a), bed +13, Skelbro.



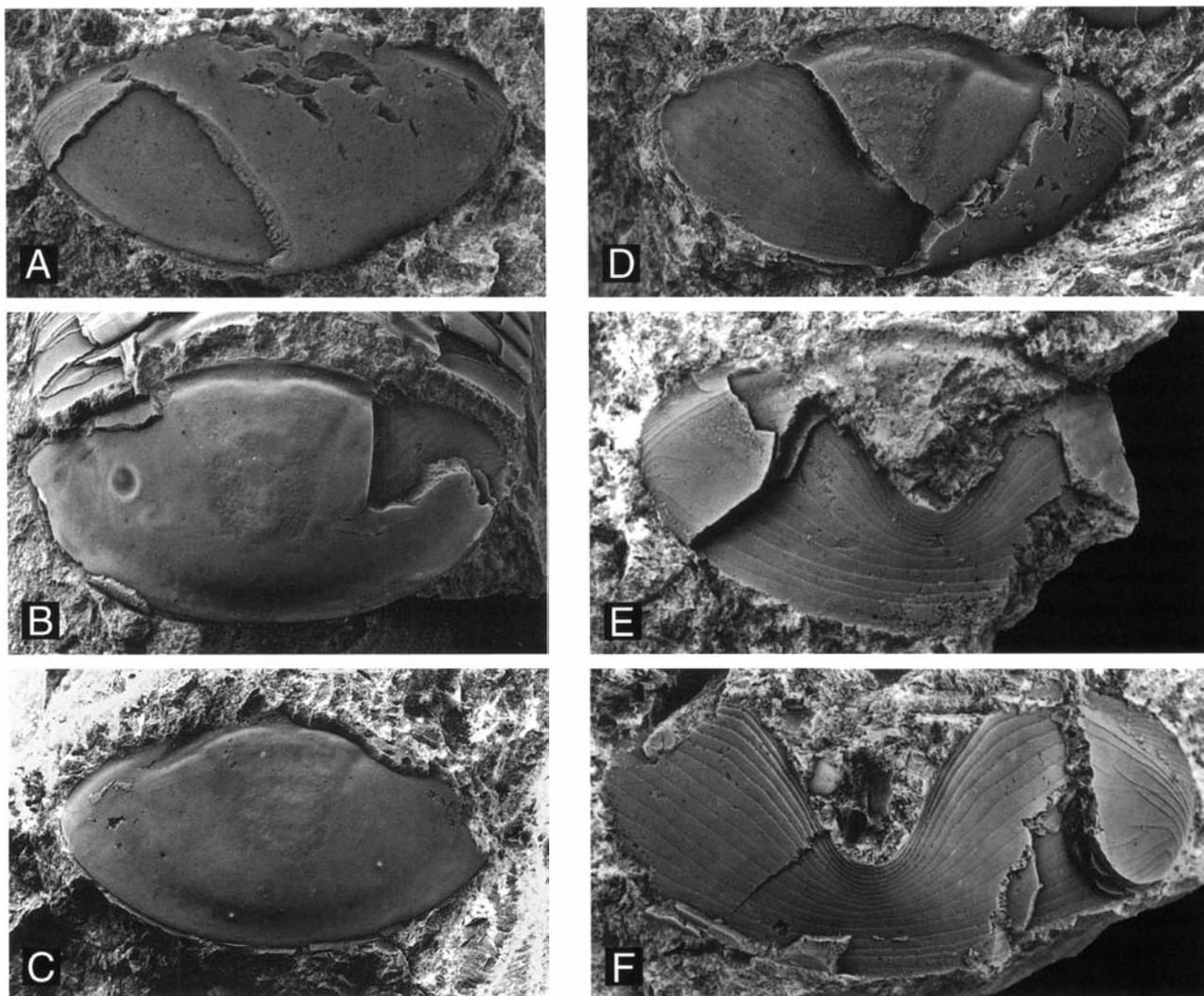


Fig. 158. *Nileus latifrons* n.sp. □A. Partly exfoliated small pygidium, showing weakly defined border on internal mould, but almost no border on external side, $\times 6$. MGUH 22.676 (F 144), bed 19, Fågelsång. □B. Paratype MGUH 22.649 (GM 1984.1617). Internal mould of large pygidium, $\times 2$. Cephalon and thorax figured on Figs. 153A, 156A–B. Duegård, Bornholm. □C. Internal mould of small pygidium showing axis, $\times 3$. MGUH 22.677 (S 1725), bed +13, Skelbro. □D. Internal mould of small pygidium showing axis and doublure, $\times 4$. MGUH 22.678 (S 1592), bed +13, Skelbro. □E. Internal mould of small pygidium showing doublure, $\times 4$. MGUH 22.679 (K 1261), bed 11, Killeröd site b. □F. Internal mould of pygidium showing doublure, $\times 3$. LO 7070 (LU 13), Fågelsång, loc. E21b.

Table 14. *Nileus latifrons* n.sp. Ranges for variation of pygidia, expressed as ratios. An unusually large E-stage specimen, 4.5 mm long, has not been included.

Size (mm)	Pygidial L:W ratio			Axial width : pygidial width			Axial length : pygidial length			Border length (sag.) : pygidial length		
	Variation	Mean	N	Variation	Mean	N	Variation	Mean	N	Variation	Mean	N
2.2–2.8 [Stage C]	0.58–0.70	0.64	3	0.34–0.38	0.36	3	0.59–0.71	0.64	3	—	0.23	2
2.4–3.5 [Stage D]	0.62–0.73	0.66	7	0.36–0.42	0.39	8	0.52–0.65	0.59	7	0.20–0.25	0.23	7
3.3–3.7 [Stage E]	0.54–0.66	0.59	4	0.34–0.40	0.38	4	0.52–0.60	0.56	4	0.19–0.24	0.23	3
3.6–5.7 [Hol.]	0.50–0.56	0.54	11	0.30–0.38	0.33	6	0.49–0.58	0.54	8	0.18–0.26	0.21	8
>6 [Hol.]	0.51–0.60	0.55	30	0.31–0.41	0.36	20	0.53–0.68	0.61	26	0.12–0.20*	0.15	19

* Exclusive of pygidia without border.

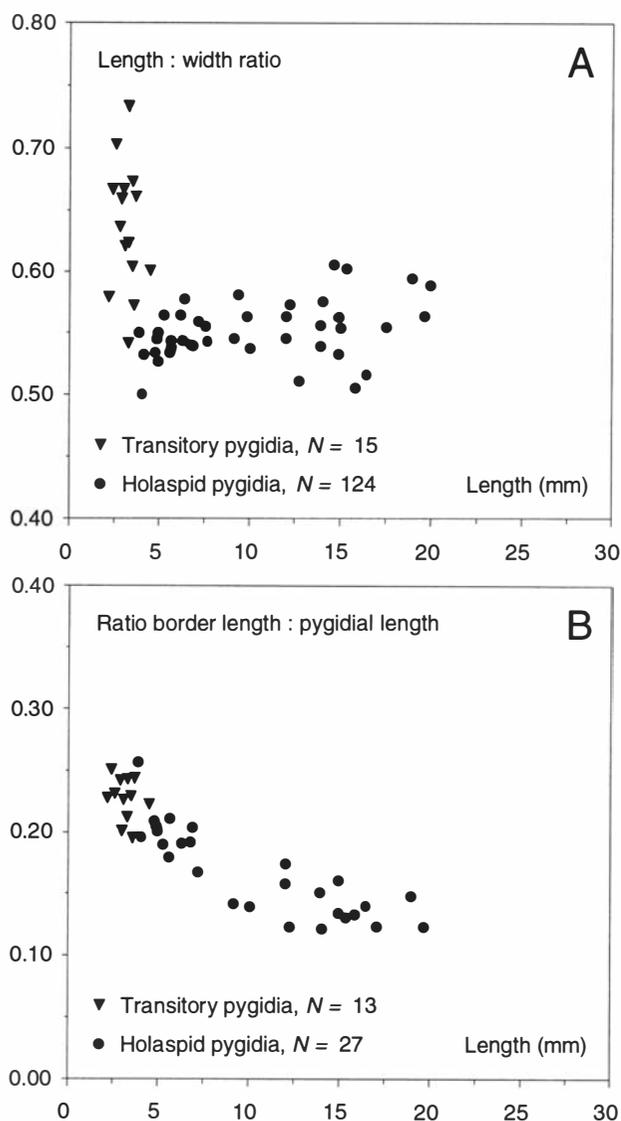


Fig. 159. Pygidia of *Nileus latifrons* n.sp. □A. Ratio between sagittal length and maximum width plotted against sagittal length. □B. Ratio between border length (sag.) and pygidial length plotted against pygidial length. Note that the border is steep in many specimens. Pygidia without a border are not included.

axial swellings seen on internal moulds, to stop short off the 'axial furrows'. One to two well-impressed terrace lines are present on the posterior crest of articulating facet. Facet provided with at least ten gently sigmoidal, fine terrace lines, running downwards-outwards.

Doublure extends below 0.75 of the pleural width (tr., dorsal projection). A low crest (panderian protuberance *sensu* Hupé 1954) crosses the doublure diagonally from one third up the anterior margin and inwards-backwards; the crest is a stopping device for the articulating facet of the succeeding thoracic segment. Terrace lines arranged in a 'herring-bone' pattern around the crest (Fig. 156B). Anterior to the crest are usually seen about seven rather coarse,

roughly transverse lines, becoming gradually shorter and with an increasing oblique outwards direction abaxially; posterior to the diagonal crest the terrace lines are more abundant and finer, also trending roughly transverse, but with an oblique outwards-backwards direction. Distally the terrace lines turn abruptly outwards and follow the anterior margin on the anterior segments, whereas the distal lines on the posterior segment are U-shaped, facing outwards.

Pygidium moderately vaulted, slender. Axis has no relief at all in adults, even on internal moulds, but a funnel-shaped axial area is occasionally outlined by muscle markings, by a faint 'wrinkling' of test surface, or by an indistinct reticulate pattern on internal moulds (e.g., Figs. 157B, 158C). For the same reason the exact dimensions of the axial area are difficult to obtain (Table 14). A barely raised axis with indistinct segmentation is usually defined on internal moulds of smaller holaspides less than 10 mm long, showing up to five segments in addition to the terminal piece. The axial segmentation is effaced on internal moulds of adults, apart from the anterior transverse furrow, separating half-ring. Four pairs of light coloured muscle markings are present in the axial area of a couple of excellently preserved testaceous specimens (Fig. 157A). Anterior pair is connected by a narrow band across sagittal area, and corresponds to the first axial ring. The posterior, clearly composite pair is the largest, and appears to contain three submarks, suggesting a total of six muscle pairs on the pygidium. A narrow, more or, typically, less well-defined border is normally present, but a few pygidia are fully convex. Anterolateral border width may be up to twice the postaxial width. Especially pygidia from the lower part of bed +13 at Skelbro, as well as holaspides less than 8 mm long, show a comparatively well-defined concave border (Fig. 157C), whereas it mostly is steeper and indistinct in pygidia from Scania and from the uppermost part of bed +13 and bed +14 at Skelbro (Fig. 157L). Within this range of variation some pygidia are convex postaxially or nearly so, but still show an anterolateral concave border. Of 24 holaspides with intact postaxial region, 3 specimens, 6.3 to 6.7 mm long, show a relatively wide border, occupying 0.16–0.21 of the pygidial length; 18 specimens, more than 8 mm long, have a more or less well-defined border occupying 0.12–0.18 of the pygidial length (mean 0.15; see Fig. 159B), and 8 specimens, 6 to 16 mm long, lack a postaxial border. The test is thickened in the flexure between pleural fields and border, so the border is most distinct on internal moulds; a concave border may actually be defined on internal moulds and not on the outside of test as demonstrated by a few, partly exfoliated specimens (Fig. 158A).

Adult pygidia usually show four long and two short well-impressed terrace lines along anterior margin and several well-impressed, openly spaced terrace lines anterolaterally on border (Fig. 157L); the entire test surface is finely punctate (the faint punctation is obliterated by even the faintest corrosion). Articulating facets provided with about 15–18 fine

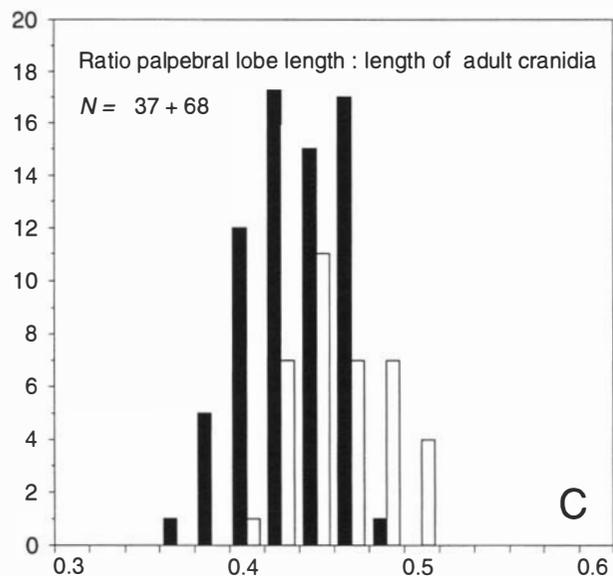
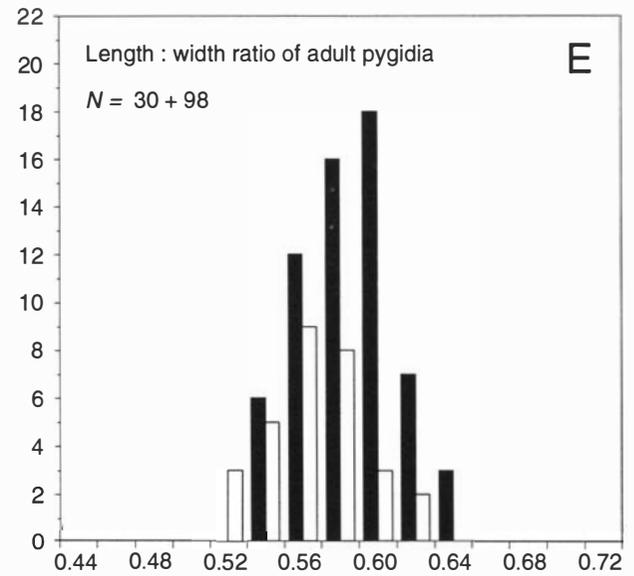
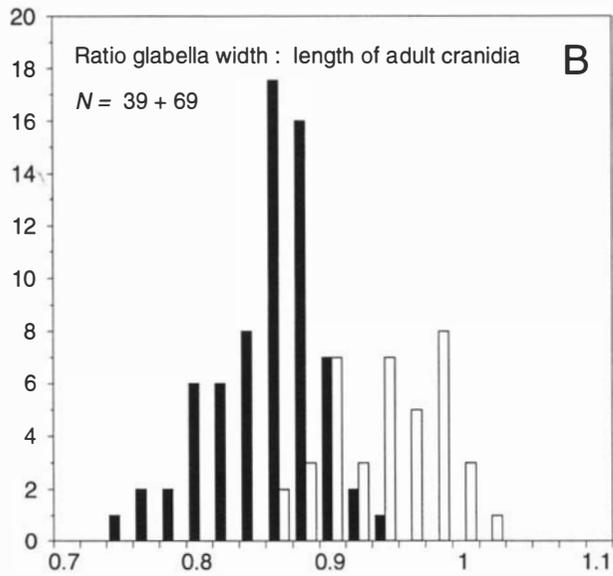
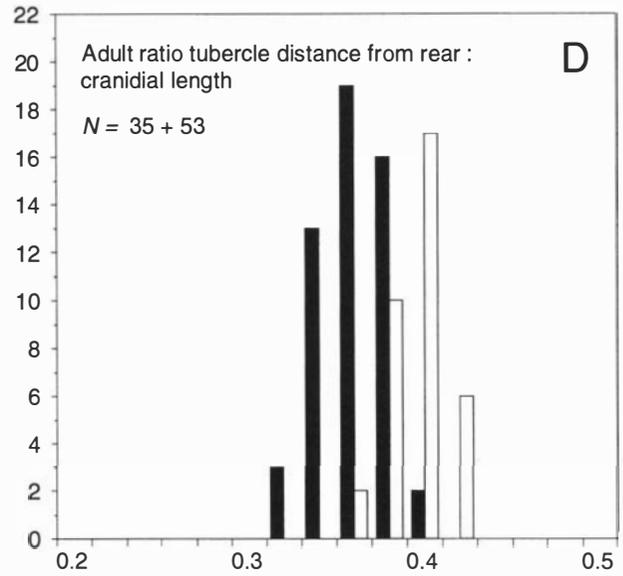
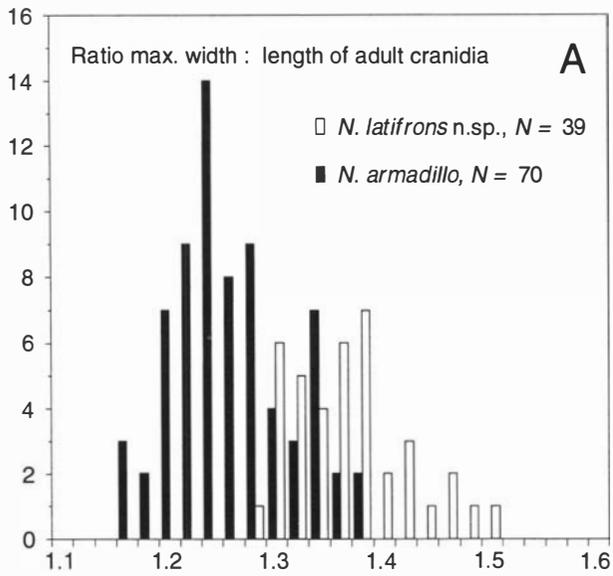


Fig. 160. *Nileus latifrons* n.sp. versus *N. armadillo*, adult specimens only (crania more than ca. 6 mm long and pygidia >5.7 mm long). □A. Comparison of adult ratios between maximum cranial width and cranial length. □B. Comparison of adult ratios between glabella width (measured between hind corners of palpebral lobes) and cranial length. □C. Comparison of adult ratios between palpebral lobe length (exsag.) and cranial length. □D. Comparison of adult ratios between the distance from posterior cranial margin to glabellar tubercle against cranial length. □E. Comparison of adult ratios between pygidial length (sag.) and maximum pygidial width.

terrace lines. Excellently preserved specimens show a 'wrinkled' pattern radiating from the axial area (Fig. 157L).

Doublure slightly to moderately concave, gently upturned around the tip of axis and provided with about 14–15 coarse terrace lines.

Juveniles. – Juvenile cranidia less than 4 mm long and transitory pygidia of *N. latifrons* n.sp. and *N. armadillo* cannot be distinguished, see separate description below of material from levels containing both species.

Cranidia less than 6 mm long differ significantly from larger specimens in several respects (cf. Fig. 155; Table 13), i.e. the cranidial W:L ratio is lower, glabella is distinctly narrower, and the glabellar tubercle is situated closer to posterior margin. The smallest specimen (S 1459, Fig. 153G) has a distinct flattened rim along the more rounded anterior cranidial margin and a lower sagittal convexity. Juvenile cranidia have a smooth test surface.

Thirty-one juvenile pygidia from levels containing only *N. latifrons* n.sp. are assigned to this species, but they are 'identified' solely by their association with identifiable adult specimens. Transitory pygidia (stages C, D and E) match the description of similar material (pp. 243–245). The E stage is represented by five pygidia, 3.3–3.7 mm long, plus a specimen 4.5 mm long. The latter presumably belongs to *N. armadillo*, although no adult specimens of this species have been found at the same level. It may alternatively represent a growth stage F individual in which the thoracic segment failed to detach during moulting.

Fourteen specimens, 3.9–5.7 mm long, of the juvenile material are holaspides. The specimens from Skelbro have a well-defined border, postaxially occupying 0.18–0.21 of the pygidial length (mean 0.20; $N = 5$). Of six specimens from Fågelsång, the smallest, 3.9 mm long, has a distinct border, postaxially occupying 0.25 of the pygidial length, the next-smallest, 4.1 and 4.8 mm long, have a border occupying 0.20–0.21 of the pygidial length, whereas no border is defined in the remaining specimens, 5 to 5.7 mm long. The three smallest specimens from Fågelsång are internal moulds, and patches of intact test in one of the specimens (4.8 mm long) suggest that no border is defined on testaceous material (Fig. 158A). None of the specimens show punctuation of test surface, perhaps reflecting preservational failure.

Affinities. – *Nileus latifrons* n.sp. occurs associated with *N. armadillo*, but is readily distinguished by the wide cranidium (Fig. 160A), the short, slightly rounded glabella (Fig. 160B), the advanced glabellar tubercle (Fig. 160D), the rather straight anterior cranidial margin without median boss, and by the slender pygidium, typically with a poorly defined border and very few terrace lines; besides, the pygidial doublure is less concave and less upturned around the tip of axis. *N. latifrons* n.sp. and *N. armadillo* probably are not close relatives. The separating characters stated for *N. latifrons* n.sp. versus *N. armadillo* also differentiate the new species from *N. orbiculatoides*.

N. latifrons n.sp. has the same basic outline as the members of the *N. depressus* group, particularly *N. depressus depressus*. Thus *N. latifrons* n.sp. and *N. d. depressus* both have a short cephalon with a broad, slightly rounded glabella, a strong cephalic convexity (both ways), a rather straight anterior cranidial margin, convex posterolateral librigenae without lateral border, and moderately vaulted, slender pygidia typically with an ill-defined or no border. *N. latifrons* n.sp. is separated by the different size and the much different terrace-line pattern, but it is possible that *N. latifrons* n.sp. is related to the *N. depressus* group, particularly as suggested by the quite similar cephalic outlines. It is even possible that *N. latifrons* n.sp. simply represents a shallow-water ecophenotype of *N. depressus* (compare discussion of *Nileus* sp. B).

Remarks. – The variation of pygidial border outline is interesting from a general taxonomical viewpoint, as it demonstrates that the border may vary from being fairly well-defined to absent within one and the same species. This is relevant in the discussion of *N. depressus* and *N. orbiculatoides* (q.v.), and indicates that a rigid use of presence/absence of a pygidial border in nileid taxonomy is unwarranted (cf. Tjernvik 1980).

The articulated specimen MGUH 22.649 in all probability represents a failed exuviation. The facial suture is open (Fig. 153A), and there is an anterior gap of 5 mm between the librigenae and the cranidial margin; the neck point (Henningsmoen 1975, p. 182) is still articulated. It appears probable that the trilobite either died during exuviation or, alternatively, that the cephalic opening diminished after accomplished exuviation. Under all circumstances the specimen seems to indicate that *Nileus* molted by opening the facial suture and then emerged through the cephalon, lying on the back (the specimen is orientated with the dorsal side down). This position is also seen in the living *Limulus* during exuviation (Henningsmoen 1975, p. 188). Furthermore, the sizeable specimen clearly suggests that even the old trilobites continued to molt.

Undifferentiated juveniles of *Nileus armadillo* and *N. latifrons* n.sp.

Figs. 161–162

Material. – Six juvenile cranidia and 16 transitory pygidia.

List of material. – □Cranidia S 1632 (im), F 117 (t) [MGUH 22.680], F 150b (t), F 161 (im), K 369a (t), LU 87b (t). □Pygidia S 1530 (im) [MGUH 22.686], S 1707 (im), S 1719a (im), S 1727 (t), S 1750 (t) [MGUH 22.685], S 1752 (t), K 369b (t) [MGUH 22.687], K 376 (t), K 1259 (t), K 1267 (t) [MGUH 22.682], K 1268 (t), F 143 (t) [MGUH 22.684], F 148 (im), F 154a (im), F 154b (pim) [MGUH 22.681], F 189 (pim) [MGUH 22.683].

Occurrence. – The material is from the *A. expansus* Zone of Skelbro (top of bed +13, bed +14), Fågelsång (beds 18–20), Killeröd (bed +35) and Killeröd site b (beds 11–12). Specimen LU 87b is from bed interval 18–20 of Fågelsång.

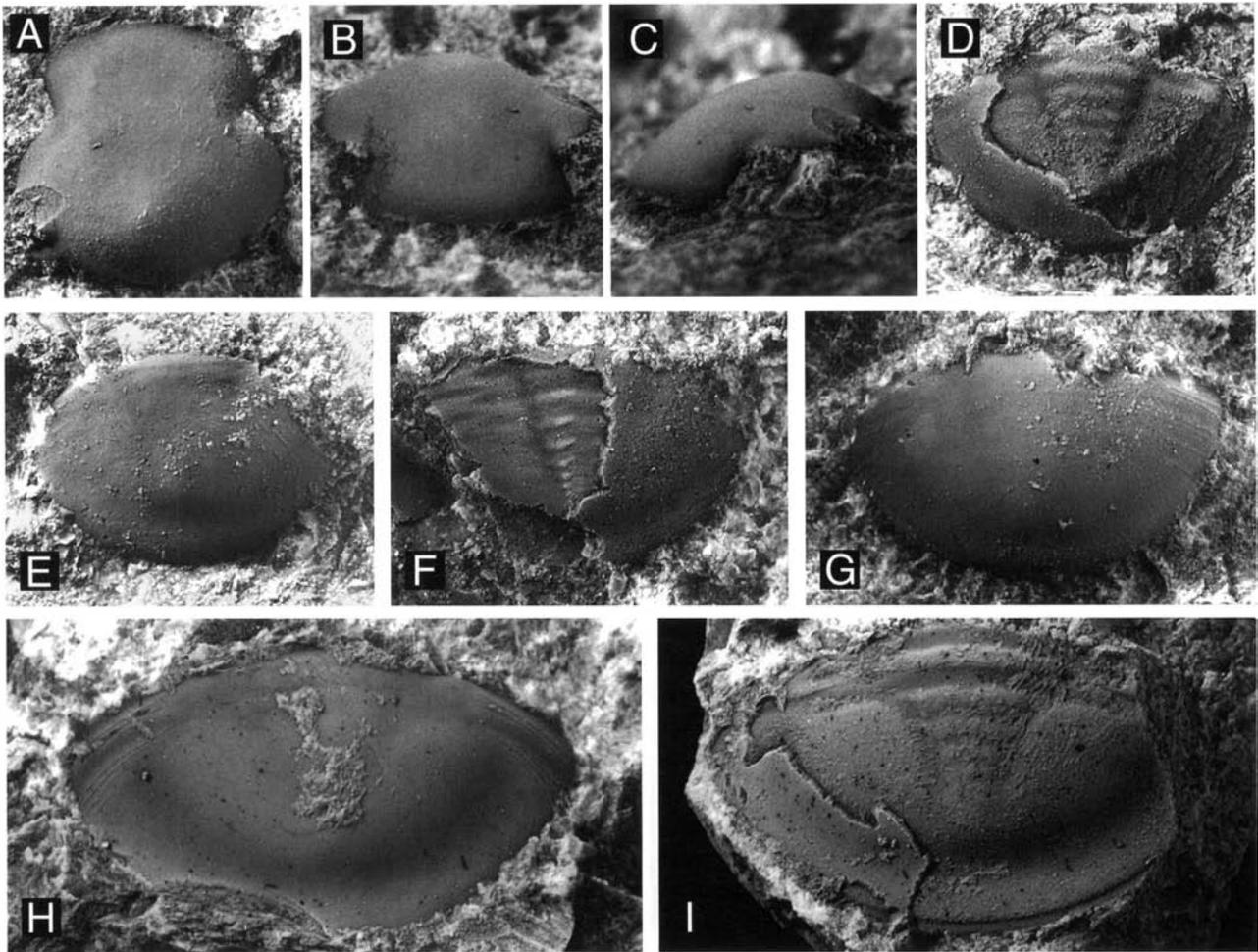


Fig. 161. Juveniles of *N. armadillo* or *N. latifrons* n.sp. □A–C. Juvenile cranidium showing comparatively strong sagittal curvature, dorsal, frontal and side views, $\times 15$. MGUH 22.680 (F 117), bed 19, Fågelsång. □D. Partly exfoliated transitory pygidium, stage D, showing axis, $\times 14$. MGUH 22.681 (F 154b), bed 19, Fågelsång. □E. Transitory pygidium, stage D, $\times 12$. MGUH 22.682 (K 1267), bed 12, Killeröd site b. □F. Partly exfoliated transitory pygidium, stage C, showing axis and pleural fields, $\times 12$. MGUH 22.683 (F 189), bed 20, Fågelsång. □G. Transitory pygidium, stage D, $\times 12$. MGUH 22.684 (F 143), bed 19, Fågelsång. □H. Transitory pygidium, stage E, showing outline of fixed segment, $\times 9$. MGUH 22.685 (S 1750), bed +13, Skelbro. □I. Internal mould of transitory pygidium, stage E, showing axis, $\times 9$. MGUH 22.686 (S 1530), bed +13, Skelbro.

Table 15. Undifferentiated juvenile cranidia of *Nileus armadillo* and *N. latifrons* n.sp. Ranges for variation, expressed as ratios of cranidial length.

Size (mm)	Maximum width of cranidium			Glabella width			Palpebral lobe length (exsag.)			Glabellar tubercle, distance to post. margin		
	Variation	Mean	N	Variation	Mean	N	Variation	Mean	N	Variation	Mean	N
1.9 mm	–	–	–	–	0.58	1	–	0.39	1	–	0.29	1
2.4–2.9 mm	1.04–1.07	1.06	2	0.69–0.75	0.72	2	0.42–0.45	0.43	2	–	0.29	1
3.2–3.9 mm	1.13–1.21	1.15	3	0.74–0.79	0.76	3	0.41–0.44	0.43	3	0.29–0.34	0.32	3

Table 16. Undifferentiated juvenile pygidia of *Nileus armadillo* and *N. latifrons* n.sp. Ranges for variation, expressed as ratios.

Size (mm)	Pygidial L:W ratio			Axial width : pygidial width			Axial length : pygidial length			Border length (sag.) : pygidial length		
	Variation	Mean	N	Variation	Mean	N	Variation	Mean	N	Variation	Mean	N
1.5 [Stage A]	–	0.68	1	–	0.31	1	–	–	0	–	0.20	1
2.1–2.4 [Stage C]	0.63–0.68	0.65	2	0.35–0.39	0.37	2	–	0.71	2	0.17–0.19	0.18	2
2.3–3.1 [Stage D]	0.62–0.66	0.64	6	0.39–0.40	0.39	4	0.61–0.65	0.63	3	0.21–0.24	0.23	5
3.6–4.5 [Stage E]	0.52–0.57	0.55	4	0.35–0.37	0.36	4	0.53–0.59	0.56	4	0.15–0.22	0.19	4

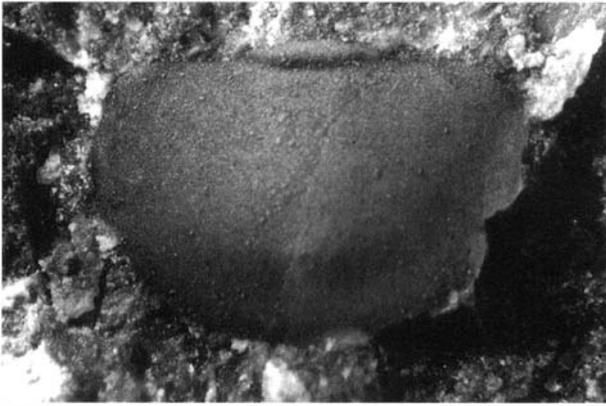


Fig. 162. Juvenile of *N. armadillo* or *N. latifrons* n.sp. Transitory pygidium, stage A, $\times 30$. MGUH 22.687 (K 369b), bed +35, Killeröd.

Description. – A tiny, somewhat damaged cranidium, 1.9 mm long, is very elongate (Table 15). Sagittal convexity moderate, but quite strong posterior to glabellar tubercle. Compared to the next-smallest cranidium, 2.4 mm long, the discussed cranidium is less convex (sag.) except posterior to tubercle, and glabella is distinctly narrower. The specimen is not suited for illustration.

Remaining cranidia, 2.4–3.9 mm long, have a fairly pronounced sagittal convexity. Compared to adult specimens, they are more elongate and the sagittal curvature is slightly less strong in front of the glabellar tubercle, whereas the curvature is markedly stronger posterior to the tubercle, which gives the central part of glabella a peculiar ‘humpbacked’ shape with highest point at glabellar tubercle (Fig. 161A–C). Axial furrows effaced, or nearly so, on testaceous specimens; palpebral lobes narrower (tr.) than in adults, and glabellar tubercle situated far back. Posterior fixigena strongly flexed downwards. No specimen show a mesial boss or a flattened rim along anterior margin. Test surface smooth.

The available pygidia are all transitory pygidia. One tiny pygidium, 1.5 mm long, with smooth test surface does not show any indication of unreleased segments; it represents stage A (Fig. 162). Axis not outlined, except for the distinct articulating half-ring, which projects in front of the straight pygidial margin. Sagittal convexity comparatively strong, with a narrow and only slightly less sloping border running the whole way; postaxial border width 0.20 of the pygidial length. Compared to specimen S 63b (see pp. 241–243) the sagittal convexity is slightly less strong and the border is better defined. The straight anterior margin appears to end laterally in gentle elevations, which probably correspond to articulating sockets; anterolateral corners of pygidium obliquely truncate.

Sparse material of transitory pygidia, representing stages C–E (Table 16), match the description on pp. 243–245, except that the C and E stage specimens generally show a narrower border, and the D stage pygidia are proportionally broader.

Remarks. – The material is from beds containing both *Nileus armadillo* and *N. latifrons* n.sp., and cannot with certainty be assigned to either of these species. It is, however, suspected that their late meraspide stages are of unequal size, but more material is needed to verify this impression. The smallest holaspide pygidia can be assigned to the respective species.

The peculiar ‘humpbacked’ juvenile cranidia are unusual and a similar development is not seen in any other of the species described here. The material probably represents *N. armadillo*.

The D stage is represented by eight pygidia, 2.3–3.1 mm long, plus a specimen 4.4 mm long (excluded from calculations in Table 16). The latter specimen is interpreted as an E-stage representative in which the anterior segment failed to detach during moulting.

Nileus exarmatus Tjernvik, 1956

Figs. 163–167

Synonymy. – □1904 *Nileus Armadillo* Dalm. [*partim*] – Schmidt, Pl. 8:16 (illustrations of pygidium) [cephalon of the same specimen is figured by Balashova 1976]. □v 1936 *Nileus armadillo* Dalm. [*partim*] – C. Poulsen, pp. 48, 50 (listed, occurrence discussed). □v 1952 *Nileus armadillo* (Dalman) [*partim*] – Skjeseth, p. 170; Pl. 2:8, 11 (occurrence, illustrations of cephalon, pygidium). □1956 *Nileus exarmatus* n.sp. – Tjernvik, pp. 209–210; Textfig. 33B; Pl. 2:16–21 (description, occurrence, illustrations of complete specimen, cranidium, hypostome, pygidium and juvenile cephalon). □v 1965 *Nileus exarmatus* Tjernvik, 1956 – V. Poulsen, pp. 74–76; Pls. 3:7, 8–10; 4:1 (description, occurrence, illustrations of complete specimen and hypostome).

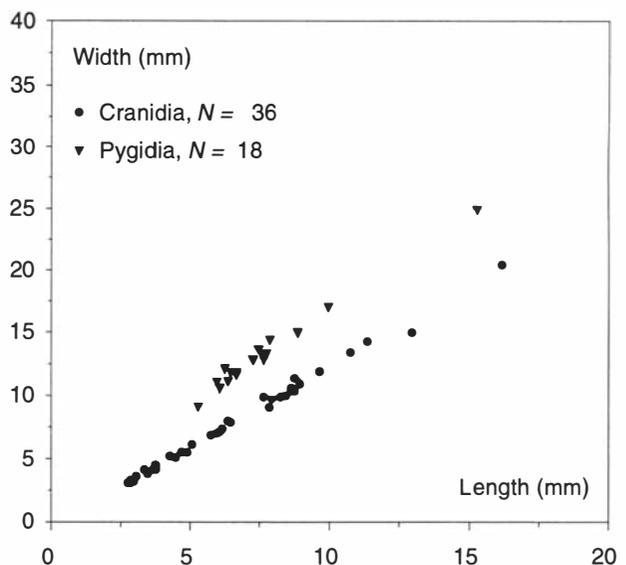


Fig. 163. Cranidia and pygidia of *Nileus exarmatus*. Maximum width plotted against sagittal length.

□1972 *Nileus* sp. indet. – Schrank, Pl. 3:1 [orig. Tjernvik 1956, Pl. 2:20] (illustrations of juvenile cephalon). □1972 *Nileus exarmatus exarmatus* Tjernvik [*partim*] – Schrank, pp. 352, 358–361; Pls. 2:1–10; 3:5, 7, 10, 11, 14; non Pl. 3:3, 4, 6, 8, 9 [= *N. orbiculatoides*]; Textfig. p. 353 (description, occurrence, phylogenetic relationships, illustrations of enrolled specimen, cranidia, pygidia, hypostomes). □1972 *Nileus* sp. aff. *limbatus* et *exarmatus* [*partim*] – Schrank, p. 364; Pls. 3:2; 4:6; 5:7, ?8, 9 (remarks on diagnostic characters, illustrations of cranidia, librigena, pygidia). □1973 *Nileus exarmatus* Tjernvik, 1956 – Modliński, p. 51, Pl. 3:4 (short description, occurrence, illustration of pygidium). □1976 *Nileus exarmatus* Tjernvik – Balashova, p. 139; Pl. 40:8 (description, illustration of cephalon). □1980 *Nileus exarmatus* Tjernvik – Tjernvik & Johansson, pp. 178–179, 187–188, 191–192, 202 (occurrence).

Holotype. – Complete specimen PUN-155, figured by Tjernvik (1956, Pl. 2:18–19).

Material. – Six complete specimens, 3 cephalata (all with a few contiguous thoracic segments), 24 cranidia, 17 juvenile cranidia and 19 pygidia.

List of material. – □ Complete specimens S 1661 (t) [MGUH 22.694], S 1770 (t) [MGUH 22.690], MGUH 9432 (im), GM 1984.1806 (t), K 17 (t) IK 21 (im) [MGUH 22.689]. □ Cephalata GM 1874.68 (pim) [MGUH 22.688], A 620 (t) [MGUH 22.698], A 659 (t). □ Cranidia S 7 (im), S 23 (im) [MGUH 22.695], S 26a (im) [MGUH 22.696], S 58 (im), S 61 (im), S 63c (im), S 89 (im), S 98c (im), S 109 (im), S 123b (im), S 161 (im), S 272a (c), S 273 (im), S 274 (im), S 295c (t), S 300 (t), S 306b (im) [MGUH 22.691], S 326 (im) [MGUH 22.697], S 373b (im), LU 20a (im), K 448 (pim), A 583 (im), A 649 (pim), A 702? (t). □ Juvenile cranidia [less than 5.5 mm long] S 26b (pim), S 40a (pim), S 46b (t), S 80a (im) [MGUH 22.692], S 80c (t), S 92 (im), S 157d (im), S 176 (pim), S 184 (t), S 188b (im), S 205a (im), S 207b (t), S 215b (pim), S 295d (t) [MGUH 22.693], S 324 (im), S 340 (im), S 373a (im). □ Pygidia S 4a (pim), S 4b (im) (partly double), S 48b (im), S 56a (t) [MGUH 22.700], S 70d (pim), S 106a (t), S 110 (em), S 157a (t), S 168c (pim), S 172a (t), S 172b (pim), S 173 (t), S 188a (im) [MGUH 22.701], S 189a (t) [MGUH 22.699], S 216c (im), S 237? (im) (lost, prep.), S 1679 (im), A 635 (im), A 685? (c).

Occurrence. – *N. exarmatus* is abundant in beds –21 and –20 at Skelbro, representing the basal part of the *M. polyphemus* Zone. A few specimens were found in beds K and M at Gårdlösa-1, belonging to the *M. simon* Zone. Cranidium LU 20a originates from an erratic boulder at Andrarum, but the sample is unmistakably Komstad Limestone (level unknown).

A few specimens have been found at Slemmestad in beds M-1 (*M. polyphemus* Zone) and M-2 (*M. simon* Zone). A damaged cranidium (A 702) and a corroded pygidium (A 685) from bed M-4 at Slemmestad (i.e. still *M. simon* Zone) are tentatively assigned to *N. exarmatus*.

Nileus exarmatus ranges in central Sweden from the *M. aff. estonica* Zone and into the *M. simon* Zone (Tjernvik 1980; see also Fig. 144), and the occurrence in the Komstad Limestone and the Huk Formation at Slemmestad thus fits the known upper range of the species. This is the first report of *N. exarmatus* from the Huk Formation at Slemmestad, but

some of the material assigned to *N. armadillo* by Skjeseth (1952, p. 170, Pl. 2:8, 11) from the Herramb Member at Ringsaker (base of Stein Limestone) also belongs to *N. exarmatus*. The species possibly occurs in Poland as well, see discussion below.

Diagnosis. – Small, relatively elongate species. Cephalon semicircular to slightly parabolic; glabella pronouncedly subrectangular; glabellar front rounded, or the anterior branches of facial suture meet at a very blunt angle; sagittal convexity rather low. Glabellar tubercle situated relatively far back. Lateral cephalic border wide and continues almost to genal angle. Pygidium with concave, narrow border of subequal width all the way; axis has a faint positive relief also on testaceous specimens. Pygidial test surface shows a few terrace lines along anterior margin and close to outer posterior margin, but is otherwise smooth. [Emended from Tjernvik 1956 and Schrank 1972.]

Description. – The material agrees with the descriptions published by Tjernvik (1956) and V. Poulsen (1965), and only a few complementary observations are added. In order to facilitate a comparison to the other Nileids described, ranges for variation of selected morphological features are shown in Fig. 166A–D and listed in Tables 17–18.

Small for a *Nileus*, largest cranidium about 13 mm long, largest pygidium 10.0 mm long. The rather poorly preserved complete specimen GM 1984.1906, 47 mm long, almost certainly belongs to *N. exarmatus*, and is the largest specimen recorded so far: the cranidium is 16.2 mm long and the pygidium is 15.3 mm long. The ratios between cephalon, thorax and pygidium in complete specimens are about 28:42:30 ($N = 2$, dorsal projection). It is uncommon that the cephalon is shorter than the pygidium, and it is the more surprising as the cephalon of *N. exarmatus* is rather elongate. However, in standard maximum measurements (see introductory chapter) the pygidial length averages 0.94 of the cephalic length, and the pygidial width averages 0.86 of the cephalic width in the two complete specimens (adults). Cephalic L:W ratio varies between 0.55 and 0.60 (mean 0.58;

Fig. 164. *Nileus exarmatus* Tjernvik. □A–B. Internal mould of complete specimen, side view showing doublure, dorsal view showing axial morphology, ×4. Previously figured by V. Poulsen (1965, Pl. 3:8–10). MGUH 9432, Skelbro beds, Skelbro. □C. Internal mould of cephalon, stereo-pair, ×2.5. MGUH 22.688 (GM 1874.68), Vasegård, Bornholm. □D–E. Internal mould of juvenile complete specimen, dorsal views of cephalon and pygidium, ×9. MGUH 22.689 (IK 21), Skelbro beds, Skelbro. □F–I. Large, enrolled specimen, dorsal, frontal and sides views, ×3. MGUH 22.690 (S 1770), Skelbro beds, Skelbro. □J–K. Internal mould of cranidium showing paired glabellar muscle insertion sites, side and dorsal views, ×6. MGUH 22.691 (S 306b), bed –20, Skelbro. □L. Internal mould of small cranidium, ×12. MGUH 22.692 (S 80a), bed –21, Skelbro. □M. Non-whitened juvenile cranidium with transparent cuticle showing dark coloured glabellar muscle insertion sites, ×12, MGUH 22.693 (S 295d), bed –20, Skelbro. □N. Small enrolled specimen, side view of cephalon, ×6. See also Fig. 165A–B. MGUH 22.694 (S 1661), bed –21, Skelbro.

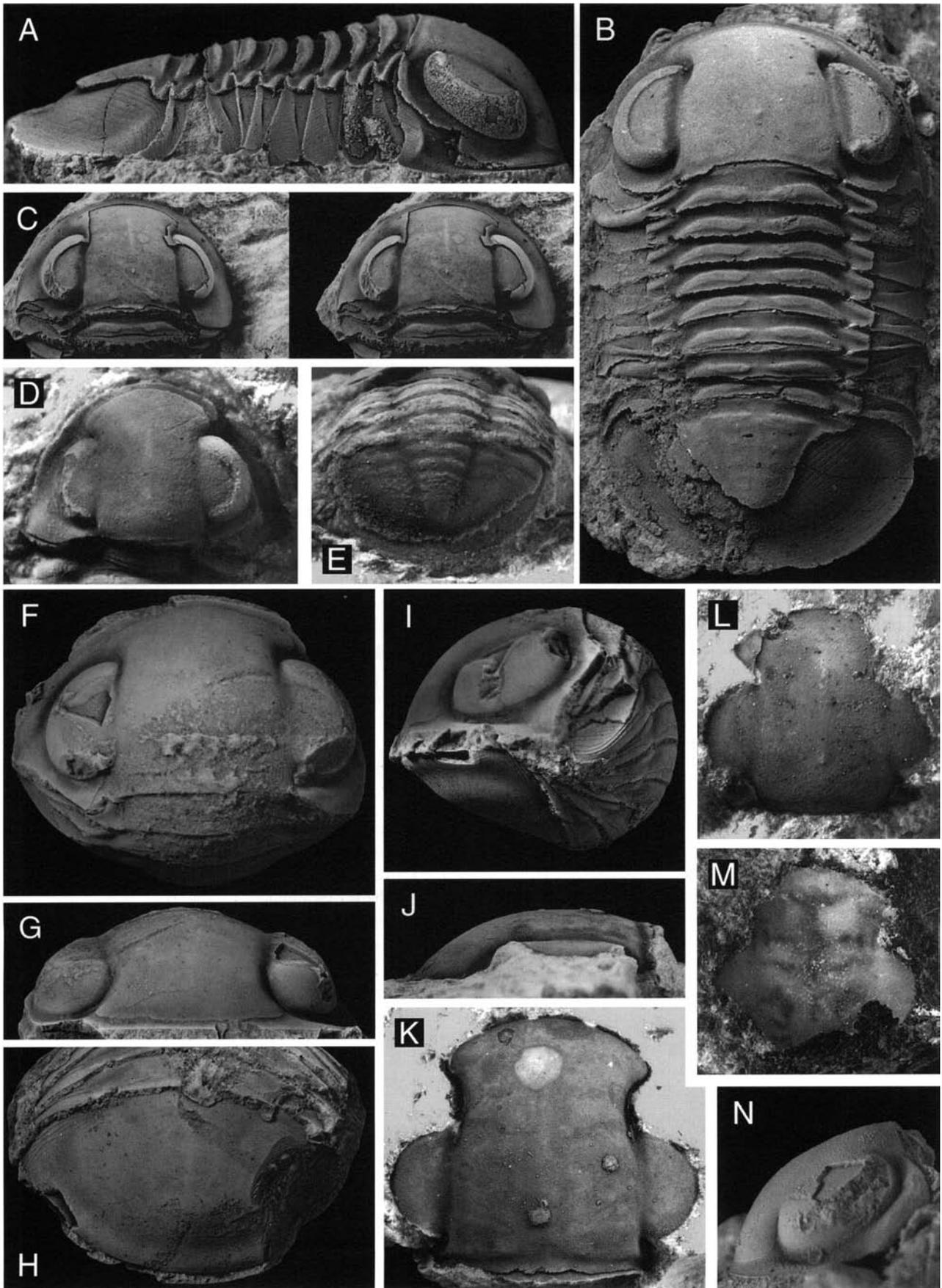


Table 17. *Nileus exarmatus*. Ranges for variation of cranidia, expressed as ratios of cranial length.

Size (mm)	Maximum width of cranidium			Glabella width			Palpebral lobe length (exsag.)			Glabellar tubercle, distance to post. margin		
	Range	Mean	N	Range	Mean	N	Range	Mean	N	Range	Mean	N
2.6–5.1	1.03–1.19	1.11	15	0.65–0.77	0.72	15	0.41–0.47	0.44	13	0.27–0.33	0.30	10
>6	1.14–1.28	1.20	21	0.69–0.83	0.77	24	0.38–0.47	0.43	24	0.27–0.33	0.30	22

Table 18. *Nileus exarmatus*. Ranges for variation of pygidia, expressed as ratios.

Size (mm)	Pygidial L:W ratio			Axial width : pygidial width			Axial length : pygidial length			Border length (sag.) : pygidial length		
	Range	Mean	N	Range	Mean	N	Range	Mean	N	Range	Mean	N
>6 [Hol.]	0.53–0.62	0.57	15	0.35–0.41	0.38	11	0.55–0.61	0.58	12	0.15–0.22	0.20	12

$N = 4$). Lateral border of cephalon wide, and it almost reaches genal angle, even though it tapers from the middle of eye (Fig. 165F). Articulating sockets in posterior margin of cephalon comparatively deeply incised. Length (exsag.) of posterior fixigenae averages 0.13 ($N = 19$) of the cranial length. Posterior branch of facial suture gently sigmoidal. Only the posterior part of the cephalic doublure is visible, showing, however, that the doublure is slightly less concave at eye level, compared to *N. armadillo*, the posterolateral outer part near genal angle, which is downflexed along margin, is wider (tr.) than in *N. armadillo*, and the posterior flattened, 'pleura-shaped' portion is separated only distally by a doublural crest, which becomes effaced adaxially.

Thorax parallel-sided until the third segment and thence tapers slightly rearwards; posterior segment 0.94 ($N = 1$) times as wide (tr.) as the anterior segment. Axis occupies 0.49 (tr.) ($N = 1$) of the thoracic width on the first segment, then expands slightly to attain a maximum width on the third segment, here occupying 0.51 ($N = 1$) of the thoracic width (tr.), to taper backwards; it occupies 0.43 ($N = 1$) of the thoracic width on the posterior segment. Axial width on the posterior segment corresponds to 0.83 ($N = 1$) of the axial width on the first thoracic segment. Pleural furrows comparatively well-impressed, and clearly visible also on testaceous material. Thoracic doublure wide, stretching below ca. 0.8 of the pleural length (tr.); it is provided with a low crest running obliquely inwards-backwards from one third up the anterior margin. Numerous terrace lines present behind the crest, running transversely, slightly backwards-outwards, whereas very short lines, typically about seven, are situated adaxially, immediately in front of and adjacent to the crest. Only the posterior segment shows a slightly different morphology.

Pygidial doublure strongly concave, and with anterior incisions to pleural furrows; it is covered with about 19 coarse terrace lines.

Juveniles. –Cranidia 2.6–5.1 mm long are by comparison to larger cranidia significantly more elongate, resulting in relatively narrow glabellas, low cranial L:W ratios etc. (Fig. 166, Table 17). Moreover, the anterior margin is also more rounded, and the sagittal convexity is less strong in the smallest juveniles, compared to adults. Relative length and position of palpebral lobes as well as position of mesial glabellar tubercle as in larger cranidia. Librigenae of juvenile cephalon carry short spines according to Tjernvik (1956, p. 210; Pl. 2:20; see also Schrank 1972, Pl. 3:1); the smallest cephalon found in the Komstad Limestone is 6.2 mm long, and shows the adult condition with rounded genal angles.

All 'exarmatus-like' small pygidia are described collectively below as 'Juvenile pygidia of *Nileus exarmatus*, *N. orbiculatooides*, and *N. depressus schranki* n.subsp.'.

Affinities. –*Nileus exarmatus* occurs associated with *N. orbiculatooides*, *N. depressus schranki* n.subsp. and *Nileus* sp. B in the Komstad Limestone. It is distinguished from these species by the subrectangular, narrow glabella (Fig. 167B), by the distinctly curved anterior cranial margin, by the lower cephalic convexity (sag.), by the rearwards position of the glabellar tubercle (Fig. 167D), and by the limited number of terrace lines on the pygidium. Furthermore, *N. orbiculatooides* shows a mesial boss on the anterior cranial margin and almost lack the sagittal glabellar keel present on internal moulds of *N. exarmatus*, and the cranidium of *N. depressus schranki* n.subsp. is characterized by a finely pitted test surface.

The relationship to the somewhat similar *N. limbatus* is discussed by Tjernvik (1956, p. 210). *N. limbatus* is presumably the ancestor of *N. exarmatus* (cf. Schrank 1972, pp. 352–353, see also introductory discussion of *Nileus* above).

Remarks. –*Nileus exarmatus* is comparatively small, which causes identification problems for pygidia, as they closely resemble juveniles of several nileid species.

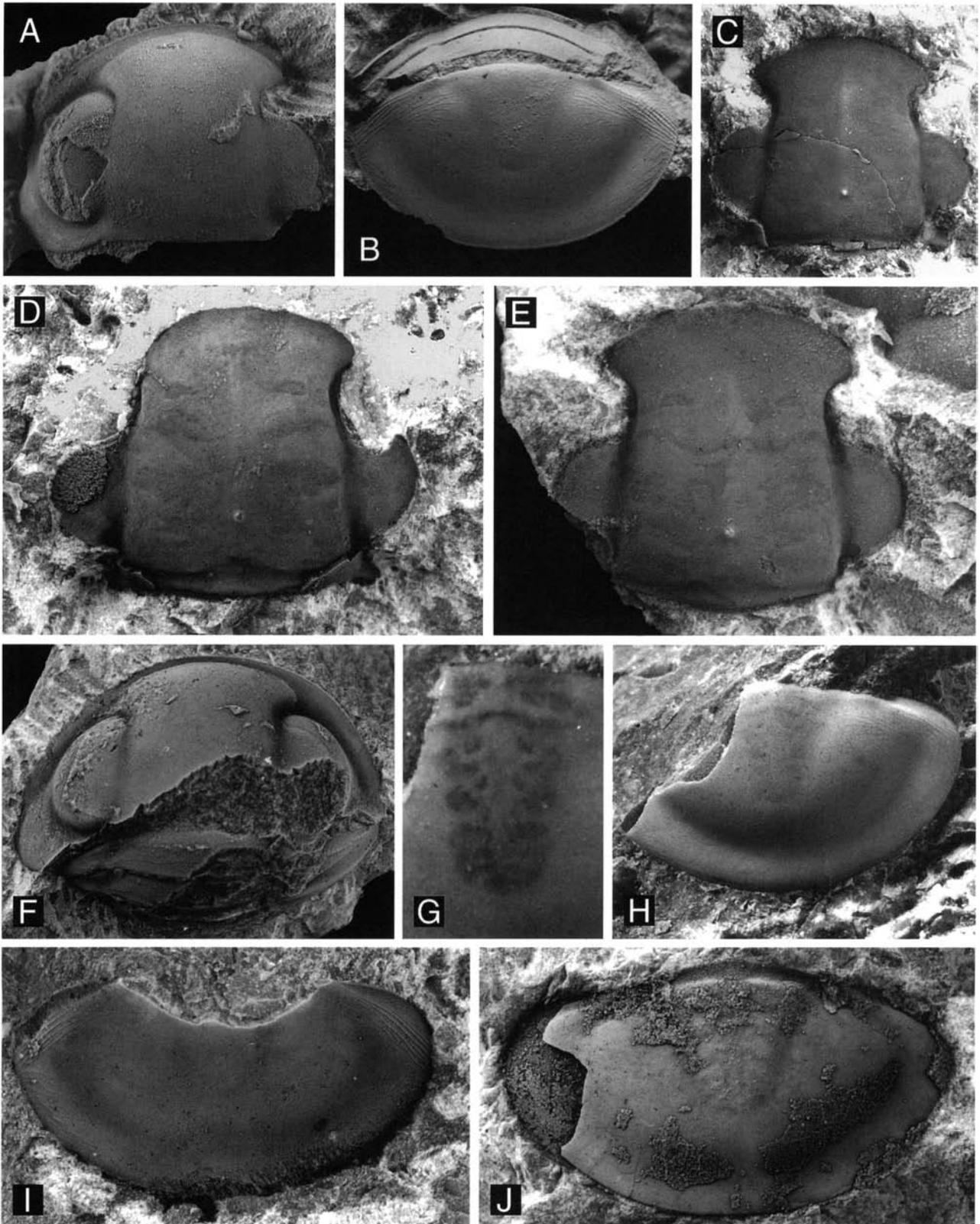


Fig. 165. *Nilus exarmatus* Tjernvik. □A–B. Small enrolled specimen, dorsal views of cephalon and pygidium, $\times 6$. Side view of cephalon shown on Fig. 164N. MGUH 22.694 (S 1661), bed –21, Skelbro. □C. Internal mould of cranidium showing faint traces of paired glabellar muscle impressions, $\times 6$. MGUH 22.695 (S 23), bed –21, Skelbro. □D. Internal mould of cranidium showing paired muscle impressions on glabella, $\times 6$. MGUH 22.696 (S 26a), bed –21, Skelbro. □E. Internal mould of small cranidium, showing paired muscle impressions on glabella, $\times 9$. MGUH 22.697 (S 326), bed –20, Skelbro. □F. Damaged cephalon, $\times 3$. MGUH 22.698 (A 620), bed M-2, Slemmestad. □G–H. Slightly damaged, but well-preserved pygidium with transparent cuticle showing coloured muscle insertion sites in axial area, and ‘*exarmatus*-type’ terrace-line pattern, $\times 8$; G non-whitened close-up of axis, $\times 16$. MGUH 22.699 (S 189), bed –21, Skelbro. □I. Slightly damaged, but well-preserved pygidium showing ‘*exarmatus*-type’ terrace-line pattern, $\times 6$. MGUH 22.700 (S 56a), bed –21, Skelbro. □J. Internal mould of pygidium showing axis, $\times 6$. MGUH 22.701 (S 188a), bed –21, Skelbro.

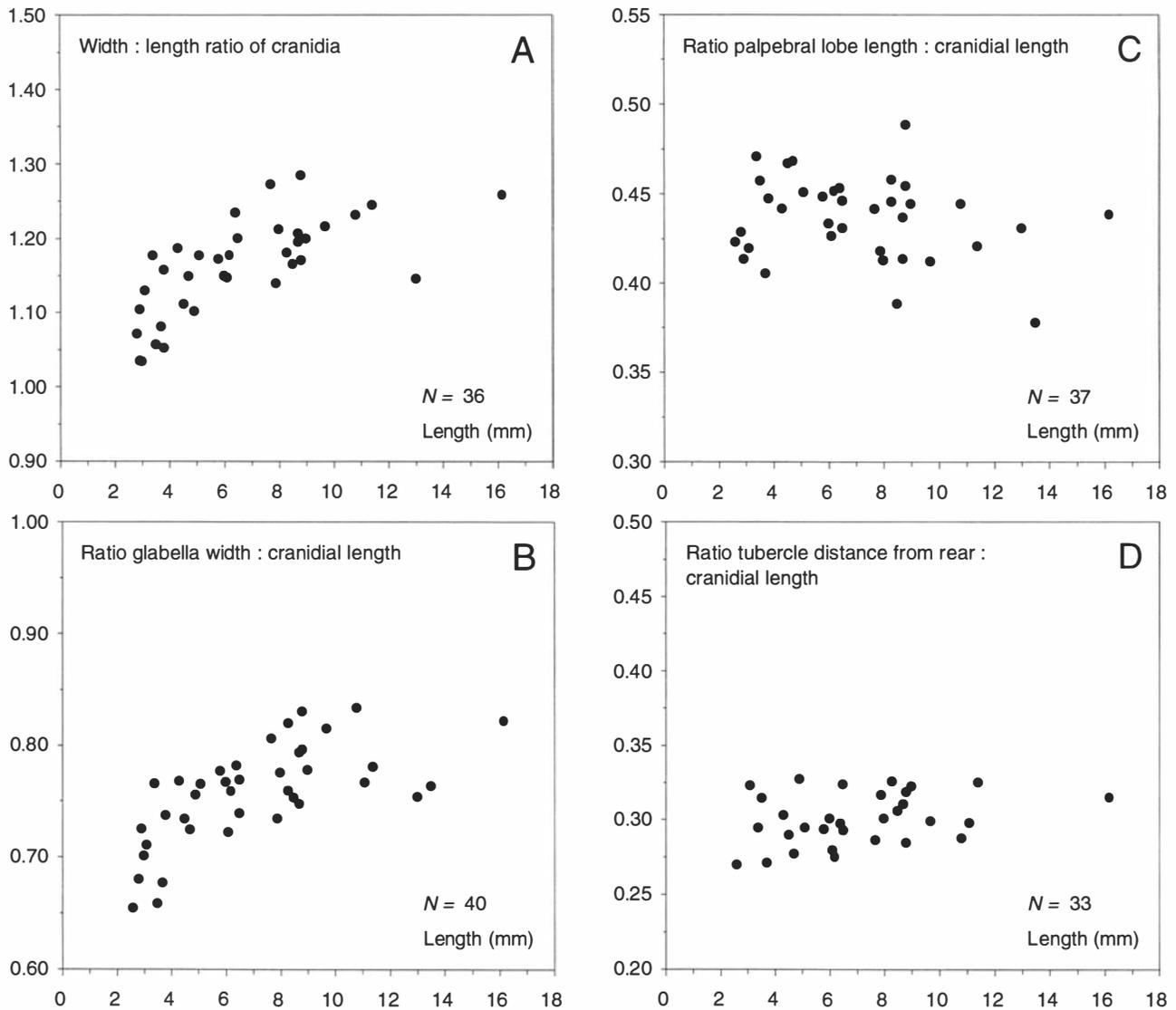


Fig. 166. Crania of *Nileus exarmatus*. □A. Width:length ratio (measured across palpebral lobes) plotted against sagittal length. □B. Ratio between glabella width (measured between posterior corners of palpebral lobes) and cranial length plotted against cranial length. □C. Ratio between palpebral lobe length (exsag.) and cranial length plotted against cranial length. □D. Relative position of glabellar tubercle plotted against cranial length.

The transitory pygidium assigned to *N. exarmatus* by V. Poulsen (1965, Pl. 3:7) cannot be confidently identified. It is here included in 'Juvenile pygidia of *Nileus exarmatus*, *N. sp. B ...*' etc. The report of *N. exarmatus* from the *M. simon* Zone of the Finngrundet core (Tjernvik 1980, p. 191, Textfigs. 3–4) is based on two juvenile pygidia, which cannot be identified at the species level (see remarks on 'Juvenile pygidia of *Nileus exarmatus*, *N. sp. B ...*' etc. herein).

V. Poulsen (1965, pp. 58, 76) emphasized the occurrence of fine terrace lines on the pygidia of *N. exarmatus* from the *M. polyphemus* Zone. However, the pygidial test is smooth in *N. exarmatus*, and the separate pygidium de-

scribed by V. Poulsen obviously represents *N. depressus schranki* n.subsp.

According to Schrank (1972, pp. 358–361) the cranium of *N. exarmatus* is characterized by a small anterior median boss as in *N. orbiculatoides*. Tjernvik (1956) originally described the anterior margin of glabella as smooth, or anterior branches of the facial suture may join at a very blunt angle. None of the available crania of *N. exarmatus* possess an anterior boss, and all of the cephalia and crania, assigned to *N. exarmatus* by Schrank and which have an anterior boss, rather belong to *N. orbiculatoides*. The crania and cephalia of *N. exarmatus* appear to have been identified as *Nileus sp.*

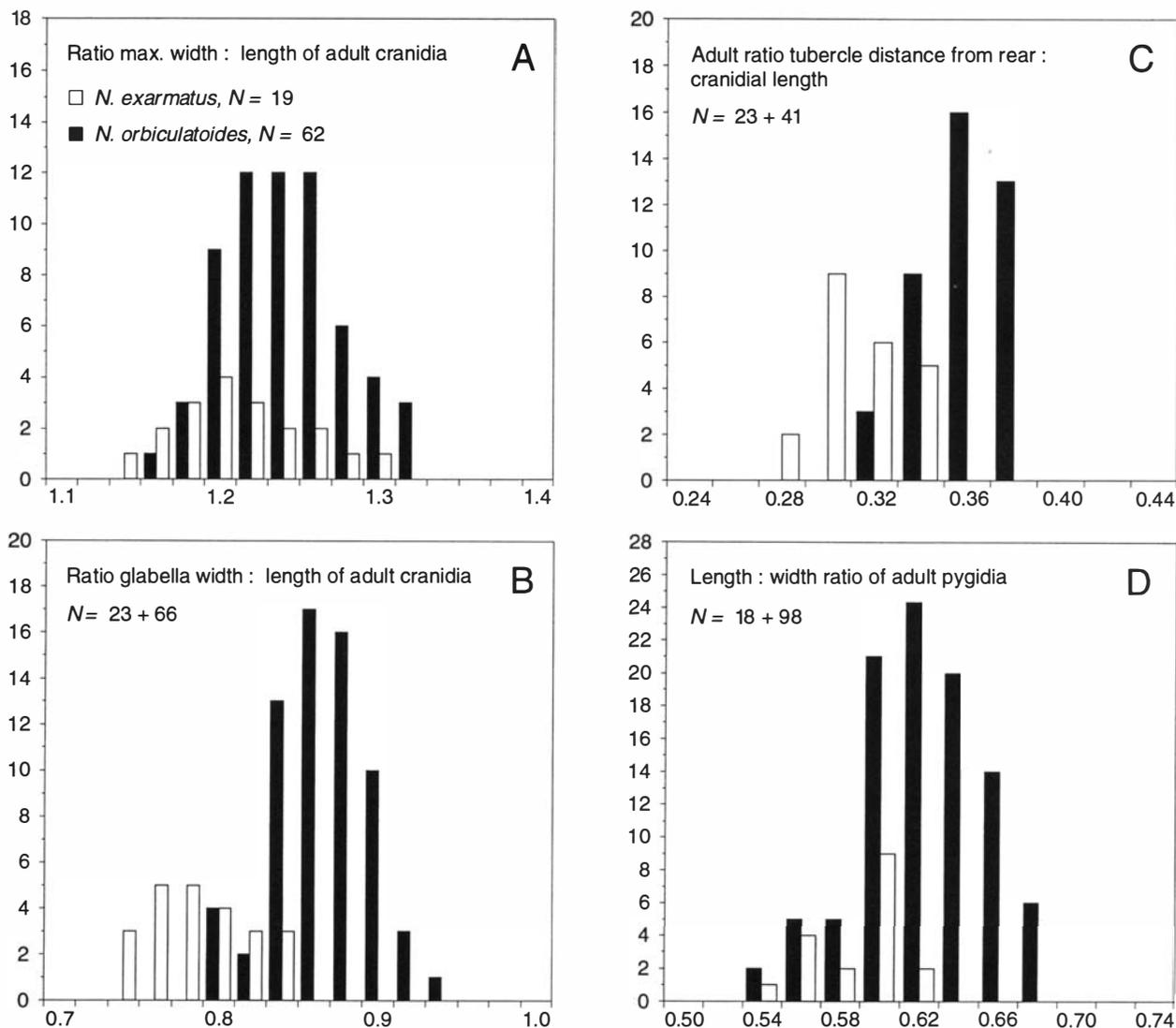


Fig. 167. *Nileus exarmatus* versus *N. orbiculatooides*, adult specimens only (cranidia >ca. 6 mm long and pygidia >5.5 mm long). □A. Comparison of adult width:length ratios of crania (measured across palpebral lobes). □B. Comparison of adult ratios between glabella width (measured between hind corners of palpebral lobes) and cranial length. □C. Comparison of adult ratios between the distance from posterior cranial margin to glabellar tubercle against cranial length. □D. Comparison of adult length:width ratios of pygidia.

aff. *limbatus* et *exarmatus* by Schrank (cf. 1972, p. 364). Cranidia of *N. depressus* are possibly also included in this group (Schrank 1972, ?Pl. 3:2, 12). Some of the pygidia grouped as *Nileus* sp. aff. *limbatus* et *exarmatus* probably belong to *N. exarmatus* (cf. Schrank 1972, Pl. 5:7; the specimen figured on Pl. 5:8, however, shows a very broad border and may represent *Nileus limbatus*).

A complete specimen from Sweden, assigned to *N. armadillo* by Schmidt (1904, Pl. 8:16), was identified as *N. exarmatus* by Balashova (1976, p. 139), who also figured the cephalon (Balashova 1976, Pl. 40:8). The specimen is rather large, compared to the material described by Tjernvik

(1956), but otherwise in accordance with his description. Measured from the figure (Balashova 1976, Pl. 40:8), the cephalon appears to be about 14 mm long, and thus corresponds to the largest specimens studied here.

Bednarczyk (1968, Pl. 1:6) figured a pygidial doublure, assigned to *N. exarmatus*, from the Zawada 1 well of Poland. The identification is questionable, as the pygidial L:W ratio appears low, and the terrace lines are not turned outwards close to the anterior margin. Another pygidium figured by Modliński (1973, Pl. 3:4), looks, however, like *N. exarmatus*, so presumably the species actually does occur in the Polish area.

Nileus orbiculatooides Schrank, 1972

Figs. 168–174

Synonymy. – □1884 *Nileus Armadillo* Dalm. [partim] – Törnquist, pp. 55–56 (occurrence). □v 1936 *Nileus armadillo* Dalm. [partim] – C. Poulsen, p. 48, 50 (listed). □v 1972 *Nileus exarmatus orbiculatooides* n.subsp. – Schrank, pp. 358–361; Textfig. p. 353; Pls. 4:1, ?2, 3–5; 5:1, ?2 (description, occurrence, illustrations of cephalon, cranidium, pygidia, hypostomes). □ 1972 *Nileus exarmatus exarmatus* Tjernvik [partim] – Schrank, pp. 358–361; Pl. 3:3–6, 8–9 (description of cranidium, illustrations of cranidia). □?1976 *Nileus armadillo* Dalman [partim] – Balashova, Pl. 40:2 (illustration of pygidium). □1980 *Nileus exarmatus orbiculatooides* n.sp. or subsp. – Tjernvik & Johansson, pp. 188, 191, 192, 203 (summary of diagnostic features, occurrence). □1980 *Nileus orbiculatooides* – Tjernvik & Johansson, pp. 191, 192, 203 (occurrence).

Holotype. – Pygidium T 791.1, figured by Schrank (1972, Pl. 4:1).

Material. – Twelve complete specimens, 12 cephalata, 102 cranidia, 121 pygidia and 17 juvenile pygidia. Additional juvenile pygidia are described elsewhere (see 'Juvenile pygidia of *Nileus exarmatus*, *N. orbiculatooides* and *N. depressus schranki*?').

List of material. – □ Complete specimens S 788a (t), S 942b (t), S 957 (c), K 8 (t) [MGUH 22.707], K 20 (t), K 22 (t), K 479 (t), K 642? (c), K 653 (c), K 690a (t), GM 1875.1492 (c), LU 156b (c). □ Cephalata S 523 (t), S 761 (pim) with thoracic segments [MGUH 22.705], S 793 (t), S 864c (t), S 989 (pim) with thoracic segments, S 1006 (t), S 1025 (t) with thoracic segments, S 1033 (t), K 560a (t), K 606a (t) with thoracic segments, K 737 (pim), LU 135-1a (t) [LO 7120]. □ Cranidia S 53 (im), S 60a (im), S 256a (im) [MGUH 22.702], S 258 (im), S 284b (im), S 288c? (im) [MGUH 22.709], S 595 (c), S 632 (pim), S 677a (im), S 808 (t), S 813 (t), S 834a (im), S 857? (pim), S 858a (t), S 858b (im), S 860d? (t), S 864b (t), S 873b? (t), S 876 (t), S 880 (t), S 884 (t), S 892 (t), S 940b (t), S 942a (t), S 965 (pim), S 968 (t), S 996 (t), S 1004 (t), S 1036 (t) [MGUH 22.704], S 1043 (im), S 1080 (t), S 1674 (im), K 25 (im), K 45 (t), K 96 (t), K 107 (t) [MGUH 22.710], K 120a (t) [MGUH 22.703], K 120b? (t), K 129 (t), K 151 (t), K 156 (t), K 184 (c), K 197 (c), K 378 (t), K 387 (c), K 419 (t) [MGUH 22.712], K 436 (t), K 441 (c), K 450a? (pim), K 484b (im), K 490 (t), K 493? (t), K 497c? (t), K 498a (t) [MGUH 22.711], K 498b (im), K 498d (t), K 509b (t), K 516 (pim), K 537a (t), K 550 (c), K 556? (pim), K 568? (im), K 570 (t), K 578 (t), K 587b (im), K 604 (t), K 608 (t), K 609b (t), K 609c (im), K 611 (pim) [MGUH 22.708], K 613 (t), K 617a? (t), K 617b (t), K 629 (c), K 632 (im), K 636 (pim), K 638 (c), K 641 (c), K 648a (pim), K 648b (im), K 662 (c), K 663 (im), K 664b? (pim), K 672b (c), K 672d? (c), K 693 (pim), K 707 (im), K 713 (c), K 751? (pim), K 762 (c), K 775 (c) DGU 1-7 (t) [MGUH 22.706], LU 15a (pim), LU 18b (im), LU 22b? (im), LU 24a (im) [LO 7079], LU 24b (im) [LO 7080], LU 24d? (t), LU 24e (t), LU 24f (im), LU 24g? (pim), LU 135-1b (t) [LO 7121]. □ Pygidia S 8? (pim), S 130 (t), S 162b? (t), S 256b (t), S 269 (im) [MGUH 22.723], S 271 (pim), S 272b (im), S 284a? (im), S 301c? (im), S 323 (im), S 345 (im) [MGUH 22.722], S 452a (t), S 454b (im), S 454c? (im), S 467 (t), S 496 (pim), S 501a (im), S 515 (t) [MGUH 22.724], S 567 (pim) [MGUH 22.721], S 701 (t), S 722 (t), S 819 (t), S 823 (t), S 826? (im), S 843 (pim), S 847 (t), S 854 (t), S 859 (t), S 860a (em), S 860c? (em), S 864a (t) [MGUH 22.719], S 866 (t), S 867 (t), S 873a (t), S 924 (t), S 925 (t), S 933? (t), S 938 (t), S 956 (t), S 993 (t) [MGUH 22.726], S 1029 (t), S 1032 (t), S 1049 (t), S 1672 (t), K 49 (t), K 52 (c), K 85 (c) with thoracic segments, K 94 (pim), K 98 (im), K 112 (c), K 135 (im), K 153 (c), K 185a (c), K 186 (t), K 190 (im) [MGUH 22.727], K 196a (c), K 196b (c), K 386 (t), K 389 (t), K 409 (t), K

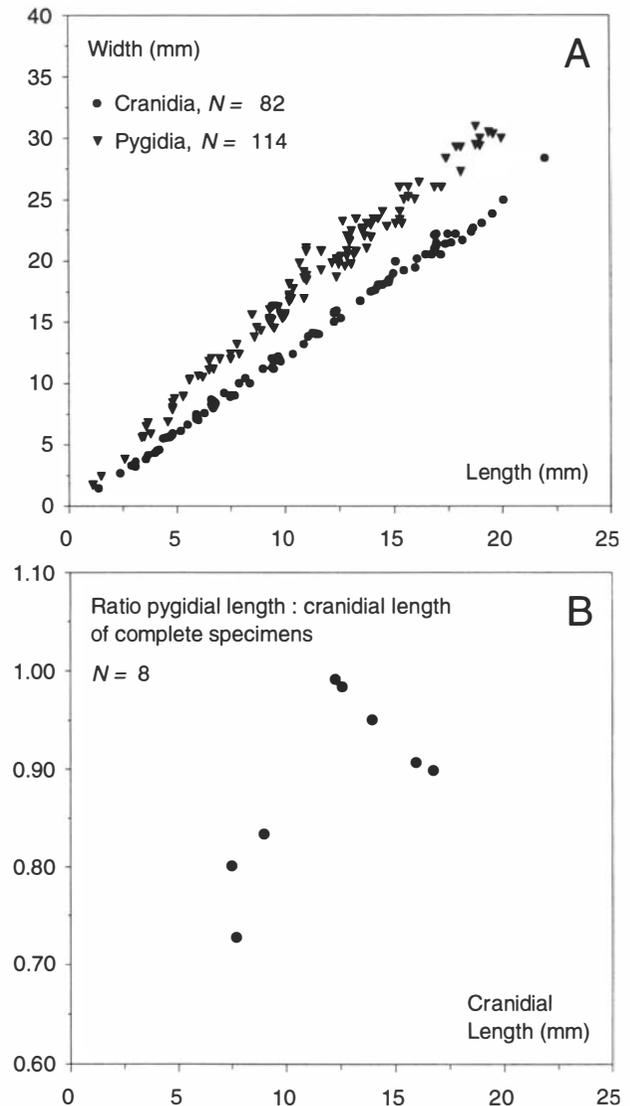


Fig. 168. *Nileus orbiculatooides*. □A. Maximum width plotted against sagittal length, cranidia and pygidia. □B. Ratio between pygidial length and cranial length of entire specimens plotted against cranial length.

Fig. 169 (opposite page). *Nileus orbiculatooides* Schrank, 1972. □A. Internal moulds of two cranidia, $\times 2$; one is shown in close-up on J. LO 7079 and LO 7080 (LU 24a, b), Andrarum. □B. Small cranidium, stereo-pair, $\times 3.5$. LO 7121 (LU 135-1b), Tommarp. □C. Internal mould of cranidium showing paired muscle impressions on glabella, stereo-pair, $\times 2$. MGUH 22.702 (S 256), bed -20, Skelbro. □D. Small cranidium, stereo-pair, $\times 5$. MGUH 22.703 (K 120a), bed -5, Killeröd. □E–G. Cranidium, dorsal (stereo-pair) $\times 2$, frontal and side views, $\times 3$. MGUH 22.704 (S 1036), bed -2, Skelbro. □H–I. Corroded small cephalon, dorsal and frontal views, showing anterior mesial boss of cranidium, $\times 4$. MGUH 22.705 (S 761), bed -13, Skelbro. □J–K. Internal mould of cranidium, dorsal and side views, $\times 3$ (close-up of one of the cranidia shown in A). LO 7079 (LU 24a), Andrarum. □L–M. Cranidium, dorsal and side views, $\times 5$. MGUH 22.706 (DGU 1-7), Skelbro.

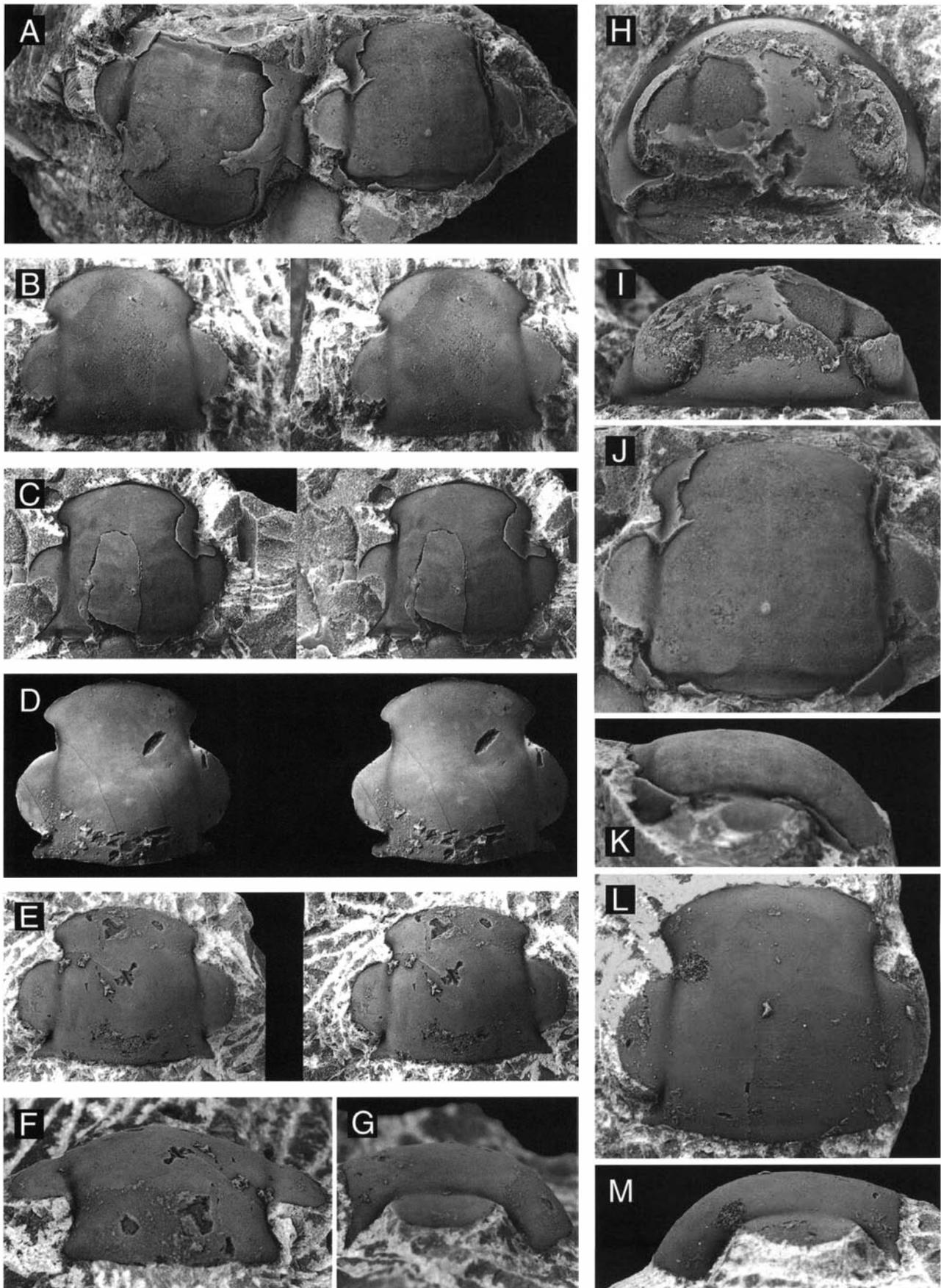


Table 19. *Nileus orbiculatoides*. Ranges for variation of cranidia, expressed as ratios of cranial length.

Size (mm)	Maximum width of cranium			Glabella width			Palpebral lobe length (exsag.)			Glabellar tubercle, distance to post. margin		
	Range	Mean	N	Range	Mean	N	Range	Mean	N	Range	Mean	N
1.4	—	0.93	1	—	0.64	1	—	0.43	1	—	—	0
2.4–4.2	1.00–1.13	1.07	9	0.69–0.81	0.73	10	0.42–0.50	0.46	10	0.28–0.33	0.30	4
4.4–5.5	1.15–1.23	1.19	7	0.75–0.85	0.79	7	0.44–0.50	0.46	6	0.29–0.39	0.32	5
>5.9	1.15–1.32	1.23	65	0.78–0.93	0.85	69	0.39–0.49	0.43	67	0.31–0.37	0.35	41

434? (pim), K 439? (pim), K 447? (im), K 450b? (c), K 452? (c), K 484a (t), K 497a (t), K 499a (t), K 504 (t), K 505 (t), K 509a (t), K 523 (t), K 537? (c), K 551? (pim), K 579 (t), K 587a (t), K 600? (c), K 602 (t), K 603 (pim), K 606b (t), K 609a (t), K 610b (t), K 610c (is), K 616 (im) [MGUH 22.728], K 618 (t), K 620 (t), K 621? (im), K 623 (t), K 625 (t), K 645? (c), K 652 (c), K 654 (pim), K 656? (c), K 659 (t), K 665 (pim), K 666? (c), K 667 (c), K 669a (pim), K 670? (c), K 672a? (c), K 672c (c), K 708? (c), K 720 (c), K 721 (c), K 764a (t), K 764b (pim), K 771 (t) [MGUH 22.720], K 772 (t), DGU 1-1 (pim) [MGUH 22.725], DGU 1-2 (t), DGU 1-5 (t), LU 5 (t), LU 9c (pim), LU 18c (im), LU 20c (pim), LU 22a (t) [LO 7077], LU 23a (t), LU 23b (pim), LU 24c (pim), LU 25 (t) [LO 7081], LU 50c? (im). □ Juvenile pygidia S 297b (pim), S 860b (im), S 940a (pim) [MGUH 22.714], S 941 (t), S 945 (t) [MGUH 22.716], S 995 (t) [MGUH 22.718], K 3 (t), K 28 (c), K 106 (t) [MGUH 22.717], K 118 (pim) [MGUH 22.713], K 431 (t), K 440 (t), K 560c (pim), K 649 (c), K 664a (t), K 669b (t) [MGUH 22.715], LU 135c (t).

Occurrence. – The species is common in the Komstad Limestone and occurs from the base of the *M. polyphemus* Zone to the top of the *M. simon* Zone at Skelbro (bed interval –21 to 0), and throughout the *M. simon* Zone in the Killeröd area (bed interval K [at Gårdlösa-1] to –1 [at Killeröd]). The museum material studied, most of which cannot be assigned to precise level, originates from Skelbro, Soldatergård, Andrarum, Tommarp and Komstad. *N. orbiculatoides* has not been found at Slemmestad.

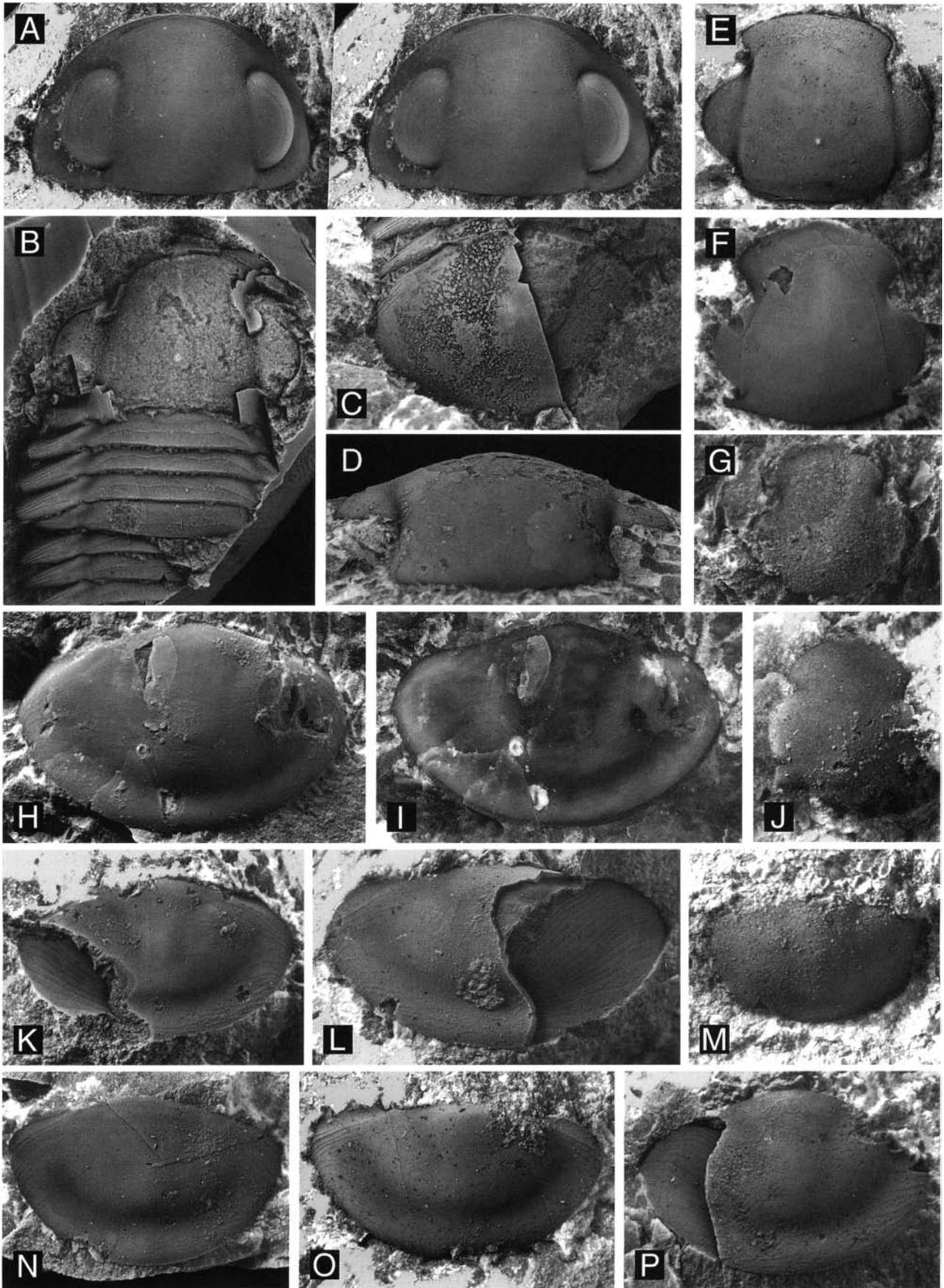
In Sweden the species occurs from the upper part of the *M. estonica* Zone, throughout the *M. polyphemus* Zone to become an especially characteristic element of the *M. simon* Zone fauna (Tjernvik & Johansson 1980; see discussion below). *N. orbiculatoides* probably also occurs in the eastern Baltic area (see remarks below).

Diagnosis. – Fairly large species; cephalon rather strongly convex (sag.); provided with obtuse mesial boss on anterior cranial margin; glabella subrectangular; cephalic test surface smooth. Pygidium with or without concave border, and covered with short, widely spaced, well-impressed, unbranching lines, present at least along anterior margin and anteriorly on border, but may also cover pleural fields and entire border. [Emended from Schrank 1972.]

Description. – Fairly large species, largest cranium 21.3 mm long, largest pygidium about 19 mm long. Length ratios between cephalon, thorax and pygidium cannot be verified, as all articulated specimens are poorly preserved. Length:length ratios between pygidium and cranium of articulated specimens varies between 0.73 and 0.98 (mean 0.89; $N = 8$), increasing with size (Fig. 168B). Cephalon semicircular in outline and strongly convex (both ways),

W:L ratio varies between 1.5 and 1.6 (mean 1.55; $N = 7$). Glabella subrectangular (Table 19), most so in the smallest specimens (Fig. 171B). A single specimen shows four pairs of barely indicated lateral impressions on glabella (Fig. 169C). Axial furrows almost straight, converge gently forwards; they are wide and shallow, slightly deeper on internal moulds, but accentuated by the change of slope between glabella and palpebral lobes. Anterior margin of cranium rounded and provided with a characteristic mesial boss. The slightly upturned boss is part of the anterior cephalic border, and almost reaches cephalic margin. Palpebral lobes moderately long (exsag.) (Table 19); they are gently convex (tr.), and slope slightly in outward direction. Mesial glabellar tubercle of moderate size on internal moulds; it is difficult to see on testaceous material. A faint sagittal keel is indicated on internal moulds, running from tubercle to about 0.2 of the cranial length from anterior margin. A minute swelling, visible only on exfoliated specimens, is situated on sagittal line immediately above the anterior mesial boss. No external indication of occipital furrow. Posterior fixigena slender triangular in outline, stretching (tr.) for about 0.15 of the cranial width at posterior margin; exsagittal length averages 0.15 ($N = 51$) of the cranial length. Anterior branches

Fig. 170. *Nileus orbiculatoides* Schrank, 1972. □A. Well-preserved small cephalon showing anterior mesial boss on cranium, stereo-pair, $\times 6$. LO 7120 (LU 135-1a), Tommarp. □B. Latex cast of damaged complete specimen showing external thoracic terrace-line distribution, $\times 3$. Pygidium shown in C. MGUH 22.707 (K 8), bed M, Gårdlösa-1. □C. Corroded, partly exfoliated pygidium, $\times 3$. Same specimen as B. □D. Frontal view of cranium showing anterior mesial boss, $\times 3$. MGUH 22.708 (K 611), bed –5, Killeröd. □E. Internal mould of atypical small cranium tentatively identified with *N. orbiculatoides*, $\times 8$. MGUH 22.709 (S 288), bed –20, Skelbro. □F. Small cranium, $\times 9$. MGUH 22.710 (K 107), bed 6, Gårdlösa-4a. □G. Corroded juvenile cranium, $\times 9$. MGUH 22.711 (K 498a), bed 1, Gårdlösa-4a. □H. Pygidium showing 'orbiculatoides-type' terrace-line pattern, $\times 3$. LO 7081 (LU 25), Tommarp. □I. As H, but without whitening, transparent cuticle shows light coloured muscle insertion sites on axis, $\times 3$. □J. Tiny juvenile cranium, $\times 25$. MGUH 22.712 (K 419), bed –5, Killeröd. □K. Small pygidium showing 'orbiculatoides-type' terrace-line pattern, $\times 3$. MGUH 22.713 (K 118), bed –5, Killeröd. □L. Partly exfoliated small pygidium showing double, $\times 9$. MGUH 22.714 (S 940), bed –4, Skelbro. □M. Tiny transitory pygidium, stage A, $\times 15$. MGUH 22.715 (K 669b), bed 7, Gårdlösa-4a. □N. Transitory pygidium, stage E, $\times 9$. MGUH 22.716 (S 945), bed –4, Skelbro. □O. Pygidium representing smallest holaspis stage, $\times 8$. MGUH 22.717 (K 106), bed –5, Killeröd. □P. Small holaspis pygidium, $\times 6$. MGUH 22.718 (S 995), bed –4, Skelbro.



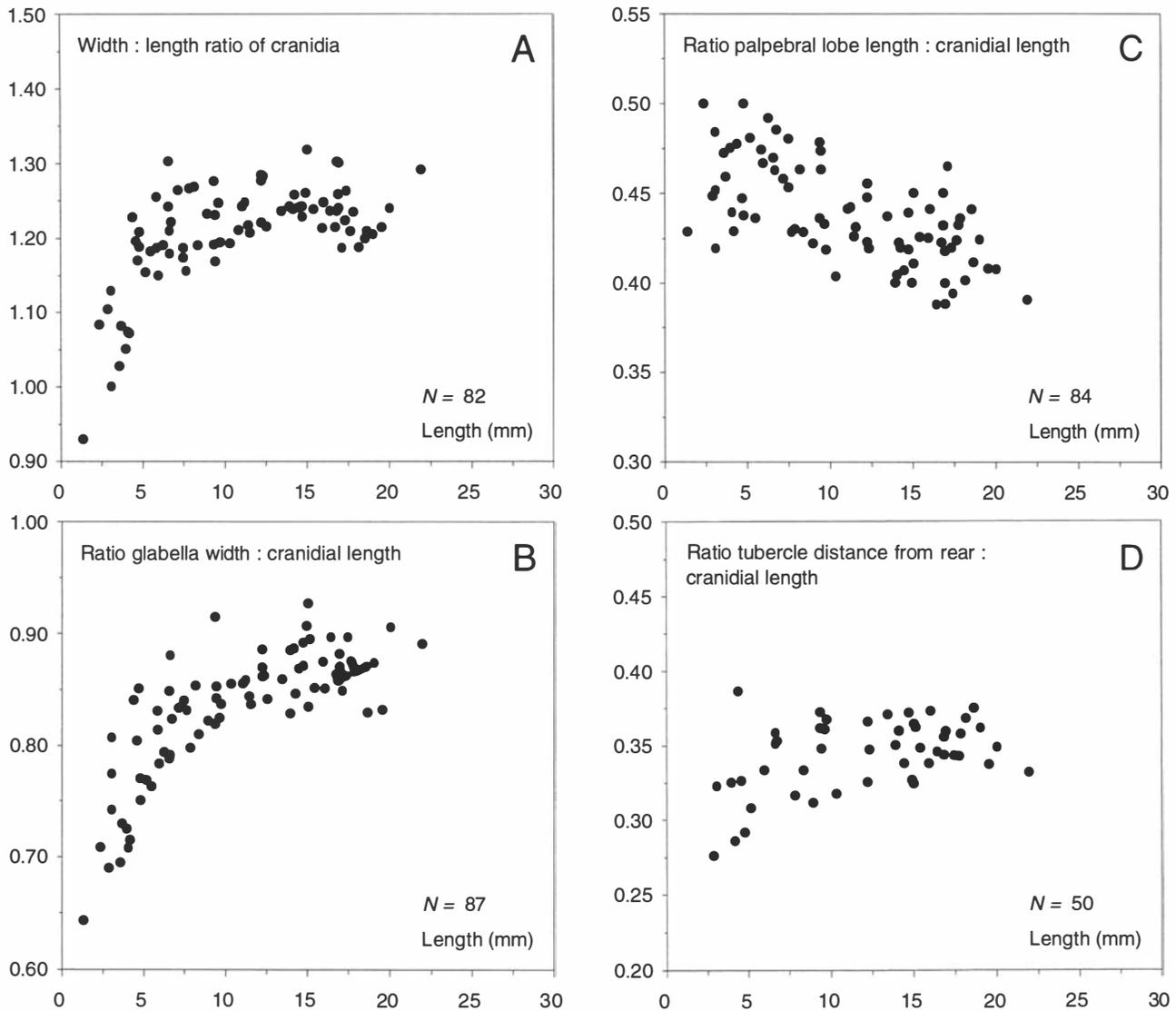


Fig. 171. Crania of *Nileus orbiculatoides*. □A. Ratio between maximum width across palpebral lobes and cranial length plotted against sagittal length. □B. Ratio between glabella width (measured between posterior corners of palpebral lobes) and cranial length plotted against cranial length. □C. Ratio between palpebral lobe length (exsag.) and cranial length plotted against cranial length. □D. Comparison of adult ratios between the distance from posterior cranial margin to glabellar tubercle against cranial length.

of facial suture curve outwards at an angle of about 35° to sagittal line in front of eyes; they meet anteriorly in a more or less angulate junction. Posterior branch of facial suture virtually straight, running obliquely backwards-outwards (at about 35° from sagittal line) from hind corner of palpebral lobe to posterior margin of cephalon.

Lateral border of cephalon is almost flat at eye level; it tapers out close to genal angle. Posterolateral part of librigena slightly convex, sloping outwards. Outer margin of librigena occasionally thickened, and on some specimens provided with one or two continuous terrace lines.

Cephalic doublure provided with at least 14 coarse, continuous terrace lines. Cephalic test surface smooth, except for the usual local 'wrinkling' displayed by well-preserved specimens.

Fig. 172 (opposite page). *Nileus orbiculatoides* Schrank, 1972. □A. Pygidium showing open 'orbiculatoides-type' terrace-line pattern, $\times 2.5$. LO 7077 (LU 22a), Andrarum. □B. Fragmentary pygidium showing comparatively dense 'orbiculatoides-type' terrace-line pattern, $\times 2.5$. MGUH 22.719 (S 864a), bed -7, Skelbro. □C. Fragmentary, partially corroded pygidium; close-up showing articulating facet, $\times 3$. MGUH 22.720 (K 771), bed 12, Gårdlösa-4a. □D. Partly exfoliated pygidium showing 'orbiculatoides-type' terrace-line pattern, and axial outline, $\times 3$. MGUH 22.721 (S 567), bed -18, Skelbro. □E. Internal mould of pygidium, $\times 4$. MGUH 22.722 (S 345), bed -20, Skelbro. □F. Internal mould of pygidium, showing axis, $\times 3$. MGUH 22.723 (S 269), bed -20, Skelbro. □G. Somewhat corroded large pygidium showing comparatively dense 'orbiculatoides-type' terrace-line pattern, $\times 2.5$. MGUH 22.724 (S 515), bed -18, Skelbro. □H. Partly exfoliated large pygidium showing open 'orbiculatoides-type' terrace-line pattern, $\times 2.5$. MGUH 22.725 (DGU 1-1), Skelbro. □I. Small pygidium showing proportionally wide border, $\times 6$. MGUH 22.726 (S 993), bed -4, Skelbro. □J. Internal mould of large pygidium showing doublure, $\times 2.5$. MGUH 22.727 (K 190), bed -3, Killeröd. □K-L. Internal mould of pygidium showing doublure (L latex cast), $\times 3$. MGUH 22.728 (K 616), bed 6, Gårdlösa-4a.

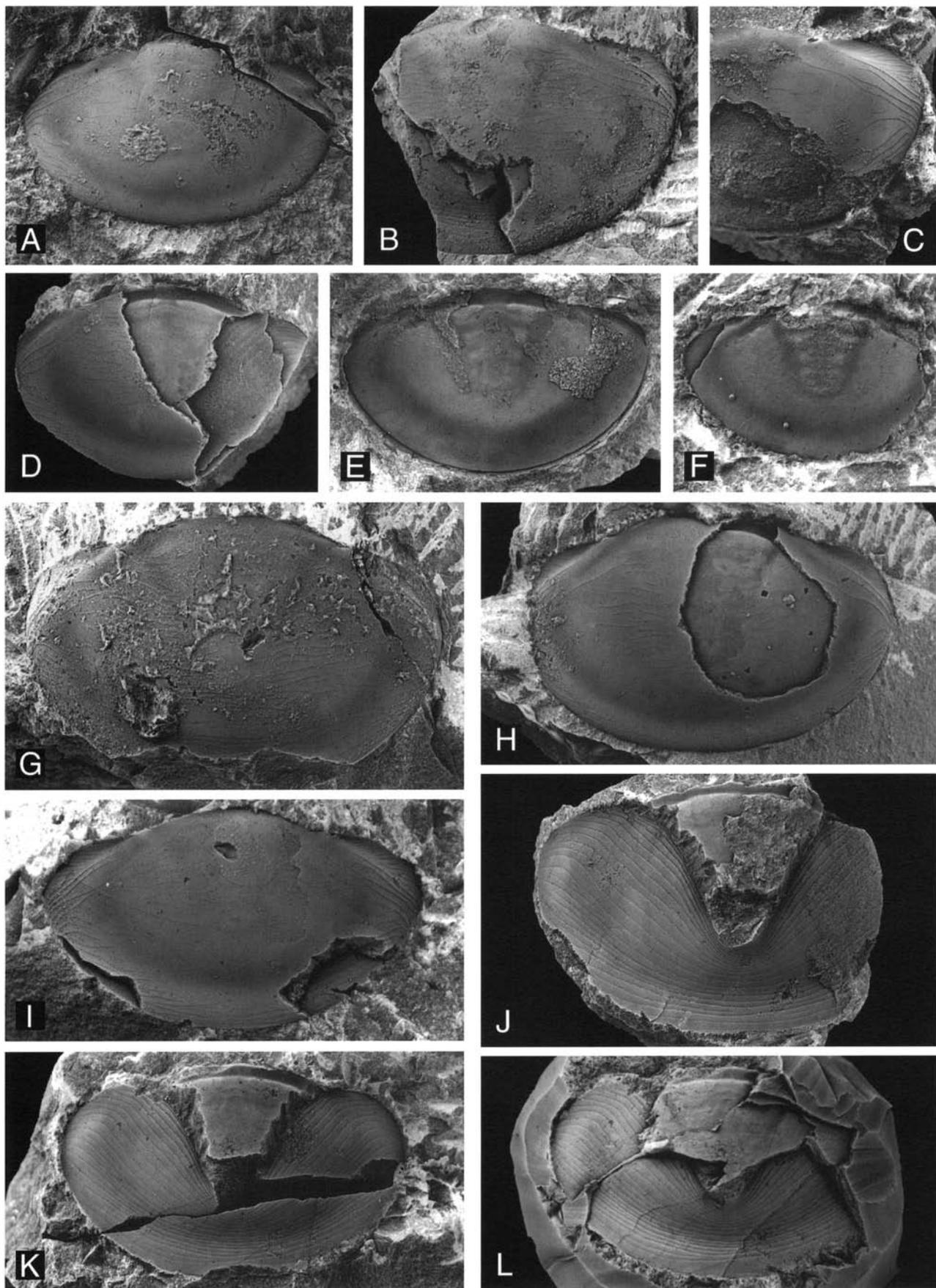


Table 20. *Nileus orbiculatooides*. Ranges for variation of pygidia, expressed as ratios.

Size (mm)	Pygidial L:W ratio			Axial width : pygidial width			Axial length : pygidial length			Border length (sag.) : pygidial length		
	Range	Mean	N	Range	Mean	N	Range	Mean	N	Range	Mean	N
1.1–1.5 [Stage A]	0.63–0.69	0.66	2	0.25–0.38	0.31	2	0.73–0.80	0.76	2	0.20–0.27	0.24	2
2.6 [Stage D]	—	0.68	1	—	—	0	—	0.58	1	—	0.31	1
3.4–5.6 [Hol.]	0.54–0.66	0.60	13	0.33–0.39	0.38	4	0.56–0.64	0.58	5	0.23–0.28	0.26	12
>6.0 [Hol.]	0.54–0.67	0.61	95	0.33–0.43	0.37	35	0.54–0.68	0.60	36	0.14–0.24	0.18	79

Hypostomes not investigated, see Schrank (1972, p. 362).

Thorax poorly preserved in the material at hand, so size relations cannot be verified. Pleural furrows weakly impressed, indistinct; articulating processes and sockets, are, on the other hand, comparatively distinct, also when the test is intact. Axis occupies 0.53 of the thoracic width (tr.) on the first segment in one specimen. A single transverse terrace line crosses the axis of each thoracic segment. One to four, typically two, terrace lines are present on the pleura posterior to articulating facet. Articulating facet shows about ten lines.

Pygidium fairly strongly vaulted. Axis has a low relief on internal moulds, is of equal width and length, truncately cone-shaped, and stretches for about 0.6 ($N = 36$) of the pygidial length (Table 20). Width at anterior margin accounts for 0.4 ($N = 23$) of the pygidial width. On testaceous material the axis has no relief at all, except in the largest specimens, but may be crudely outlined by the terrace-line pattern. Accordingly, it is impossible to measure the axis in most specimens. Internal moulds show a very short anterior half-ring, followed by four faint axial segments, outlined by lateral swellings, in addition to a rounded, ill-defined terminal piece, which is fused with the posterior pair of axial swellings. Only the first ring furrow behind the anterior deep articulating furrow is fairly defined. A couple of specimens show faint, light coloured muscle markings in the axial region (Fig. 170I). Four pairs are present, just as in the much better preserved pygidia of *N. latifrons* n.sp. (*q.v.*), but compared to that species they appear slightly smaller, and are limited to the lateral part of axis. The posterior pair is the largest and visibly composite, consisting of three sub-marks. Anterior proximal pleural furrow is very shallow and inconspicuous on outside of test. Border concave, quite wide, and almost of the same width all the way. Border width and concavity appear to be constant throughout the stratigraphical range, but juvenile pygidia show markedly wider borders and the width tends to decrease with increasing size of specimen (Fig. 173B).

Adult pygidia exhibit the characteristic 'orbiculatooides-type' terrace-line pattern, consisting of well-impressed, openly spaced, rather short, unbranching and usually slightly undulating lines, present at least along the anterior margin and anterolaterally on border. Terrace lines may also more or less cover the pleural fields and border, while the axial area

always is smooth. Larger pygidia tend to show the most extensively distributed terrace lines. The first areas to be 'invaded' by lines, in addition to the areas with omnipresent lines, are the flexure between the pleural fields and border, or the central lateral portions of the pleural fields. The various terrace-line patterns are apparent from Fig. 172. Line density generally about 2–3 lines/mm on the pleural fields in pygidia more than 10 mm long; the articulating facet shows about 12–16 gently sigmoidal lines. The best preserved pygidia also show a very fine pitting of the test surface, and a couple of specimens exhibit fine 'wrinkles' radiating from the posterior part of axis. The terrace lines, although distinct, are rarely impressed on internal moulds. Doublure strongly concave and provided with 18–21 continuous, coarse terrace lines.

Juveniles. – The majority of juvenile cephalae and cranidia are identified by the presence of an anterior mesial boss, whereas most of the pygidia show only a general Nileid morphology. The material described is from beds containing only *N. orbiculatooides*; additional small pygidia are dealt with in the section on 'Juvenile pygidia of *Nileus exarmatus*, *N. sp. B*', etc.

Three specimens out of twenty-four juvenile cephalae and cranidia, 1.4 to 6.3 mm long (cranidial length), including the two smallest cranidia (1.4 and 2.4 mm long), lack the anterior mesial boss, seventeen specimens have a boss, and the remaining four specimens are damaged anteriorly. The smallest specimen with an anterior boss is 2.9 mm long. All available cephalae, down to 3.7 mm long, have rounded genal angles. Compared to larger cranidia, the juveniles are less convex sagittally, comparatively more convex transversely with poorly defined axial furrows, and glabella is almost confluent with palpebral areas. The most conspicuous difference from adult specimens is the cephalic elongation with significantly lower W:L ratios (Table 19). As a consequence of the elongation the glabellar tubercle is situated relatively far back, about 0.30 of the cranidial length from posterior margin. Even the smallest specimens are elongate and of rather low sagittal convexity; the strongly convex (sag.) growth stage with 'hump-shaped' glabella is not present in *N. orbiculatooides* (cf. 'Und. juveniles of *N. armadillo* and *N. latifrons* n.sp.'). Cranidium S 288c, tentatively assigned to *N. orbiculatooides* as the facial sutures meet under an obtuse

angle, is more strongly convex (sag.) than the remaining specimens studied (Fig. 170E).

Pygidia K 560b and K 669b, 1.1 and 1.5 mm long, respectively, represent growth stage A. The preservation is not good, but the smallest pygidium matches specimen S 63b (see pp. 241–243). The larger pygidium, 1.5 mm long, are slightly less convex, and the prominent articulating half-ring is either missing or not preserved (Fig. 170M).

One pygidium, 2.6 mm long, probably represents stage D, while all remaining specimens, 3.4 to 5.5 mm long, are holaspides. They match the description on p. 244. Specimens up to 4.9 mm long have an almost smooth test surface with a few lines along anterior margin and on the border along outer margin ('*exarmatus*-type' terrace-line pattern), whereas specimens 4.8 to 5.5 mm long exhibit an '*orbiculatoides*-type' pattern with terrace lines spreading onto the pleural fields. Pygidium S 942, about 5 mm long, is part of a complete specimen with a cranidium 7 mm long, i.e. the larger juvenile pygidia match cranidia showing adult morphology.

Affinities. – *N. orbiculatoides* shows strong affinity to the slightly larger *N. armadillo*, and is most likely its ancestor. Differences are enumerated in the section on *N. armadillo*.

Nileus exarmatus is smaller than *N. orbiculatoides*, and has a more elongate glabella (Fig. 167B), an evenly rounded anterior margin lacking a mesial boss, and the pygidium has fewer dorsal terrace lines, restricted to the anterior part; various features of *N. orbiculatoides* and *N. exarmatus* are compared in Fig. 167A–E. *Nileus exarmatus* has been suggested as a possible ancestor to *N. orbiculatoides*, see discussion below.

The *N. depressus* group is readily separated from *N. orbiculatoides* on basis of the different pygidial terrace-line pattern. Isolated cranidia and cephalae of the associated *N. depressus schranki* n.subsp. can be separated by the lower sagittal convexity, the gently arcuate anterior margin lacking a mesial boss, the curved and slightly better impressed axial furrows, and by the different test ornamentation.

N. orbiculatus is much smaller than *N. orbiculatoides*, the central portion of glabella is slightly circular, there is no anteriomesial boss, the anterior lateral expansion of glabella is short (exsag.), the lateral cephalic border is very narrow, the cranidium is partly or entirely covered with terrace lines (unpublished) and the pygidia lack any indications of a concave border. The naming of *N. orbiculatoides* after *N. orbiculatus* erroneously suggests a relationship between these species; Tjernvik (1980) pointed out that the forms presumably are rather distant.

The differences from *N. orbiculatoides svalbardensis* were discussed by Fortey (1975a, pp. 43–44). I do not regard *N. svalbardensis* as a subspecies of *N. orbiculatoides*, as the lack of a cranidial mesial boss, the coarse punctuation of cephalic test and the rather few terrace lines on the pygidial doubleure suggest a separation at the species level. *N. svalbardensis* is more likely related to the *N. depressus* group.

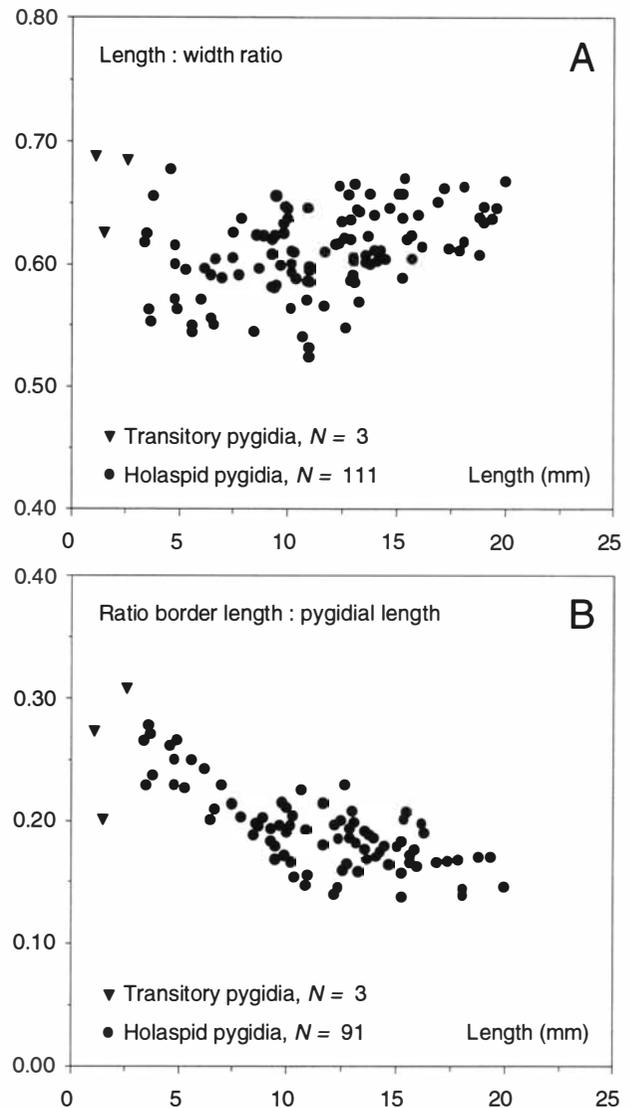


Fig. 173. Pygidia of *Nileus orbiculatoides*. □A. Ratio between sagittal length and maximum width plotted against sagittal length. □B. Ratio between border length (sag.) and pygidial length plotted against pygidial length.

Remarks. – Schrank (1972) defined *Nileus orbiculatoides* as a subspecies of *N. exarmatus*; Fortey (1975a, p. 43) elevated it to species rank. Most of the cranidia and cephalae assigned to *N. exarmatus* by Schrank (1972, Pl. 3:3–6, 8–9) in fact belong to *N. orbiculatoides* (see discussion of *N. exarmatus* for details).

The first representatives of *N. orbiculatoides* appear in the upper part of the *M. estonica* Zone of Sweden, and, according to Tjernvik (1980), a 'transitional form' then continues throughout the *M. polyphemus* Zone, to be succeeded by *N. orbiculatoides* (s.str.) in the *M. simon* Zone. Tjernvik (1980) referred to the early, supposedly transitional form as *N. exarmatus orbiculatoides* n.sp./subsp.; it is characterized by a pygidium with concave border and external terrace lines at

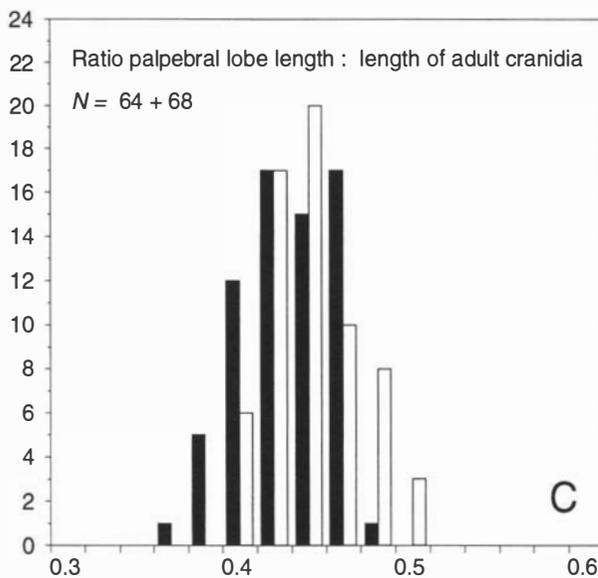
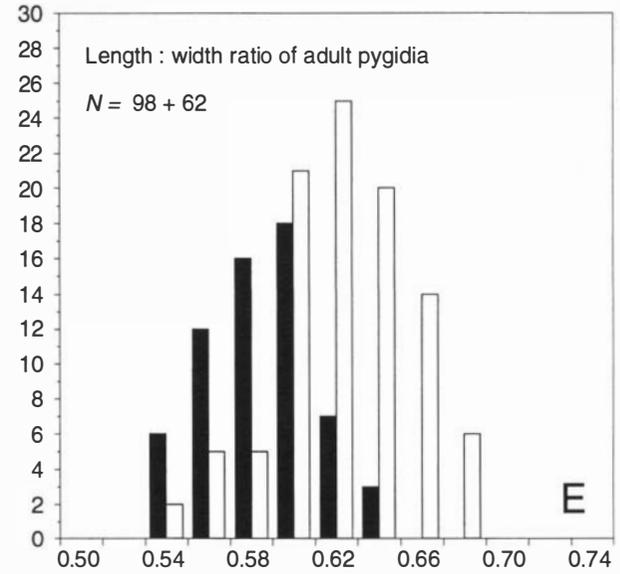
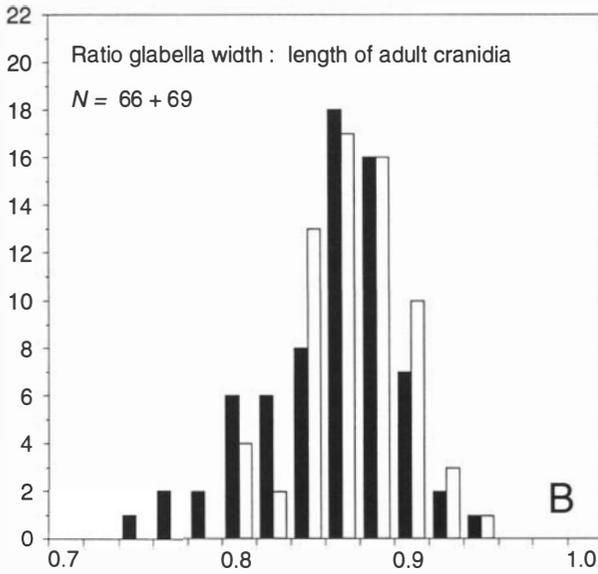
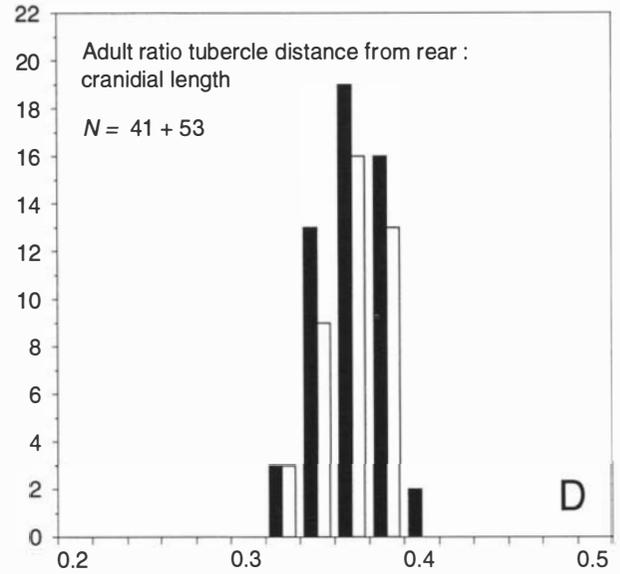
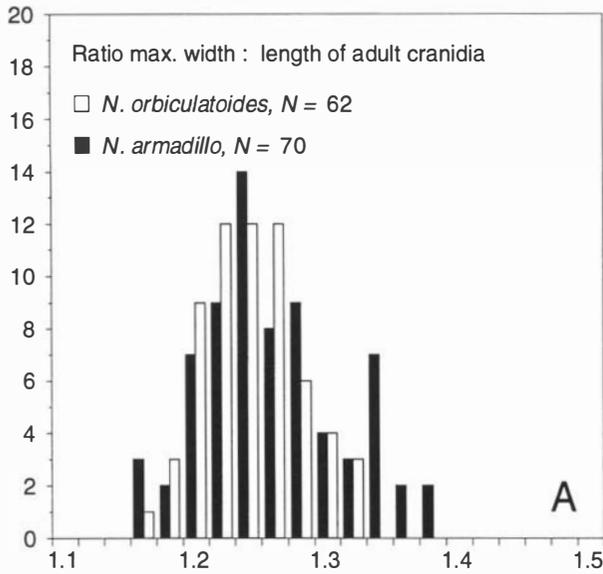


Fig. 174. *Nileus orbiculatoides* versus *N. armadillo*, adult specimens only (crania more than ca. 6 mm long and pygidia >5.7 mm long). □A. Comparison of adult ratios between maximum cranial width and cranial length. □B. Comparison of adult ratios between glabella width (measured between hind corners of palpebral lobes) and cranial length. □C. Comparison of adult ratios between palpebral lobe length (exsag.) and cranial length. □D. Comparison of adult ratios between the distance from posterior cranial margin to glabellar tubercle and cranial length. □E. Comparison of adult ratios between pygidial length (sag.) and maximum pygidial width.

first limited to the anterior part of the border and pleural fields, but they then gradually spread over the pygidium during the *M. polyphemus* Zone (Tjernvik 1980, p. 203). *N. orbiculatooides* (*s.str.*) is, according to Tjernvik, characterized by a pygidium with a poorly defined or effaced concave pygidial border and with more widely distributed, yet still openly spaced terrace lines, covering the entire pygidium except for the axial region. Tjernvik (1980) attached importance to *N. orbiculatooides* '*s.str.*' as a characteristic species of the *M. simon* Zone of Sweden.

The new material of *N. orbiculatooides* from the Komstad Limestone shows no trend towards a narrower or vanishing pygidial border, and no systematic change in degree of pygidial terrace-line coverage. Hence the specimens would in Tjernvik's terminology be referred to as 'transitional', but even the latest pygidia from the top of the *M. simon* Zone exhibit the same morphology. It is concluded that the characters relate to environment rather than evolution (see also *N. latifrons* n.sp.), so that deeper-water (muddy-substrate?) representatives of *N. orbiculatooides* are characterized by pygidia with a well-developed concave border and comparatively few dorsal terrace lines, whereas shallower-water (slightly coarser-substrate?) representatives had a poorly developed pygidial border, if not fully convex, and show a more extensive, openly spaced dorsal terrace-line pattern.

Pending further studies of the distribution of possible ecophenotypes of *N. orbiculatooides*, all Scandinavian forms are best included in *N. orbiculatooides* Schrank without distinction of subspecies.

Törnquist (1884, pp. 55–56) stated that specimens from the 'Lower Red *Orthoceras* Limestone' of the Siljan region, assigned to *N. armadillo*, are rather small and show facial sutures meeting in an ogive, whereas later specimens have smoothly merging facial sutures. The specimens referred to with a mesial boss most likely belong to *N. orbiculatooides*.

Juvenile pygidia of *Nileus exarmatus*, *N. sp. B*, *N. orbiculatooides*, and *N. depressus schranki* n.subsp.

Figs. 175–178

Material. – 107 juvenile pygidia that cannot be assigned to species.

List of material. – (For explanation of stages A–F, see description below). □Stage A S 63b (t) [MGUH 22.729]. □Stage B S 123a (t) [MGUH 22.730], S 185a (im), S 207a (t) [MGUH 22.731]. □Stage C S 100b (t) [MGUH 22.732], S 134b (im), S 135b (im) [MGUH 22.734], S 140b (im), S 151a (im), S 163 (fragmentary, t), S 168a? (im), S 187a (pim) [MGUH 22.733], S 449 (im), S 454a (im). □Stage D S 16b (t), S 18 (im), S 22b (t) [MGUH 22.736], S 22c (im), S 26c (is), S 27b (t), S 27d (t), S 57? (pim), S 66 (em), S 70a (im), S 90a (t) [MGUH 22.735], S 90b (t), S 128b (t), S 134a (t) [MGUH 22.737], S 135a (im), S 151b (im) [MGUH 22.738], S 162a (t), S 205a (im), S 205c (t), S 215a (pim), S 223 (im), S 289a (im), S 295a (im) [MGUH 22.739], S 301a (im), S 343 (t), S 429 (t), S 511? (c), MGUH 9434 (im), K 435 (t). □Stage E S 46a (t), S 59 (im), S 60b (im), S 63a (im) [MGUH 22.743], S 79 (im), S 80b (im), S 80d (pim), S 87b? (em), S 98a (pim), S 107a (t) [MGUH 22.752], S 132a (t) [MGUH 22.741], S 133 (pim) [MGUH 22.742], S 140a (im), S 157b (t), S 185b (im) [MGUH 22.746], S 201 (pim), S 297a (im) [MGUH 22.745], S 338 (im) [MGUH 22.744], S 354? (im), S 651 (t) [MGUH 22.740], S 664 (t), S 1678a (is), K 543c (im). □Stage F S 22a (t), S 27a (im), S 27e (t) [MGUH 22.748], S 38 (im) [MGUH 22.747], S 48a (t), S 50a (t), S 55 (im), S 67 (t) [MGUH 22.753], S 70c (t) [MGUH 22.749], S 75 (im), S 80e (im), S 87a (t), S 102 (pim), S 105a (im), S 110 (em), S 125 (t), S 128a (t), S 132b (t), S 135c (em), S 135d (fragment, im), S 138 (t), S 157c (t), S 169a (im), S 172c (pim), S 172d (pim), S 188c (im), S 204 (t), S 208a (t), S 216b (im), S 263 (im), S 294 (pim), S 298a (im), S 306a (im) [MGUH 22.750], S 309 (im), S 313 (im) [MGUH 22.751], S 331 (im) [MGUH 22.754], S 357 (fragment, t), S 368 (c), S 405 (c), S 527 (t), S 1669 (t), K 497b (im).

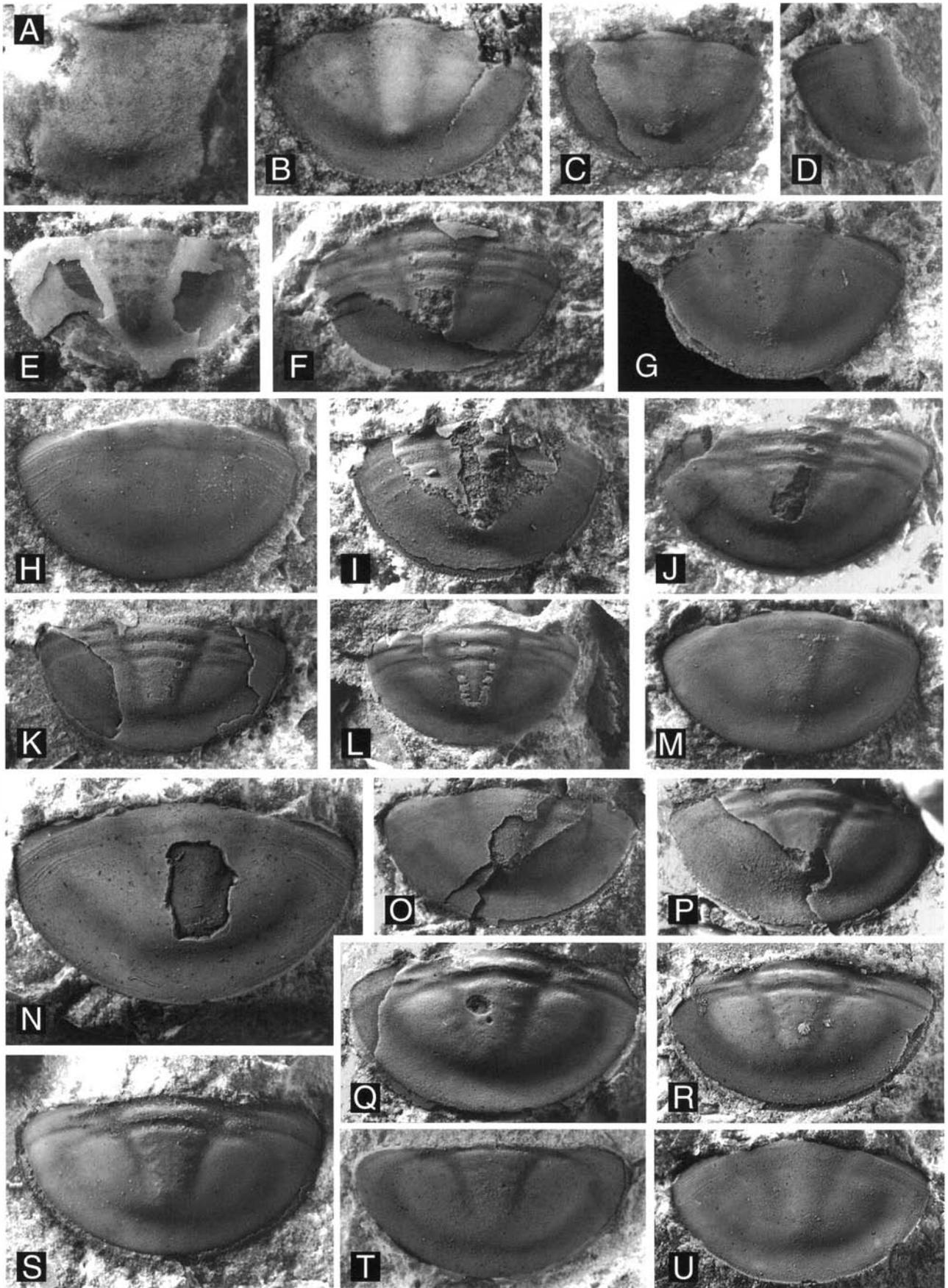
Occurrence. – The majority of the material originates from beds –21 and –20 at Skelbro, Zone of *M. polyphemus*. A few specimens are from beds –19 and –18, Skelbro (also Zone of *M. polyphemus*), bed N, Gårdlösa-1 (basal part of the *M. simon* Zone) and beds 1–3, Gårdlösa-4a (upper part of the *M. simon* Zone).

Description. – All pygidia are juveniles less than 6 mm long, lacking adult characteristics, and, consequently, impossible to assign to species. The material is divided into six groups, referred to as stages A–F (Fig. 177). The stated pygidial length includes unreleased segments.

Stage A: A somewhat damaged tiny pygidium is only 1.3 mm long (Fig. 175A); it has a comparatively high sagittal convexity, although being rather elongate (Table 21). Axis remarkably long and narrow, axial L:W ratio 1.43; it is provided with a distinct, articulating half-ring extending in front of the almost straight anterior margin of pygidium. Paradoablural area barely concave and steep, so the pygidium is basically without border. Doublure narrow and of uniform width, sagittally extending below about 0.25 of the pygidium. The transitory pygidium appears to be provided with only one unreleased segment, delimited by a faint

Table 21. Juvenile pygidia of *N. exarmatus*, *N. sp. B*, *N. orbiculatooides*, and *N. d. schranki*. Ranges for variation, expressed as ratios.

Size (mm)	Pygidial L:W ratio			Axial width : pygidial width			Axial length : pygidial length			Border length (sag.) : pygidial length		
	Range	Mean	N	Range	Mean	N	Range	Mean	N	Range	Mean	N
1.3 [Stage A]	–	~0.6	1	–	~0.3	1	–	0.77	1	–	0	1
1.7–2.0 [Stage B]	0.61–0.68	0.66	3	0.33–0.36	0.36	3	0.71–0.76	0.74	3	0.18–0.20	0.18	3
2.1–3.1 [Stage C]	0.58–0.67	0.62	10	0.35–0.42	0.38	8	0.68–0.73	0.70	9	0.21–0.29	0.25	9
2.5–3.7 [Stage D]	0.51–0.64	0.59	27	0.35–0.41	0.38	24	0.59–0.71	0.64	26	0.21–0.28	0.24	22
2.7–4.0 [Stage E]	0.61–0.63	0.57	21	0.32–0.41	0.38	18	0.57–0.63	0.60	18	0.21–0.27	0.24	17
3.3–5.9 [Hol.]	0.50–0.61	0.56	37	0.32–0.39	0.34	28	0.47–0.69	0.58	30	0.19–0.28	0.23	31



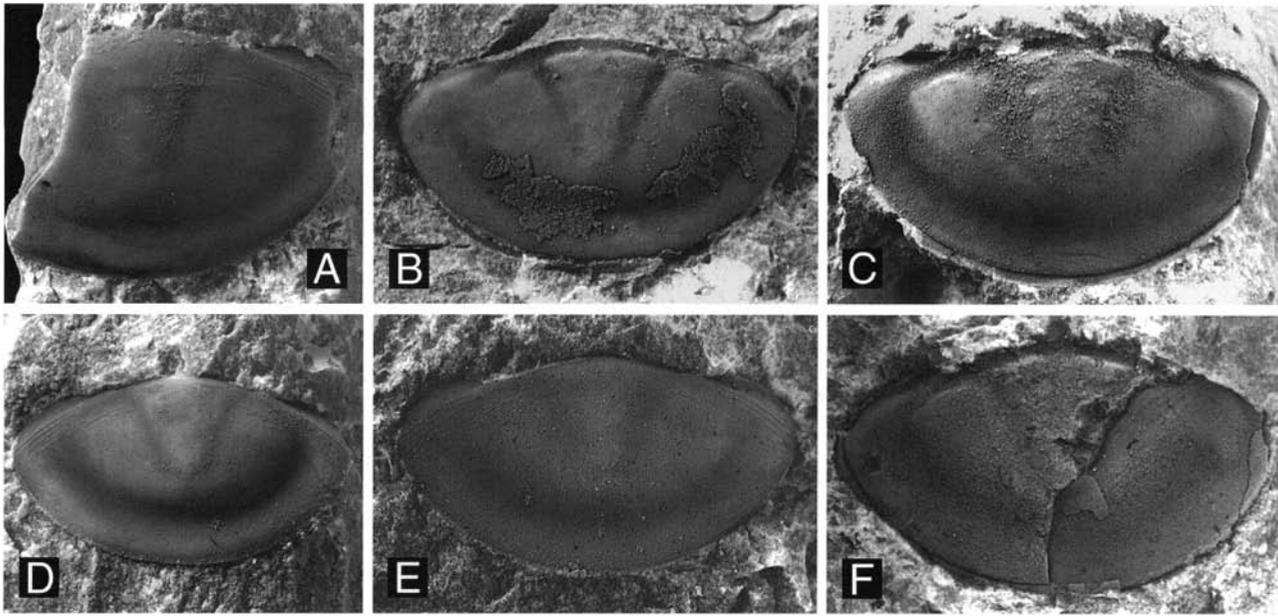


Fig. 176. Undifferentiated juvenile pygidia of *Nileus exarmatus*, *N. sp. B.*, *N. orbiculatoides*, and *N. d. schranki* n. subsp. from Skelbro. □A–C, E–F. Small holaspid pygidia lacking characteristics serving to separate species. □A. Specimen showing 'exarmatus-type' terrace line pattern, $\times 6$. MGUH 22.749 (S 70-5c), bed –21. □B. Internal mould showing axis, $\times 6$. MGUH 22.750 (S 306a), bed –20. □C. Internal mould, $\times 6$. MGUH 22.751 (S 313), bed –21. □D. Transitory pygidium, stage E, $\times 9$. MGUH 22.752 (S 107a), bed –21. □E. Holaspid showing 'exarmatus-type' terrace line pattern, $\times 9$. MGUH 22.753 (S 67), bed –21. □F. Partly exfoliated small holaspid showing doubleure, $\times 6$. MGUH 22.754 (S 331), bed –20.

Fig. 175. Undifferentiated juvenile pygidia of *Nileus exarmatus*, *N. sp. B.*, *N. orbiculatoides*, and *N. d. schranki* n. subsp. from Skelbro. □A–S. Transitory pygidia. □A. Stage A showing well-defined articulating ring and virtually no concave border, $\times 30$. MGUH 22.729 (S 63b), bed –21. □B. Stage B, showing concave border, $\times 20$. MGUH 22.730 (S 123a), bed –21. □C. Stage B, $\times 15$. MGUH 22.731 (S 207a), bed –21. □D. Fragmentary specimen, stage C, $\times 9$. MGUH 22.732 (S 100b), bed –21. □E. Non-whitened specimen with transparent cuticle showing dark coloured muscle insertion sites in axial region, stage C, $\times 12$. MGUH 22.733 (S 187a), bed –21. □F. Internal mould, stage C, $\times 9$. MGUH 22.734 (S 135b), bed –21. □G. Stage D, $\times 9$. MGUH 22.735 (S 90a), bed –21. □H. Specimen showing typical terrace line pattern, stage D, $\times 9$. MGUH 22.736 (S 22b), bed –21. □I. Internal mould showing doubleure, stage D, $\times 12$. MGUH 22.737 (S 134), bed –21. □J. Internal mould, stage D, $\times 9$. MGUH 22.738 (S 151b), bed –21. □K. Internal mould, stage D, $\times 9$. MGUH 22.739 (S 295-4a), bed –21. □L. Internal mould, stage D, $\times 9$. Previously figured by V. Poulsen (1965, Pl. 3:7). MGUH 9434, bed –21. □M. Stage E, $\times 9$. MGUH 22.740 (S 651), bed –18. □N. Large specimen, stage E, but possibly representing smallest holaspid instar, $\times 9$. MGUH 22.741 (S 132-2), bed –21. □O. Partly exfoliated specimen showing doubleure, stage E, $\times 9$. MGUH 22.742 (S 133), bed –21. □P. Internal mould, stage E, showing part of the doubleure, $\times 9$. MGUH 22.743 (S 63a), bed –21. □Q. Internal mould, stage E, $\times 9$. MGUH 22.744 (S 338), bed –20. □R. Internal mould, stage E, $\times 9$. MGUH 22.745 (S 297a), bed –20. □S. Internal mould of Stage E, $\times 9$. MGUH 22.746 (S 185), bed –21. □T–U. Small holaspid pygidia. □T. Internal mould, $\times 6$. MGUH 22.747 (S 38), bed –21. □U. Specimen showing 'exarmatus-type' terrace line pattern, $\times 6$. MGUH 22.748 (S 27e), bed –20.

furrow. Dorsal test surface smooth; 5–6 terrace lines on the doubleure are visible through the transparent test.

Similar tiny pygidia are also described for *N. orbiculatoides* (two specimens) and 'Juvenile specimens of *N. armadillo* and *N. latifrons* n. sp.' (one specimen). The tiny cranidium in Fig. 169J, may represent the matching cranidial growth stage showing a distinct articulating half-ring.

Stage B: Three pygidia, 1.7–2 mm long, resemble stage A, but show a well-developed concave border (Fig. 175B–C), and the sagittal convexity is therefore much less pronounced. L:W ratio 0.7 in two pygidia measuring 1.7 mm, and 0.6 in the pygidium measuring 2.0 mm. Axis long, narrow, L:W ratio varies between 1.25 and 1.44, smallest in the largest specimen; it is raised above pleural fields, and shows a fairly pronounced sagittal convexity, like stage A. Border well-defined, strongly concave. Doubleure wider than in stage A, extending below about one third of the pygidium, with only a small axial incision. Two unreleased thoracic segments delimited by faint, shallow furrows. External test surface smooth.

Stage C: Ten pygidia, 2.1–3.1 mm long, have three unreleased thoracic segments, best outlined on internal moulds. Compared to stages A and B, the pygidia are distinctly less convex (sag.), and show a wider concave border and a wider doubleure. Axis long and narrow, L:W ratio 1.07–1.27 (mean 1.17; $N = 8$); it is slightly raised above the pleural fields, and shows three fairly well-defined rings anteriorly on internal moulds, whereas the segmentation usually is difficult to

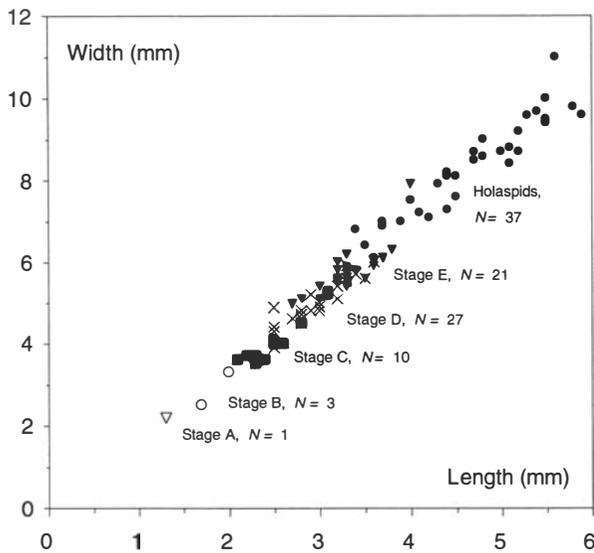


Fig. 177. Juvenile pygidia of *Nileus exarmatus*, *N. orbiculatoides*, *N. depressus schranki* n.subsp., and *N. sp.* B. Maximum width plotted against sagittal length.

recognize on testaceous material. The rings are, however, often indicated by pairs of coloured muscle markings. The unreleased segments are well set off on internal moulds, where each segment has a proximal pleural furrow inside the paradoublural line, but which shallow up at intersection with paradoublural line, and instead interpleural furrows become well-marked distally. Interpleural furrows may be seen inside the paradoublural line as very shallow, narrow furrows. Border wide, concave, and present only on the pygidium, proper. This may be the only way to recognize the unreleased segments, when the test is intact. No dorsal terrace lines have been seen in any specimen, but the material is dominated by internal moulds. Concave doublure moderately wide, widest posteriorly; small axial embayment. Doublure show about 8–10 terrace lines.

Stage D: Twenty-nine pygidia, 2.5–3.7 mm long, have two unreleased segments. This group closely resembles stage C, but is relatively shorter, the axis is less elongate, more triangular, and the doublure is wider. Axis slightly raised above pleural fields; it is about as wide as long, L:W ratio varies between 0.90 and 1.15 (mean 1.01; $N = 24$). Some of this variation may, though, reflect the difficulties of measuring the anterior width precisely, when the test is intact. Internal moulds show two well-defined axial rings corresponding to the unreleased segments, whereas the pygidial axis, proper, shows five axial segments in addition to the terminal piece; the segments are outlined by paired lateral swellings. Dorsal test surface shows a few transverse terrace lines, marking the limits of the anterior segments, but is otherwise smooth. The concave doublure is quite wide and approximately of equal width all the way, with the position of the unreleased segments marked by low crests. The doublure, which carries 13–14 terrace lines, can sometimes be discerned through the fairly thin, transparent test.

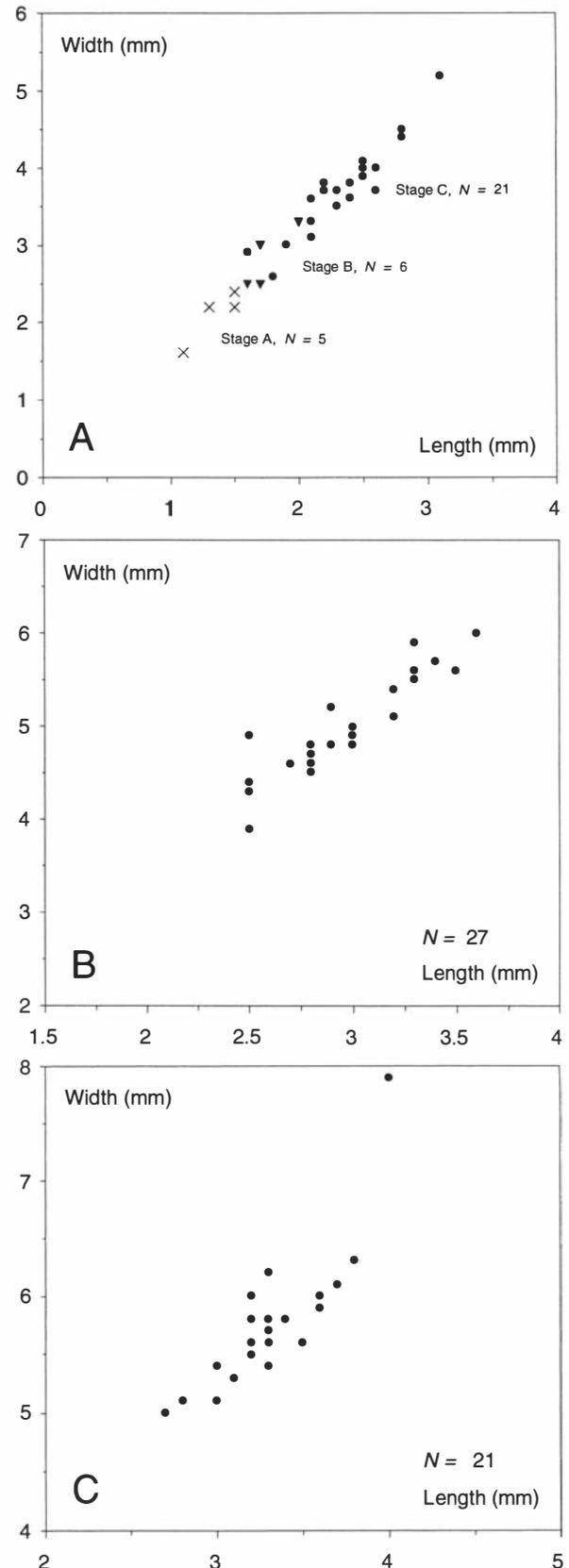


Fig. 178. □A. Combined scatter plot of the smallest juvenile pygidia of *Nileus*, including material of all species available. Maximum width is plotted against sagittal length. □B–C. Juvenile pygidia of *Nileus exarmatus*, *N. sp. B.*, *N. orbiculatoides* and *N. depressus schranki* n.subsp. Maximum width plotted against the sagittal length, stage D (in B) and stage E (in C).

Stage E: Twenty-three pygidia, 2.7–4.0 mm long, show one unreleased segment; they are similar to 'Stage D', except for the different number of fixed segments, but the axis is also slightly wider, axial L:W ratio varies between 0.89 and 0.95 (mean 0.93; $N = 18$). A few transverse terrace lines run along the anterior margin and also mark the limit of the unreleased segment. Scattered lines may, furthermore, be present along the posterior margin. Doublure wide, markedly concave; it is provided with 14–15 continuous, fairly coarse terrace lines.

Stage F: Forty-two pygidia, 3.3–5.9 mm long, are holaspides, but lack the terrace-line pattern characterizing the fully adults. Axis barely raised above pleural fields, and may be difficult to discern on testaceous material, unless outlined by coloured muscle markings; no axial furrows developed. Concave border well-defined, but relative width decreases with size. Among specimens with intact test, ten small pygidia, 3.3–4.4 mm long, show a '*N. exarmatus*-type' terrace-line pattern, with a few transverse lines close to the anterior margin and single lines along the outer posterior margin. Eight larger specimens, 4.8–5.9 mm long, plus a single pygidium 4 mm long, show a '*N. orbiculatoides*-type' terrace-line pattern, with short, openly spaced lines on the pleural fields in addition to transverse lines along the anterior and posterior margins. The surface of specimen S 70c, exhibiting an '*orbiculatoides*-type' terrace-line pattern, also seems to be very finely pitted, suggesting that the specimen presumably belongs to *N. orbiculatoides*. Doublure very wide and similar to larger holaspides.

Remarks. – The features which serve to identify adult specimens are not developed in the described early growth stages. This is the rule for nileids, but with occasional exceptions, particularly among taxa showing dense terrace-line sculpture in the holaspid stage (see *N. depressus* subspp. and *N. implexus* n.sp.). The material at hand originates from beds containing four different species of *Nileus*; if the juveniles reflect the adult frequencies, which is not necessarily the case, the material is dominated by *Nileus* sp. B, with *N. exarmatus* as an important smaller constituent, whereas *N. depressus schranki* n.subsp. and *N. orbiculatoides* may be represented only by a few specimens.

In order to survey species related differences all available transitory pygidia of *Nileus* were pooled and compared. It appeared that no significant size differences between species are evident for stages A to C (Fig. 178A), but from stage D and onwards. Accordingly, the hazards of dealing with a mixed material should be kept in mind.

The stated length of the transitory pygidia includes the unreleased thoracic segments; it is not possible to gauge only the pygidium itself in a proper way, as the outline of the fixed segments often is effaced on testaceous material. Measurements of well-preserved specimens showed that the pygidium (*s.str.*) on the average accounts for 0.60, 0.74 and 0.82 of the sagittal length in stages C, D, and E, respectively, and in the size order of 0.82 for stage A and about 0.78 for stage B.

Transitory pygidia of stage D exhibit a wide length range in the majority of species studied, and the stage most likely includes two instars. The material is therefore interpreted as representing six meraspid stages, with an instar sequence A-B-C-D¹-D²-E (-F). About 10% of the specimens of stages C to E are unusually large, and appear to represent the succeeding instar, but with failed detachment of a segment. A few of the large E-stage specimens of *N. depressus* (described elsewhere) are clearly pathological with a partly detached segment (e.g., Fig. 190L), and they also show a terrace-line pattern matching stage F, but most of the inferred 'abnormal' large specimens show normal, fixed segments. In all cases subtraction of the length, accounted for by the suspected extra segment, places the specimens in the succeeding size group. The 'failed moults' strongly indicate that only one segment was released between the C/D¹/D²/E/F stages, which entails that the generation of thoracic segments must have been uneven.

Because of the generalized nature of juvenile nileids, a number of previous identifications cannot be upheld, which concerns the two small pygidia, identified as *N. limbatus* by Skjeseth (1952, p. 170; Pl. 2:9–10) (D and B stage), the transitory pygidium (stage D) assigned to *N. exarmatus* by V. Poulsen (1965, p. 75; Pl. 3:7), and the three juvenile pygidia, assigned to *N. e. exarmatus* and *N. e. orbiculatoides* by Schrank (1972, Pls. 2:2–3; 5:2). Tjernvik (1980, Textfigs. 3–4) reported *N. exarmatus* from the *M. simon* Zone in the Finngrundet core, but based on two transitory pygidia (B 400, B 401, coll. Uppsala Univ., representing stages E and D).

Fortey (1975a, p. 42; Pl. 10:6) described and figured a transitory pygidium, assigned to *Nileus glazialis costatus*, characterized by the absence of a concave border and by possessing at least 6 axial rings and 4 unreleased thoracic segments. The material of *Symphysurus* from the Komstad Limestone is undescribed, but contains several hundreds of juvenile pygidia, of which the smallest ones are alike the specimen in question, and it almost certainly belongs to *Symphysurus arcticus* Fortey, 1975. On the other hand, the juvenile pygidium assigned to *Symphysurus arcticus* by Fortey (1975a, pp. 62–63; Pl. 21:10, 12), is exceedingly similar to the juveniles of *Nileus* from the Komstad Limestone, and rather likely belongs to *Nileus 'glazialis' costatus*.

Nileus depressus group

syn. *Nileus glazialis* group, Tjernvik, 1980

Fig. 179

The *Nileus depressus* group (as defined here) includes:

Nileus depressus depressus (Boeck, 1838)

Nileus depressus glazialis Schrank, 1973

Nileus depressus costatus Fortey, 1975

Nileus depressus teres Tripp, 1976

Nileus depressus tengriensis Weber, 1948

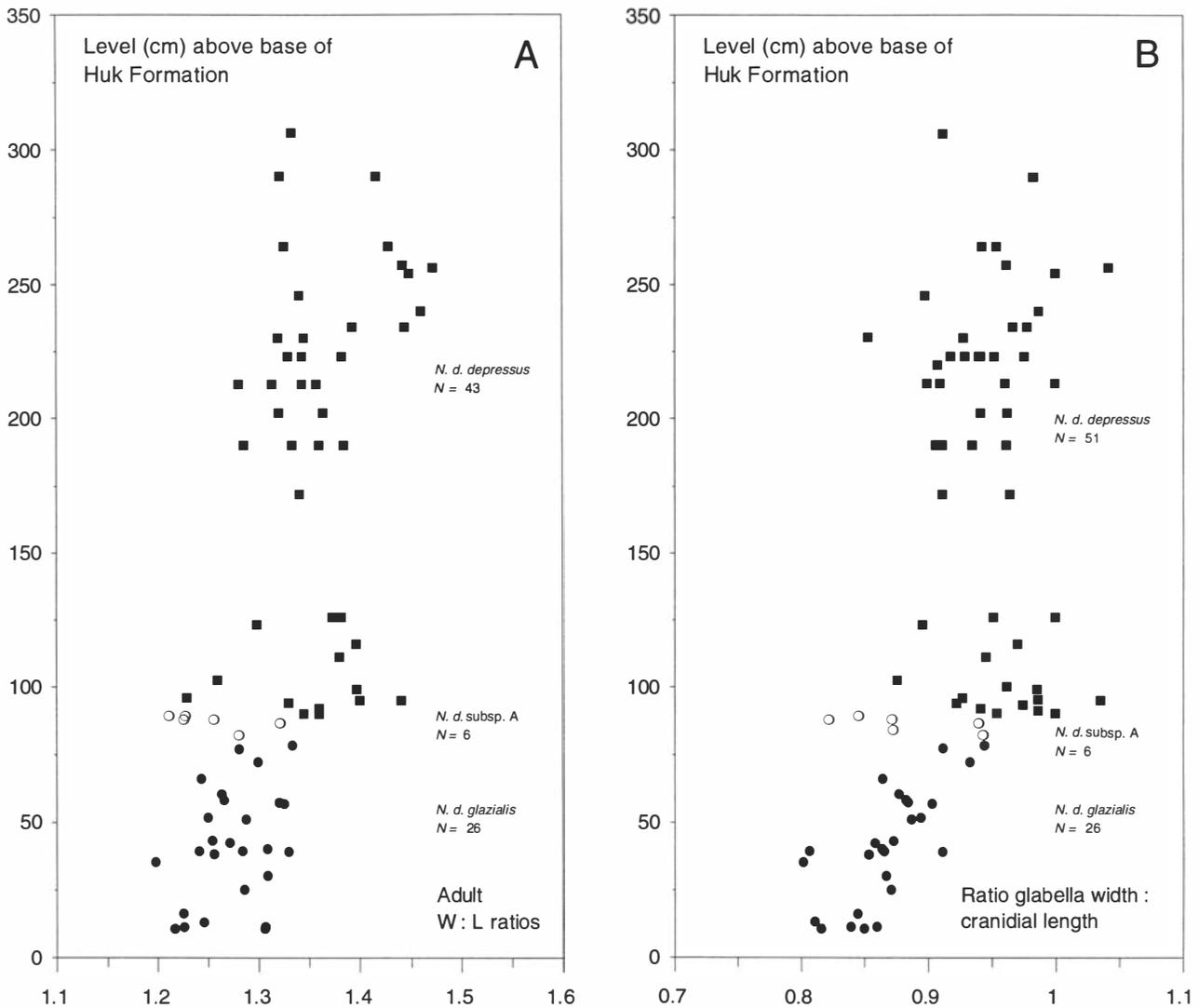


Fig. 179. Cranidia of *Nileus depressus*, Slemmestad. Adult specimens only (>5 mm long). The x-axes refer to Fig. 28. □A. Adult ratios between maximum cranial width (measured across palpebral lobes) and cranial length (sag.) plotted against stratigraphic occurrence. ○B. Adult ratios between glabella width (measured between posterior corners of palpebral lobes) and cranial length plotted against stratigraphic occurrence.

Nileus depressus schranki n.subsp.

Nileus depressus serotinus n.subsp.

Nileus depressus parvus n.subsp.

Nileus depressus subsp. A

Possibly related species:

Nileus chiton Pander, 1830 [*nomen dubium*]

Nileus transversus Lu, 1957

Nileus transversus Koroleva, 1982

Nileus huanxianensis Zhou in Zhou *et al.*, 1982

Nileus implexus n.sp.

Nileus planiceps n.sp.

Nileus latifrons n.sp.

Nileus sp. B (aff. *schranki*)

Members of the *N. depressus* group are small, and characterized by the presence of a 'depressus-type' terrace-line pattern on the pygidium, i.e. the entire pygidium (\pm the axial area) is covered with densely spaced terrace lines. The presence or absence of terrace lines on the pygidial axis is of no diagnostic value at the subspecies level (cf. Tjernvik 1980). The cranium usually has a more or less centrally rounded glabella, the anterior part of the cranium is somewhat truncate, and the eyes are large. The pygidial border is occasionally rather ill-defined or absent. It also appears to be a general feature that the test is rather thick by comparison to other species of *Nileus*, so furrows, tubercles etc., as seen on internal moulds, are comparatively well-defined.

The *N. depressus* group ranges at least from the middle Arenig to Caradoc, and it is very likely that a detailed study of

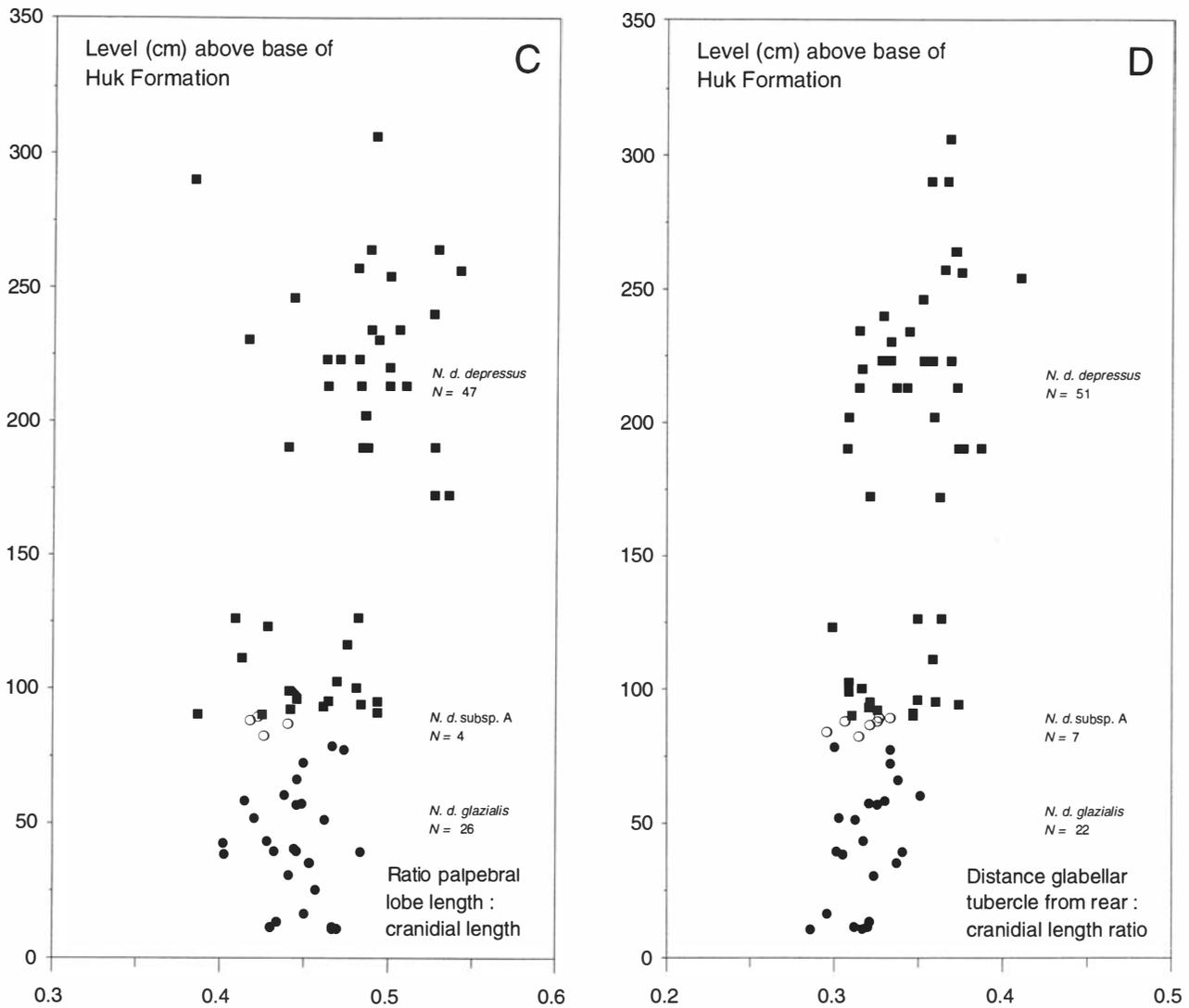


Fig. 179 (continued). □ C. Adult ratios between palpebral lobe length (exsag.) and cranial length plotted against stratigraphic occurrence. □ D. Adult ratios between the distance from posterior cranial margin to glabella tubercle and cranial length (sag.) plotted against stratigraphic occurrence.

Nileus on a global scale will lead to the identification of additional members and related species.

N. depressus depressus (Boeck) has a rather strongly convex cephalon (both ways) with an almost straight anterior cranial margin, a quite rounded glabella, strongly vaulted librigena (particularly in stratigraphically late specimens), and a very finely pitted surface lacking terrace lines; the pygidial border is ill-defined and occasionally absent; pygidial doublure with 15–20 lines in early specimens, and 13–15 lines in late. All furrows, as seen on internal moulds, are comparatively well-impressed.

N. depressus glazialis Schrank has a moderately convex (sag.) cephalon, the anterior cranial margin is gently rounded, the surface of cephalon is mostly smooth, but a few terrace lines may be present; compared to *N. d. depressus* the

cephalon is slightly more elongate; the pygidium has a narrow, concave border; pygidial doublure with 11–16 terrace lines.

N. depressus schranki n. subsp. is slightly more elongate than other subspecies of *N. depressus*, the cephalic convexity (sag.) is comparatively moderate to low, the anterolateral expansion of glabella is strong, the cephalic border continues almost to genal angle, the surface of cranidium is finely pitted; the pygidium has a comparatively well-defined concave border and the axial area, with a very few exceptions, is lacking terrace lines. The pygidial doublure is provided with 17–20 terrace lines.

N. depressus serotinus n. subsp. has a rather strongly convex cranidium (sag.), anterior cranial margin straight, truncate, palpebral lobes unusually long, cranial test surface

presumably smooth; pygidium without border and covered, axis inclusive, with terrace lines. Pygidial doublure provided with 15–16 terrace lines.

N. depressus parvus n. subsp. is minute, the cranidium is very strongly convex (sag.), axial furrows effaced (on testaceous material), palpebral lobes very long, glabellar tubercle situated far from posterior margin, and anterior branches of facial suture are subparallel, so glabella does not expand anterolaterally. Pygidium without border, and covered, axis exclusive, with terrace lines. The pygidial doublure is probably only weakly concave and provided with just 11–12 terrace lines.

N. depressus subsp. A resembles *N. d. glazialis*, but has a cranidium covered with terrace lines; the cranidial furrows, as seen on internal moulds, are fairly well-impressed; the pygidium shows densely spaced, very fine terrace lines and the pygidial doublure is provided with 18–19 terrace lines.

The non-Scandinavian *N. depressus costatus* Fortey, 1975 has a moderately convex cranidium (sag.), the anterior cranidial margin is fairly rounded, the cephalic axial furrows are effaced, even on internal moulds, but glabella appears rather elongate; the pygidium is without border, and has a doublure covered with only 8–12 terrace lines.

N. depressus teres Tripp, 1976 shows a straight anterior cranidial margin, large eyes, fairly strong cephalic convexity, 'depressus-type' terrace-line pattern on pygidium etc. and clearly belongs to the *depressus* group. The species is distinguished by its effaced cephalic axial furrows, the unusually large palpebral lobes, the smooth cephalic surface, and the well-developed pygidial border (cf. Tripp 1976).

Few details are available with regard to *N. depressus tengriensis* Weber, 1948, but the large palpebral lobes, the truncate cranidium, the fairly broad glabella and the presence of a 'depressus-type' terrace-line pattern on the pygidium clearly points to an assignment to *N. depressus*. The pygidium shows a concave border (see Weber 1948; Poletaeva in Khalfin 1960).

Remarks. – *Nileus depressus* has been more or less ignored since the days of Brögger (1882) (cf. Schmidt 1904; Tjernvik 1956; Tjernvik & Johansson 1980). In recent years it has been discussed solely by Schrank (1972), but he had only a cast of the lectotype pygidium at his disposal, and did not discover the subtle terrace-line pattern on this poorly preserved specimen.

The available material of *N. depressus* collected from the Hukodden Limestone and Lysaker Member (Huk Fm.) at Slemmestad, comprising more than 300 specimens, is divided among three groups, tentatively referred to as subspecies, viz. *N. depressus glazialis*, *N. depressus* subsp. A, and *N. depressus depressus* (in order of stratigraphical appearance). This succession resembles the occurrence in south central Sweden of *N. glazialis* subsp. 1, *N. glazialis glazialis*, and *N. glazialis* subsp. 2 in the sense of Tjernvik (1980) (see Fig. 146). *N. glazialis* subsp. 2 *sensu* Tjernvik is considered identical to

N. depressus depressus, and *N. glazialis* Schrank is ranked as a subspecies of *N. depressus*, and interpreted somewhat differently from Tjernvik (1980) (for details, see discussion of *N. d. glazialis*). Tjernvik assumed that the three subspecies represent a phylogenetic lineage, exhibiting a gradual evolution during the *M. polyphemus* to *A. expansus* Zones, and they were singled out as good index fossils (Tjernvik 1980, p. 203). The gradual changes regard an increasing glabella roundness, changing surface ornamentation, vanishing pygidial border etc. Some of these trends are also evident in the new material (cf. Fig. 179A–D), but the variable morphology is believed to mirror environmental changes mainly and not evolution. *N. glazialis* subsp. 1 and *N. glazialis glazialis sensu* Tjernvik 1980 are considered ecophenotypes of the same species. It follows that the usefulness of *N. 'glazialis'* for stratigraphy is more limited than indicated by Tjernvik. The possible phylogenetic relations within the group are remarked upon in the introductory section on *Nileus*.

Nileus depressus depressus (Boeck, 1838)

Figs. 180–186

Synonymy. – □1838 *Trilobites depressus* Ss. & Bk. Mscr. – Boeck, p. 142 (brief diagnosis). □v 1882 *Nileus Armadillo* Dalm. Var. *depressa*, Sars & Boeck [*partim*] – Brögger, pp. 62–64, Pl. 7:6–6a (description, occurrence, illustrations of cephalon and pygidium). □cf. 1904 *Nileus Armadillo* Dalm. [*partim*] – Schmidt, Pl. 8:12, 17, 17a (illustrations of cephalon with thoracic segments and pygidium with terrace lines). □v 1941 *Nileus armadillo* Dalman, var. *depressa* (Sars et Boeck MS) – Størmer, p. 142 (short discussion of species, designation of neotype). □cf. 1960 *Nileus armadillo* Dalman – Balashova, Pl. 6:1 (illustrations of enrolled specimen). □v 1972 *Nileus depressus* (Sars & Boeck, 1838) – Schrank, p. 367, Pl. 7:1 [*non* Pl. 7:2 = *Nileus cf. latifrons* n.sp.] (short description, occurrence, illustration of cast). □cf. 1976 *Nileus armadillo* Dalman [*partim*] – Balashova, pp. 138–139; Pl. 40:10 (illustrations of pygidial terrace-line pattern). □1980 *Nileus glazialis* subsp. 2 – Tjernvik & Johansson, pp. 192, 193, 194, 203 (short comments on diagnosis, occurrence listed). □cf. 1984 *Nileus depressus* (Boeck, 1838) – Wandås, Pl. 11D (side view of complete specimen).

Lectotype. – Here designated, complete specimen figured by Brögger (1882, Pl. 7:6, 6a). A cast is figured by Schrank (1972, Pl. 7:1a–c). Størmer (1941) designated another specimen as lectotype, because the one figured by Brögger (1882) was lost at that time. However, the specimen referred to by Størmer has never been figured, and it is not clear whether or not it originated from the original Sars & Boeck collection. Hence it is taken as a neotype. The description by Brögger was based on original material (cf. Brögger 1882, p. 63).

Material. – Ten complete specimens, 8 cephalae, 66 cranidia, 2 librigenae, 75 pygidia, 39 juvenile pygidia.

List of material. — □ Complete specimens A 111 (pim) [MGUH 22.767], A 119a (pim), A 132 (pim) [MGUH 22.776], A 193 (t) [MGUH 22.761], A 199 (im), A 288 (t) [MGUH 22.757], A 577 (im) [MGUH 22.768], A 819 (t) [MGUH 22.755], A 1006 (pim), A 1090 (t) [MGUH 22.790]. □ Cephalon A 54 (pim) [MGUH 22.756], A 110 (im), A 274 (pim) [MGUH 22.765], A 569 with thoracic segments (im) [MGUH 22.758], A 840a (pim) [MGUH 22.762], A 844 (pim), A 1094 with thoracic segments (t), A 1099 with thoracic segments (t). □ Cranidia A 50 (im), A 55 (im), A 57 (im), A 66 (pim), A 71? (im), A 76 (im), A 79a (pim), A 83? (im), A 100 (pim), A 123 (im), A 136b (im), A 138a? (im), A 138b (pim), A 139 (im), A 141? (im), A 159 (im), A 162a (im) [MGUH 22.770], A 162b (im), A 166a? (t), A 168a (im), A 170 (im), A 173 (pim), A 176 (pim), 203 (im), 206? (im), A 216 (im) [MGUH 22.760], A 229 (pim) [MGUH 22.759], A 240 (pim) [MGUH 22.764], A 243 (im), A 260 (im) [MGUH 22.769], A 270a (im), A 272 (im) [MGUH 22.766], A 293a (im), A 293b (im), A 309a (pim), A 309c (im), A 327 (c), A 344a (t), A 346 (pim), A 794 (im), A 798b (is), A 799 (im), A 804 (im), A 805 (im), A 814c (pim), A 837 (im), A 839 (im), A 851 (t), A 860 (im), A 865 (im), A 880a (c), A 880c (im), A 900 (t) [MGUH 22.763], A 936 (im) A 938 (c), A 944 (im), A 956 (im), A 973 (im), A 984 (im), A 991 (c), A 1001 (pim), A 1016 (im), A 1019 (im), A 1039? (im), A 1084? (im), A 1092 (im). □ Librigenae A 129c (double), A 822 (t). □ Pygidia A 36 (t), A 52 (im), A 58 (im) [MGUH 22.772], A 64 (t), A 75 (im), A 91 (im), A 93 (im) [MGUH 22.771], A 95 (im), A 99 (pim), A 104 (im), A 118 (im), A 119b (im), A 124 (pim), A 125 (im), A 126 (im), A 129a (t), A 130 (im), A 131a (im), A 131b (im), A 135 (im), A 136a? (pim), A 144 (im), A 145? (im), A 147 (t), A 148 (pim), A 149 (c), A 160 (im), A 162c (im), A 163? (im), A 166b (pim), A 175 (pim), A 179 (t), A 189 (im), A 190? (im), A 192 (im), A 205 (t) [MGUH 22.787], A 218 (pim), A 258 (im), A 268 (im), A 270b (im), A 287 (im), A 295 (im), A 297 (im), A 323 (pim), A 329 (im), A 333a (im), A 347 (pim), A 356? (im), A 803 (c), A 808 (pim), A 812 (im), A 818 (im), A 821 with thoracic segments (im), A 825 (pim), A 838 (pim) [MGUH 22.788], A 840b (pim), A 861 (t) [MGUH 22.789], A 873 (im), A 880b (t), A 888b (c), A 891 (t), A 906 (is) [MGUH 22.777], A 936 (im), A 962 (pim), A 963 (pim), A 977 (im) [MGUH 22.774], A 996 (im) [MGUH 22.773], A 1017 (im), A 1036 (im), A 1068 (pim), A 1083 (t) [MGUH 22.780], A 1087 (pim), A 1089a (pim), A 1089b (im), A 1091a? (im). □ Juvenile pygidia A 27 (t), A 30 (t), A 79b (im) [MGUH 22.783], A 101 (t) [MGUH 22.778], A 105 (im), A 129b? (im), A 137 (pim), A 143 (t) [MGUH 22.782], A 164 (c), A 171? (im), A 187 (t) [MGUH 22.779], A 196 (t), A 201 (t) [MGUH 22.784], A 281a (em) [MGUH 22.786], A 281b (em), A 284 (im), A 318 (im), A 319 (im), A 333b (im), A 338 (im), A 343 (im), A 344b (im), A 350 (im), A 358 (im), A 363 (pim), A 369 (im) [MGUH 22.775], A 798a (im), A 800 (c), A 814a (t) [MGUH 22.785], A 814b (t), A 826 (c), A 835 (t), A 853 (pim), A 888a (pim), A 913 (t) [MGUH 22.781], A 926 (t), A 966 (t), A 1085 (im), A 1091b (im).

Occurrence. — *Nileus depressus depressus* occurs frequently in bed interval M-7 (Hukodden Limestone) to A-23 (Lysaker Member) at Slemmestad, representing almost the entire *M. limbata* Zone. *N. d. depressus* or a closely resembling subspecies reappears in the Svartodden Limestone Member (*A. 'raniceps'* Zone), see discussion below.

N. depressus depressus is firmly believed to correspond to *N. glazialis* subsp. 2 *sensu* Tjernvik (1980), reported from the *M. limbata* Zone of Sweden. *N. d. depressus* or a closely similar subspecies is also present in the eastern Baltic area, see discussion below.

Diagnosis. — Small form. Cephalon quite convex (both ways) with truncate anterior cranidial margin; glabella broad, central part rounded; cephalic axial furrows comparatively well-defined on outside of test; librigenae strongly vaulted posterolaterally, and without lateral border posterior to midlevel of eye; cephalic test surface usually lacks terrace lines. Py-

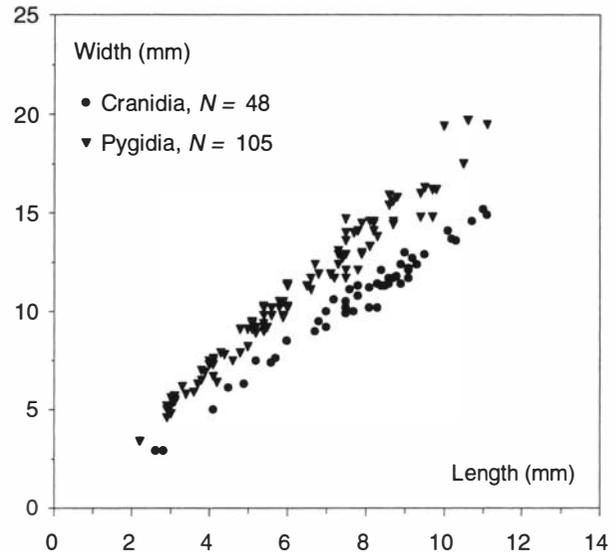


Fig. 180. Cranidia and pygidia of *Nileus depressus depressus*. Maximum width plotted against sagittal length.

gidium covered with 'depressus-type' terrace-line pattern, normally less dense on axis; border steep, ill-defined and occasionally absent. [Emended from Boeck 1838.]

Description. — Small for a *Nileus*, largest measurable cranidium 11.2 mm long, largest pygidium 12.0 mm long. The damaged cranidium A 973 may originally have been about 12–12.5 mm long. Ratios between cephalon, thorax and pygidium are 28:47:25 (dorsal projection) in two complete specimens from beds M-7 and A-5; cephalon is possibly relatively shorter in later specimens. In articulated specimens the length and width of pygidium average, respectively, 0.87 ($N=2$) and 0.86 ($N=4$) of the cephalic length and width.

Cephalic outline slightly reniform in early specimens, more strongly so in late; L:W ratio varies between 0.52 and 0.61 (mean 0.57; $N=10$), with a trend towards a relatively wider cephalon in the latest representatives. Cephalic L:W ratio averages 0.60 for six specimens from beds M-7 to A-5, and 0.54 for four specimens from beds A-9 to A-18. The rather wide range of cranidial W:L ratios (Fig. 183B; Table 22) is possibly augmented by compaction. Glabella about as wide as long (Table 22), and delimited from palpebral lobes by wide and shallow axial furrows, which, though, are better defined externally than in most other nileids; they are well-impressed on internal moulds. Furrows arcuate, giving the central portion of glabella a rounded appearance; the degree of 'roundness' is, however, varying, but generally more pronounced than in earlier subspecies of *N. depressus*. Anterior branches of facial suture diverge for a short distance in front of eyes at an angle of about 30–35° to sagittal line, to turn almost straight inward, and merge smoothly at front. Anterior cranidial margin is therefore truncate; some early speci-

Table 22. *Nileus depressus depressus*. Ranges for variation of crania, expressed as ratios of cranial length.

Size (mm)	Maximum width of cranium			Glabella width			Palpebral lobe length (exsag.)			Glabellar tubercle, distance to post. margin		
	Range	Mean	N	Range	Mean	N	Range	Mean	N	Range	Mean	N
2.6–2.8	1.04–1.12	1.08	2	0.68–0.73	0.70	2	0.46–0.50	0.48	2	0.32–0.35	0.32	2
4.1–4.9	1.22–1.36	1.29	3	0.82–0.85	0.84	3	0.49–0.53	0.51	3	0.34–0.36	0.35	3
>5.2	1.23–1.47	1.36	43	0.85–1.04	0.95	47	0.38–0.54	0.47	47	0.30–0.41	0.35	51

mens, particularly from bed M-7, have a slightly more rounded anterior margin. Transverse glabellar convexity rather low, sagittal convexity moderate to fairly strong; moderate convexities predominate among specimens from the Hukodden Limestone. Palpebral lobes comparatively long (Fig. 183C; Table 22). Crania from the Hukodden Limestone tend to show shorter lobes, exsagittal length corresponds on average to 0.46 ($N = 17$) of the cranial length, compared to crania from the Lysaker Member, showing average lobe lengths corresponding to 0.49 ($N = 30$) of the cranial length (Fig. 179C). Mesial glabellar tubercle quite prominent on internal moulds, whereas it is difficult to see on testaceous material. The latest specimens from bed interval A-13 to A-19 generally show a more advanced tubercle, average distance from posterior margin is 0.37 of the cranial length ($N = 8$) (Fig. 179D). Occipital region as in *N. d. glazialis*, although the muscle insertion sites flanking the mesial expansion of the occipital furrow appear marginally better defined in *N. d. depressus*. A few internal moulds show paired very shallow muscle imprints on glabella (Fig. 181E–F); all muscle areas are in rare specimens with well-preserved test outlined by a dullness of the test surface. Posterior branch of facial suture usually straight, and runs obliquely backward-outwards at an angle of about 30° to sagittal line; exsagittal length of posterior fixigena averages 0.16 times the cranial length ($N = 41$). Outer margin of librigena may be thickened. Posterolateral portion of librigena in early specimens from beds M-7 to A-5 similar to *N. d. glazialis*, with a lateral border tapering rearwards from midlevel of eye to stop shortly before genal angle (Fig. 181A). Late specimens from beds A-7 to A-18 have a strongly vaulted, steeply sloping, almost vertical posterolateral librigena, and no posterior continuation of lateral border from midlevel of eye (Fig. 181C, L). The changes in librigenal morphology is associated with a slightly increased sagittal convexity of cephalon. A few cephalon from bed M-7 show terrace lines posterolaterally on glabella, on palpebral lobes, along posterior margin and posterolaterally on librigena, whereas other specimens from the same bed seem to lack terrace lines. Some cephalon from bed A-1 also show terrace lines posteriorly on librigena, and a single cranidium from bed A-20 carries terrace lines posterolaterally on glabella, but the majority of cephalon of *N. depressus depressus* are smooth except for a very delicate pitting of the test, which is obliterated by even the faintest corrosion. A pitted test has, actually, been

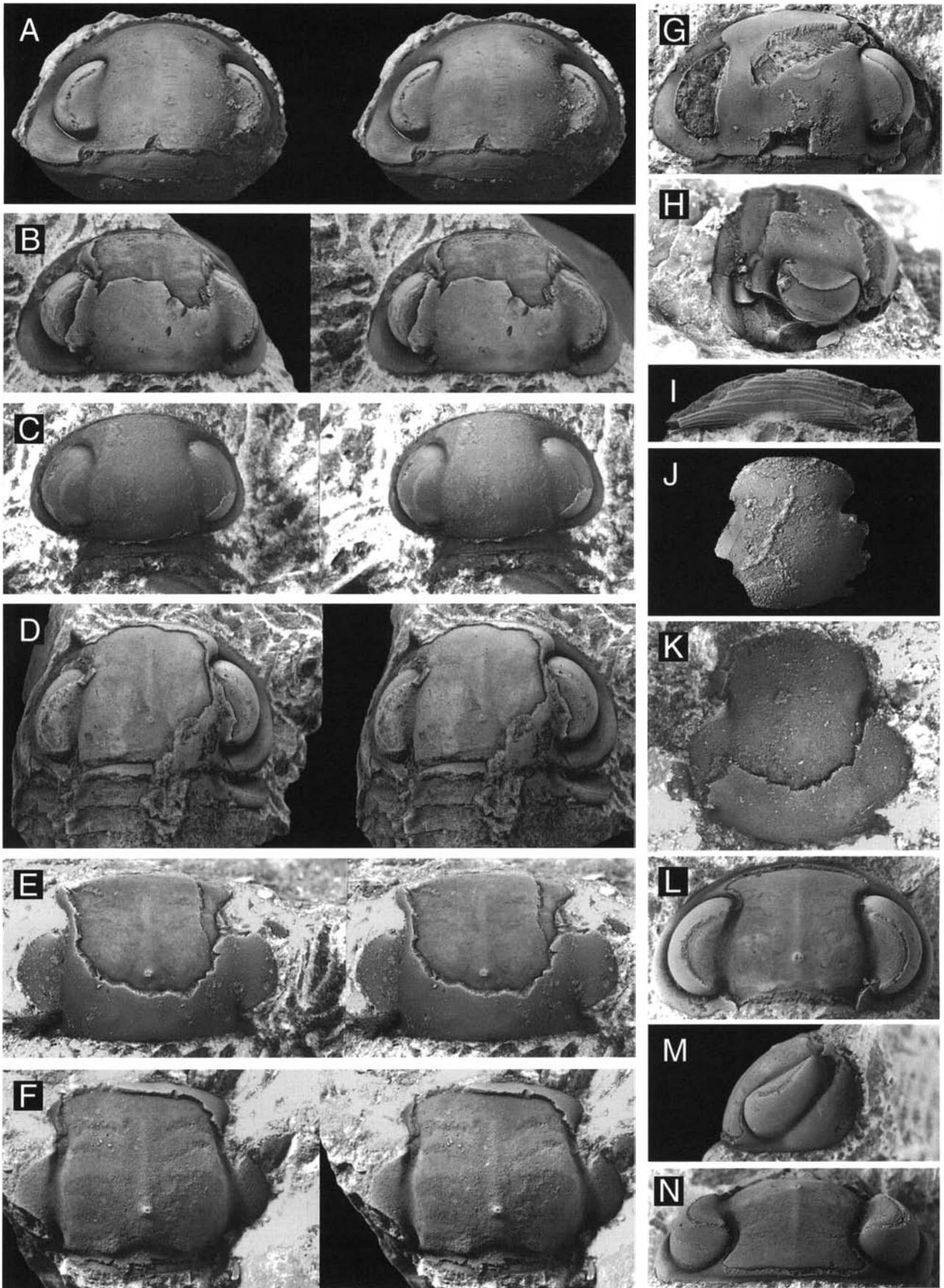
observed with certainty only in five specimens (from bed interval M-7 to A-13), the surface of the remaining material is corroded. Two specimens (from bed A-8 and A-20) may lack the pits.

Cephalic doublure extends mesially for about 0.3 of the cephalic length, tapers backward; posterolateral width (tr.) about 0.25 of mesial width (sag.). Doublure strongly concave, inner part subvertical; it is provided with 10–12 coarse, continuous terracel lines; hypostomal socket almost smooth, except for a few short lines just inside margin.

Hypostome not yet identified.

Thorax tapers gently rearwards; posterior segment is nearly 0.9 times as wide (tr.) and about 0.8 times as long as the anterior segment ($N = 3$). Axis occupies on average 0.51 ($N = 4$) of the pleural width on the first segment, expands almost imperceptibly towards the third segment and thence tapers rearward. Axial width on posterior segment averages 0.85 ($N = 4$) of the axial width on anterior segment. Axis delimited by the position of the unusually distinct articulating processes on anterior margin and by shallow 'pseudo' axial furrows, formed by the row of oblique, short pleural furrows running immediately behind the articulating pro-

Fig. 181. *Nileus depressus depressus* (Boeck, 1838). □A. Early cephalon showing sagittal 'wrinkling' of cuticle and comparatively wide lateral border, stereo-pair, $\times 3$ (compare B–C, illustrating the stratigraphic variability of librigena steepness), . Entire specimen MGUH 22.755 (A 819) (pygidium shown in Fig. 184L), bed M-7, Slemmestad. □B. Partly exfoliated cephalon, stereo-pair, $\times 3$. MGUH 22.756 (A 54), bed A-1, Slemmestad. □C. Late small cephalon showing steep librigenae and narrow lateral border, stereo-pair, $\times 5$. Complete specimen MGUH 22.757 (A 288), bed A-18, Slemmestad. □D. Largely exfoliated cephalothorax, stereo-pair, $\times 3$. MGUH 22.758 (A 569), Lysaker Member, Slemmestad. □E. Partly exfoliated late cranidium showing faint traces of paired muscle impressions on glabella and a rather truncate anterior margin, stereo-pair, $\times 4$. MGUH 22.759 (A 229), bed A-13, Slemmestad. □F. Internal mould of cranidium showing paired muscle impressions on glabella, stereo-pair, $\times 4$. MGUH 22.760 (A 216), bed A-11, Slemmestad. □G–H. Somewhat damaged cephalon, dorsal ($\times 3$) and side ($\times 4$) views, the latter showing detail of doublure. Complete specimen MGUH 22.761 (A 193), bed A-9, Slemmestad. □I. Damaged cephalon, ventral view showing anterior part of doublure, $\times 4$. MGUH 22.762 (A 840), bed M-7, Slemmestad. □J. Corroded juvenile cranidium, $\times 9$. MGUH 22.763 (A 900), bed M-9, Slemmestad. □K. Partly exfoliated juvenile cranidium, $\times 9$. MGUH 22.764 (A 240), bed A-13, Slemmestad. □L–N. Exfoliated late cephalon showing very steep librigenae, dorsal, side and frontal views, $\times 4$. MGUH 22.765 (A 274), bed A-14, Slemmestad.



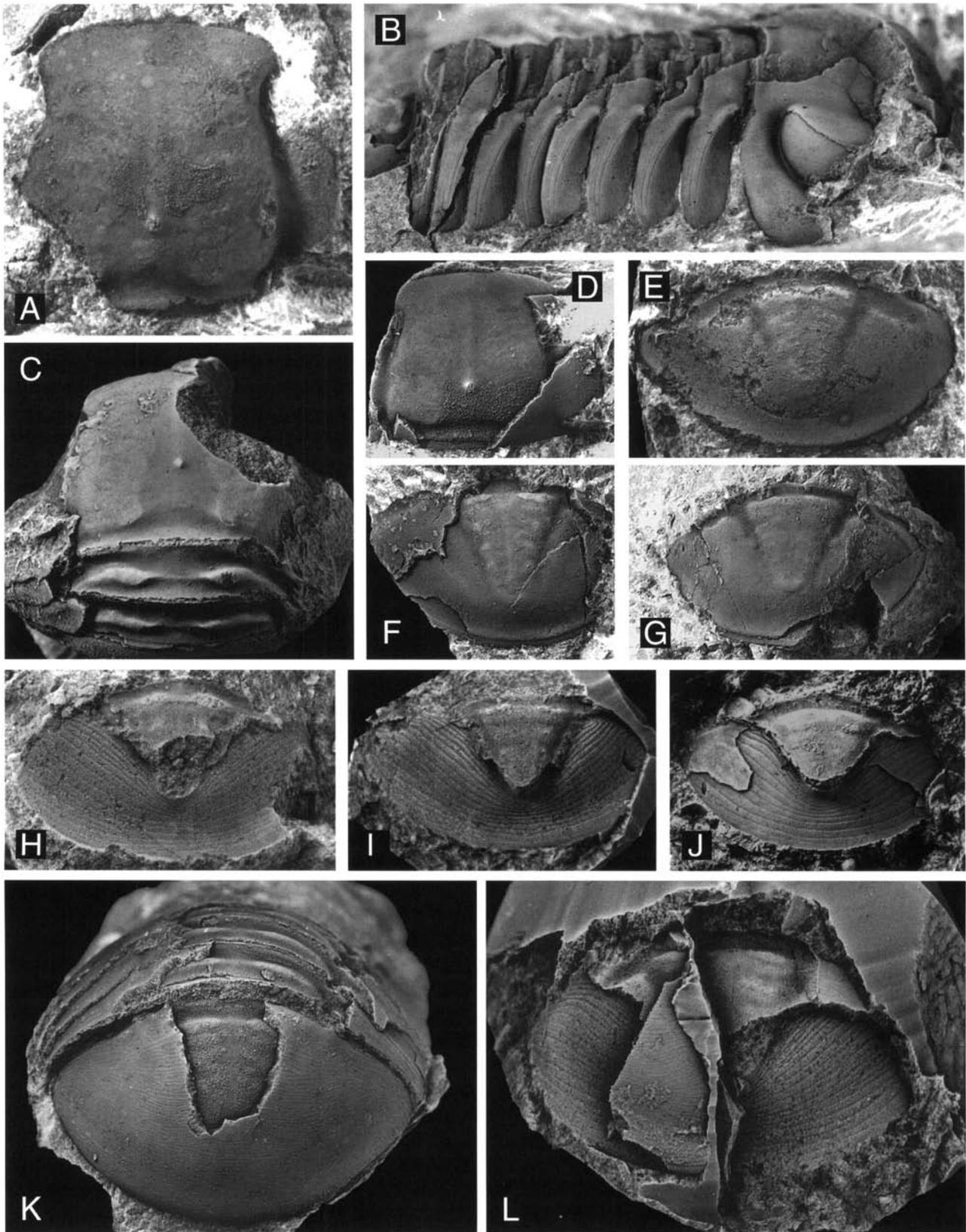


Fig. 182. *Nileus depressus depressus* (Boeck, 1838). □A. Internal mould of cranium showing paired muscle-insertion sites on glabella, $\times 6$. MGUH 22.766 (A 272), bed A-14, Slemmestad. □B. Compacted entire specimen, side view showing thoracic articulation, $\times 4$. MGUH 22.767 (A 111), bed A-4, Slemmestad. □C. Internal mould of complete specimen, close-up of anterior thoracic segments and posterior part of cephalon, showing muscle-insertion sites, $\times 6$. MGUH 22.768 (A 577), Lysaker Member, Slemmestad. □D. Internal mould of small, late cranium, $\times 6$. MGUH 22.769 (A 260), bed A-13, Slemmestad. □E. Internal

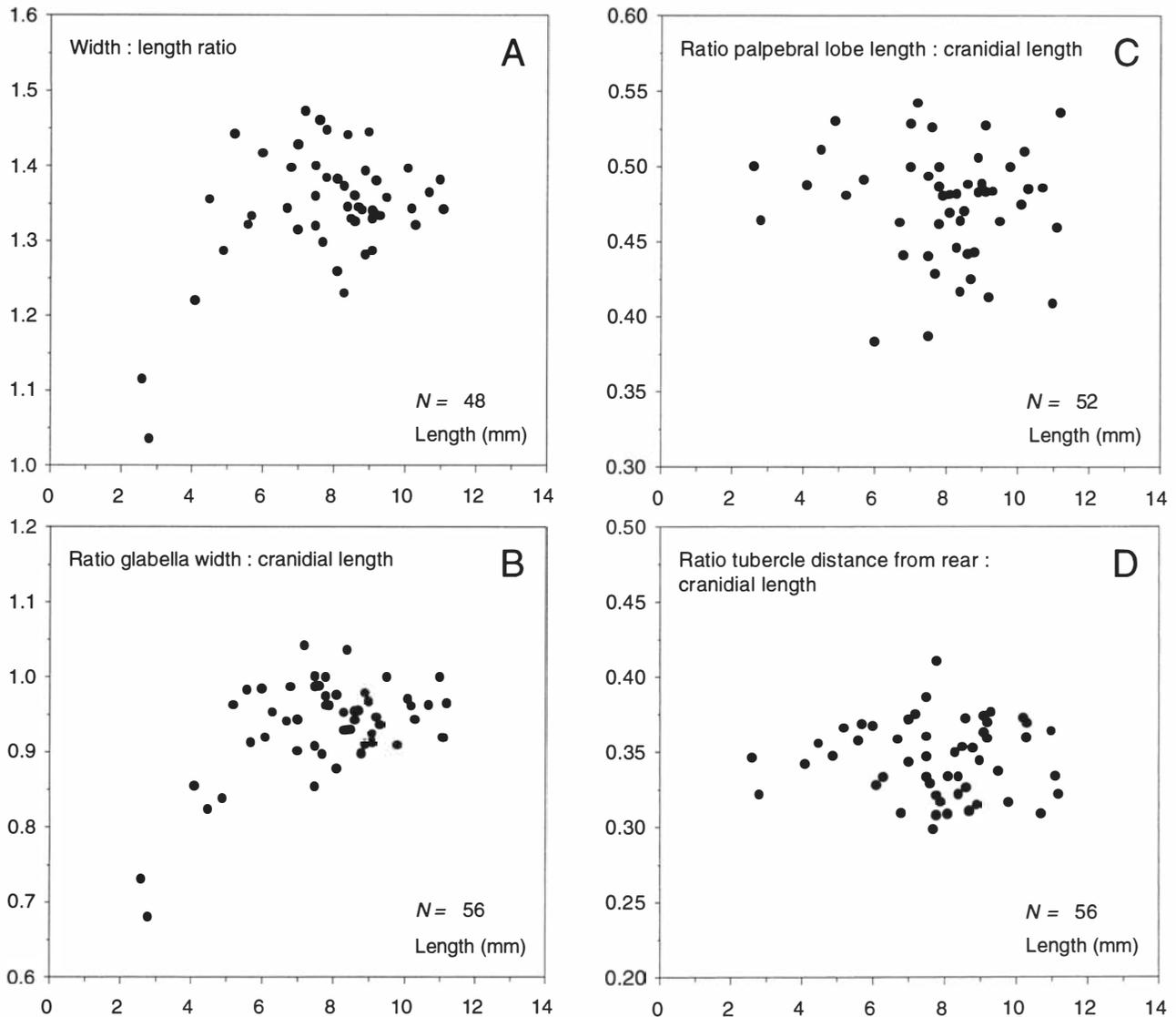


Fig. 183. Crania of *Nilæus depressus depressus*. □A. Ratio between maximum width across palpebral lobes and cranial length plotted against sagittal length. □B. Ratio between glabella width (measured between posterior corners of palpebral lobes) and cranial length plotted against cranial length. □C. Ratio between palpebral lobe length (exsag.) and cranial length plotted against cranial length. □D. Relative position of glabellar tubercle plotted against cranial length.

mould of pygidium showing axis, $\times 5$. MGUH 22.770 (A 162a), bed A-7, Slemmestad. □F. Internal mould of pygidium showing axis, $\times 6$. MGUH 22.771 (A 93), bed A-3, Slemmestad. □G. Internal mould of pygidium showing axis, $\times 3$. MGUH 22.772 (A 58), bed A-1, Slemmestad. □H. Internal mould of pygidium showing doublure, $\times 4$. MGUH 22.773 (A 996), bed M-10, Slemmestad. □I. Latex cast of internal mould of pygidium showing doublure, $\times 4$. MGUH 22.774 (A 977), bed M-10, Slemmestad. □J. Latex cast of internal mould of small pygidium showing doublure, $\times 6$. MGUH 22.775 (A 369), bed A-23, Slemmestad. □K. Well-preserved pygidium showing external 'depressus-type' terrace-line pattern, $\times 4$. Entire specimen MGUH 22.776 (A 132), bed A-5, Slemmestad. □L. Latex cast of pygidium showing doublure and portion of exterior terrace-line pattern, $\times 6$. MGUH 22.777 (A 906), bed M-9, Slemmestad.

cesses on each segment. These furrows are well-impressed on internal moulds, more so than in most other nileids described here. All specimens show three to five transverse, fine terrace lines on the pleurae. The axis of an early specimen from bed M-7 is covered with terrace lines; muscle insertion sites are indicated by irregularities in the pattern (Fig. 181A). There are no lines in the pleural furrows flanking the axis. Specimens of *N. d. depressus* from beds A-4 to A-18 have an almost smooth thoracic axis, with only a single or a few transverse lines present.

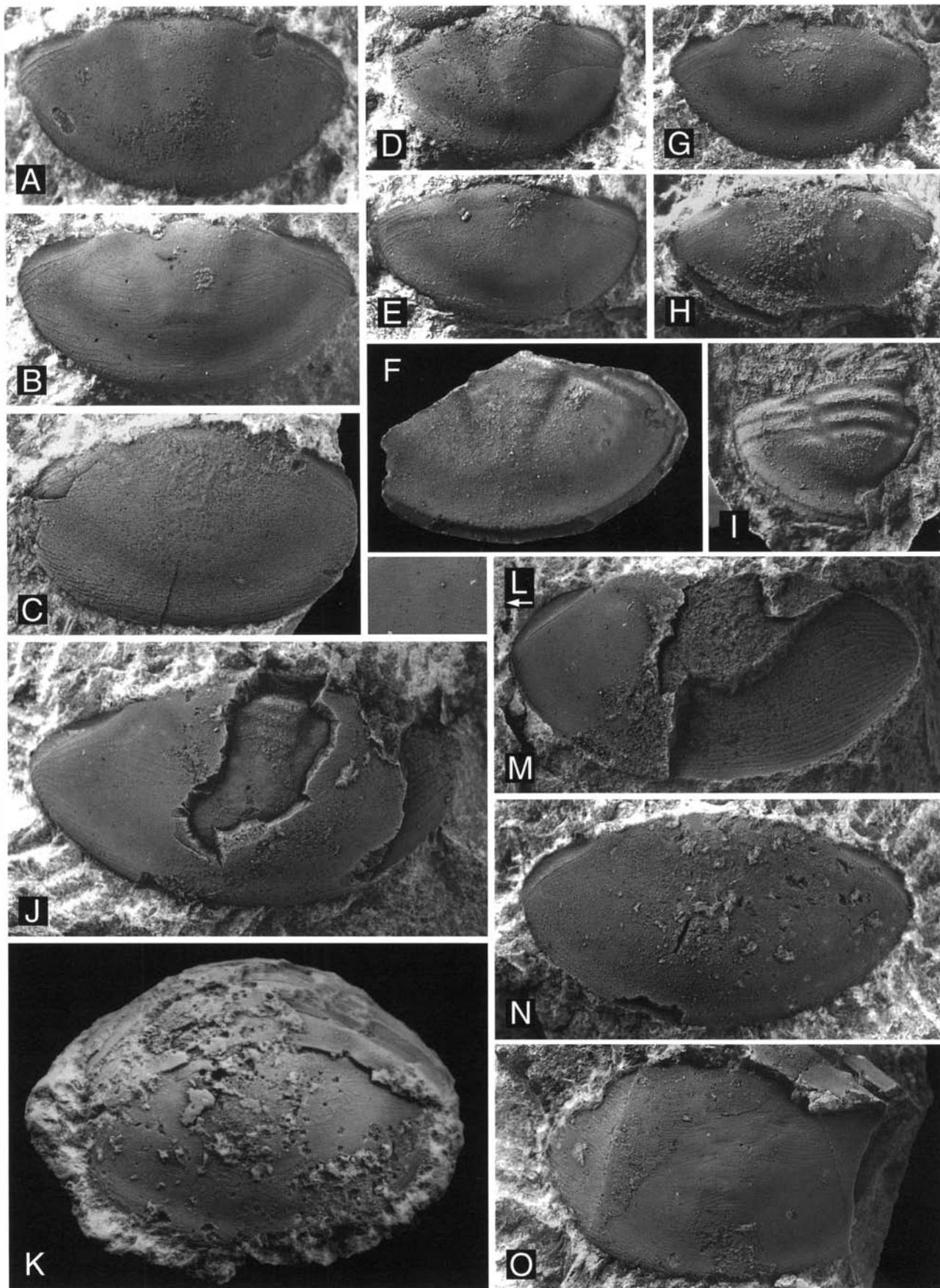


Table 23. *Nileus depressus depressus*. Ranges for variation of pygidia, expressed as ratios.

Size (mm)	Pygidial L:W ratio			Axial width : pygidial width			Axial length : pygidial length			Border length (sag.) : pygidial length		
	Range	Mean	N	Range	Mean	N	Range	Mean	N	Range	Mean	N
2.2–3.0 [Stage D]	0.63–0.65	0.64	2	—	0.38	2	—	—	0	—	0.27	2
2.8–3.4 [Stage E]	0.54–0.63	0.57	8	0.35–0.41	0.37	6	—	—	0	0.26–0.28	0.27	7
3.3–5.4 [Hol.]	0.53–0.61	0.56	22	0.30–0.39	0.35	15	—	—	0	0.20–0.24	0.22	17
>5.5 [Hol.]	0.51–0.66	0.58	60	0.32–0.44	0.38	49	—	—	0	0.13–0.22	0.18	39

Pygidium (ratios shown in Table 23) very similar to that of *N. depressus glazialis*. The most important difference concerns the border, which is much steeper, often almost as steep as the pleural fields, and, consequently, comparatively ill-defined; some pygidia are fully convex. Furthermore, the anterior pleural furrow, defined on internal moulds between axis and inner termination of articulating facet, is wider, and the pygidial test ornamentation is less distinctly engraved, and usually not impressed on internal moulds; only three exfoliated specimens in the material at hand show very faint imprints of terrace lines. The line density on the pleural fields is rather variable (Fig. 48); the variation is essentially not size-related (Fig. 185C). There is a drop in line densities between beds A-2 and A-3, and the pygidia generally show low densities up to bed A-11. Specimens from bed A-20 again show high densities. For remarks on the meandering terrace-line density, see section on autecology. One pygidium from bed M-7 shows terracelines all over axis with the same density as

on the pleural fields, while another specimen from the same bed has sparser and shorter lines in the axial area, compared to the density on the pleural fields, which appears to be the typical condition for *N. d. depressus*, at least in bed interval M-7 to A-7. Specimens from bed A-11 and A-20 have no terrace lines on axis; a single pygidium from bed A-4 has preserved a small patch of axial test showing fine pits, similar to those seen on well-preserved cephalia, and it is possible that the apparently smooth axis of late specimens actually is pitted. Doublure moderately to strongly concave (differences due to compaction?). Fifteen to twenty lines were counted across the doublure in pygidia from bed interval M-7 to A-13, while pygidia from beds A-22 and A-23 show a total of thirteen to fifteen lines.

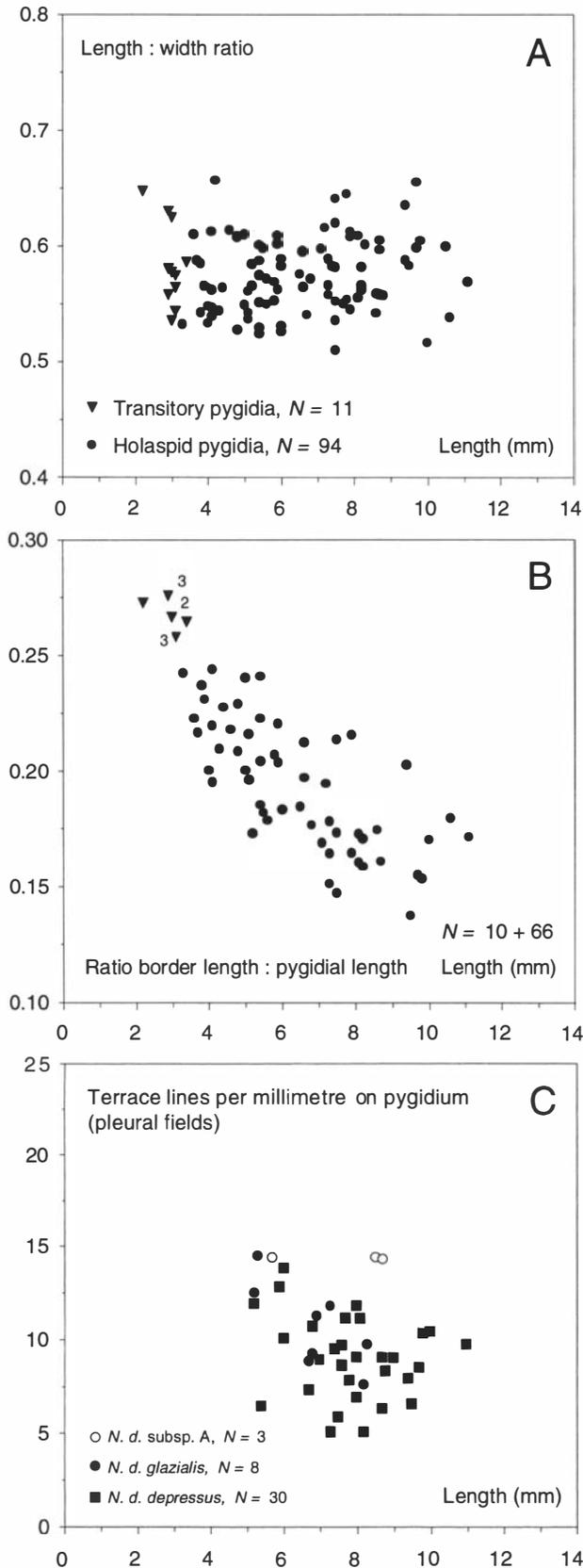
Juveniles. – By comparison to larger specimens, cranidia less than 5 mm long have a slightly more rounded anterior margin, a less strong sagittal convexity (particularly pronounced in the smallest specimens) and a relatively elongate glabella. Palpebral lobes appear but slightly narrower (tr.), and are situated relatively posteriorly, the distance from posterior margin of cranidium to hind corner of lobe is equivalent to about 0.11–0.13 of the cranial length. Test surface of the small cranidia seemingly smooth.

Two D-stage pygidia, 2.2 and 3.0 mm long, and ten E-stage pygidia, 2.8–3.3 mm long, match the description on pp. 244–245. Most E-stage specimens have a smooth test surface, except for single terrace lines outlining the fixed segment, whereas specimen A 143 exhibits an openly spaced ‘*orbiculatoides*’ pattern on the pleural fields.

Holaspid pygidia, 3.5 to 5.4 mm long ($N=23$), have a few terrace lines on the pleural fields, arranged in an ‘*orbiculatoides*’ pattern. These pygidia usually also have a better defined concave border compared to fully adult specimens. Axis is but faintly raised above pleural fields. Only three pygidia, less than 5.4 mm long (the smallest specimen is 4.3 mm long) show the adult terrace-line pattern.

Affinities. – *Nileus depressus depressus* is envisaged as a descendent of *N. d. glazialis* (Fig. 146), but may, in fact, simply represent a different ecophenotype. The early cephalia of *N. d. depressus* are very similar to those of *N. d. glazialis*, but can be distinguished by the wider glabella, the more truncate anterior cranial margin, the finely pitted test surface and the but slightly narrower anterior border. The later cephalia of *N. d.*

Fig. 184. *Nileus depressus depressus* (Boeck, 1838). □A. Small holaspid pygidium showing almost smooth cuticle surface, ×9. MGUH 22.778 (A 101), bed A-3, Slemmestad. □B. Small holaspid pygidium showing ‘*orbiculatoides*-type’ terrace line pattern, ×8. MGUH 22.779 (A 187), bed A-8, Slemmestad. □C. Rather small pygidium, showing extensive terrace lines and proportionally broad concave border; the terrace lines are, though, shorter and more irregular than in a fully developed ‘*depressus*-type’ terrace line pattern, ×6. MGUH 22.780 (A 1083), bed M-9, Slemmestad. □D. Transitory pygidium, stage E, ×9. MGUH 22.781 (A 913), bed M-9, Slemmestad. □E. Transitory pygidium, stage E, showing open ‘*orbiculatoides*-type’ terrace line pattern, ×9. MGUH 22.782 (A 143), bed A-6, Slemmestad. □F. Internal mould of small holaspid pygidium, ×9. MGUH 22.783 (A 79b), bed A-3, Slemmestad. □G. Transitory pygidium, stage E, ×9. MGUH 22.784 (A 201), bed A-9, Slemmestad. □H. Somewhat corroded transitory pygidium, stage E, ×9. MGUH 22.785 (A 814a), bed M-7, Slemmestad. □I. Latex cast of internal mould of transitory pygidium, stage D, ×10. MGUH 22.786 (A 281a), bed A-16, Slemmestad. □J. Small holaspid pygidium showing open ‘*orbiculatoides*-type’ terrace line pattern, ×6. MGUH 22.787 (A 205), bed A-10, Slemmestad. □K. Corroded pygidium showing fully developed ‘*depressus*-type’ terrace line pattern, ×5. Cephalon figured in #F180:A. Complete specimen MGUH 22.755 (A 819), bed M-7, Slemmestad. □L–M. Partly exfoliated pygidium showing doublure and dorsal ‘*depressus*-type’ terrace line pattern, ×5; close up ×8. MGUH 22.788 (A 838), bed M-7, Slemmestad. □N. Slightly corroded pygidium showing rather ill-defined border, ×5. MGUH 22.789 (A 861), bed M-7, Slemmestad. □O. Partly compacted showing comparatively open ‘*depressus*-type’ terrace line pattern, ×6. Complete specimen MGUH 22.790 (A 1090), bed A-7, Slemmestad.



depressus are relatively wide, influencing the cranial W:L ratio (Fig. 186A), and they also have strongly vaulted librigenae, a stronger sagittal convexity, an even wider and more rounded glabella (see Fig. 186B), and a still narrower anterior border. The pygidia of the two forms are very similar (Fig. 186E–F), and isolated specimens may be difficult to assign to subspecies. The border of *N. d. depressus* is, however, generally poorly defined or absent, internal moulds show a more distinct anterior pleural furrow, and the doublure of early specimens usually show a higher number of terrace lines than present in *N. d. glazialis*.

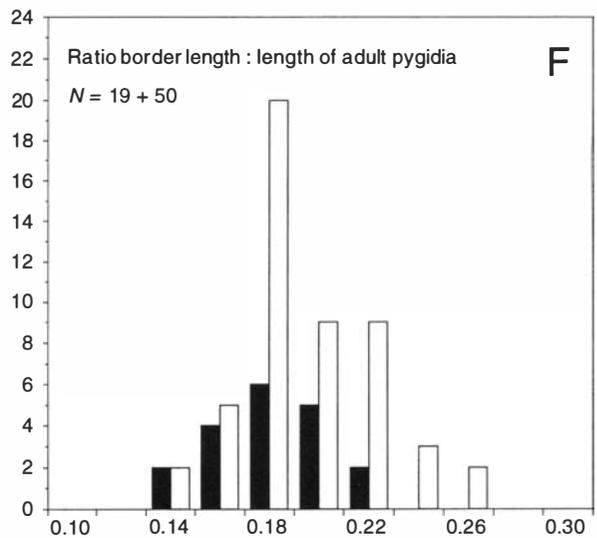
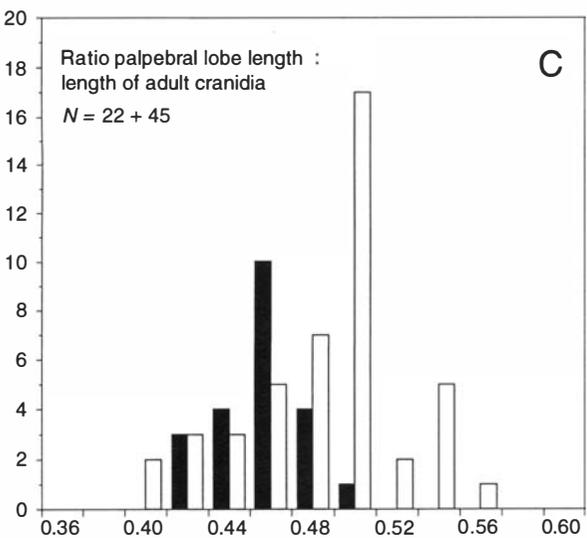
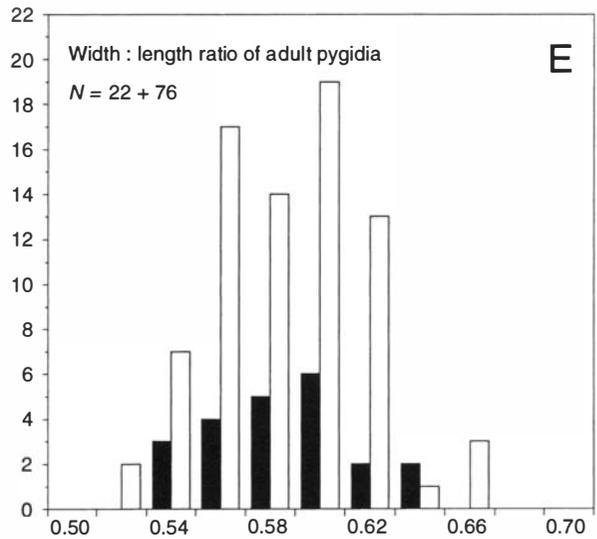
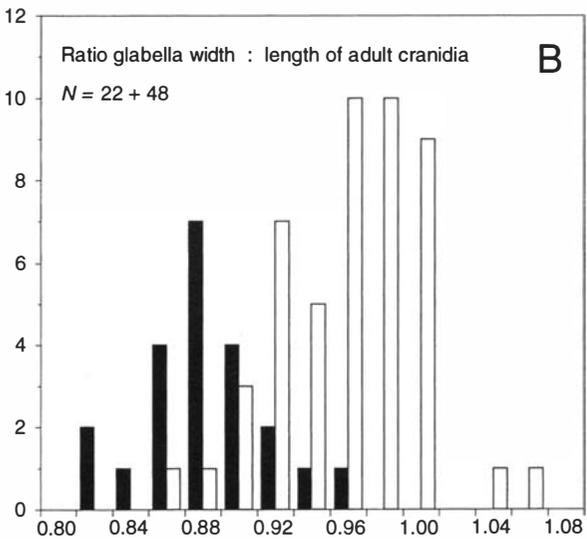
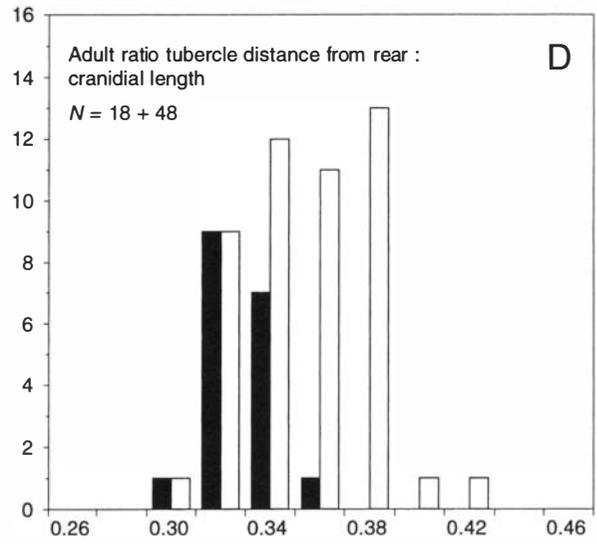
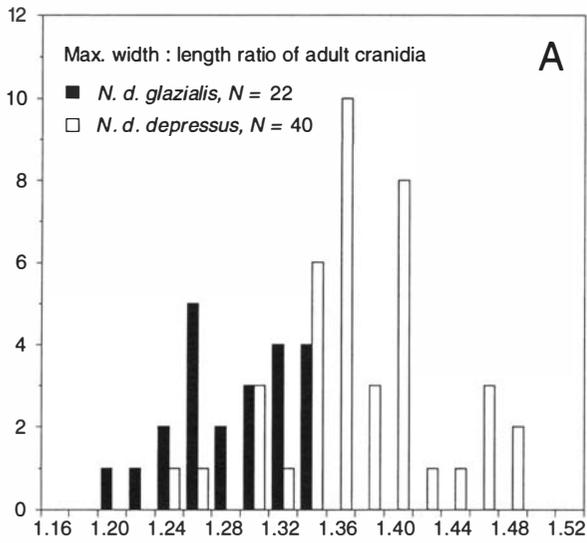
N. depressus depressus resembles *N. depressus serotinus* n.subsp. in a number of aspects, and the two forms are thought to represent different ecophenotypes. For differences, see section on the new subspecies.

The differences from other members of the *N. depressus* group are discussed in connection with the descriptions of the individual subspecies. *N. depressus depressus* is readily separated from other nileids by the small size, the slightly rounded, wide glabella, the pitted cephalic test, the moderate cephalic convexity (sag.), the pygidial terrace-line pattern and the ill-defined pygidial border. A salient diagnostic character of late representatives of *N. d. depressus* is the strongly vaulted librigena.

Remarks. – *Nileus depressus depressus* is quite common in the *M. limbata* Zone at Slemmestad, but the limestones are rich in clay, so the test surfaces are most often more or less corroded, which is critical for recognition of the surface ornamentation. However, it appears that *N. depressus* is a widespread and common species, hitherto incorrectly referred to as *N. glazialis* (see discussion of *N. depressus glazialis* below). The rounded glabella, the delicate pitting of the cephalic test surface, and the poorly developed or absent

Fig. 185 (this page). □A–B. Pygidia of *Nileus depressus depressus*. □A. Ratio between sagittal length and maximum width plotted against sagittal length. □B. Ratio between border length (sag.) and pygidial length plotted against pygidial length. □C. Pygidia of *Nileus depressus depressus*, *N. d. glazialis* and *N. d.* subsp. A. Terrace-line density on the pleural fields (lines/mm) plotted against pygidial length.

Fig. 186 (opposite page). *Nileus depressus depressus* versus *N. d. glazialis*, adult specimens only (cranidia and pygidia >5 mm long). □A. Comparison of adult ratios between maximum cranial width (measured across palpebral lobes) and cranial length. □B. Comparison of adult ratios between glabella width (measured between hind corners of palpebral lobes) and cranial length. □C. Comparison of adult ratios between palpebral lobe length (exsag.) and cranial length. □D. Comparison of adult ratios between the distance from posterior cranial margin to glabellar tubercle and cranial length. □E. Comparison of adult ratios between pygidial length (sag.) and maximum pygidial width. □F. Comparison of adult ratios between pygidial border length (sag.) and pygidial length (sag.).



pygidial border suggest that *N. depressus depressus* corresponds to *N. glazialis* subsp. 2 *sensu* Tjernvik (1980).

Russian authors have repeatedly stated that the pygidium of *N. 'armadillo'* is covered with terrace lines (Volborth 1863; Schmidt 1904; Balashova 1976); such pygidia have been figured by Schmidt (1904, Pl. 8:17–17a) and Balashova (1976, Pl. 40:10). The terrace-line pattern of the illustrated Russian specimens is unmistakably of '*depressus*-type', and it appears, accordingly, that *N. depressus* occurs also in the eastern Baltic area, at least in the *A. expansus* Zone (B2b *sensu* Schmidt 1904, 1907), but perhaps also earlier (BII β , BII γ ; see Schmidt 1907). It is uncertain which subspecies is present, but one of the cephalia figured by Schmidt (1904, Pl. 8:12; see also Balashova 1960, Pl. 6:1a–c) resembles *N. depressus depressus*. It is suspected that the inadequately known *N. chiton* Pander, 1830 is related to the *N. depressus* group, as especially indicated by its steep librigena (cf. Pander 1830, pp. 132–133).

Wandås (1984, Pl. 11D) figured a complete specimen of *N. depressus* from the Svartodden Limestone of Oslo. The specimen closely resembles *N. depressus depressus* and either belongs to this subspecies, or is a close relative. An exfoliated cranidium, 9 mm long, from 'Etage 4' at Huk (GM 1919.62) has a wide, centrally rounded glabella, a straight anterior margin, and a fairly prominent glabellar tubercle, and is in all probability a late, as yet undescribed member of the *N. depressus* group. The specimen differs from *N. depressus depressus* by having short (exsag. length 0.41 of cranidial length), but quite wide palpebral lobes, and the glabellar tubercle is situated only 0.27 of the cranidial length from posterior margin.

Nileus depressus glazialis Schrank, 1973

Figs. 187–191

Synonymy. – □ 1882 *Nileus Armadillo* Var. *depressa*, Sars & Boeck [*partim*] – Brøgger, pp. 62–64; non Pl. 7:6–6a [= *N. depressus depressus*] (description, occurrence). □ v cf. 1952 *Nileus armadillo* (Dalman) [*partim*] – Skjeseth, p. 170; Pl. 2:7 (illustrations of enrolled specimen). □ v 1972 *Nileus exarmatus lineatus* n. subsp. – Schrank, pp. 363–364; Pl. 3:13; Pl. 5:3–6; Textfig. p. 353 (description, occurrence, illustrations of pygidia). □ v 1972 *Nileus* sp. aff. *limbatus* et *exarmatus* [*partim*] – Schrank, Pl. 3:12 (illustrations of cranidium). □ 1973 *Nileus exarmatus glazialis* nom. nov. pro *Nileus exarmatus lineatus* Schrank, 1972 – Schrank, p. 1186 (change of name, *N. lineatus* preoccupied). □ 1980 *Nileus glazialis* n. subsp. no. 1 – Tjernvik & Johansson, pp. 179, 191, 203 (summary of diagnostic features, occurrence).

Holotype. – Pygidium T 794.2, figured by Schrank (1972, Pl. 5:3). The specimen is from an erratic boulder also containing *Nileus orbiculatoides* and *Aegerina erratica*, which caused Schrank (1972, p. 363) to suggest an origin from the upper part of the *M. estonica* Zone, an interpretation questioned by

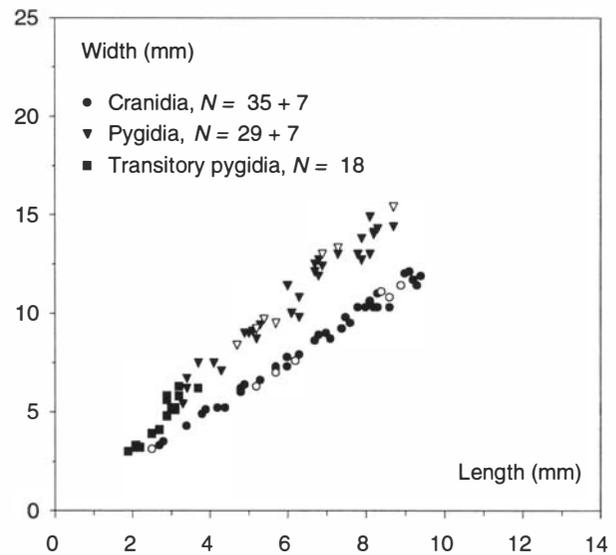


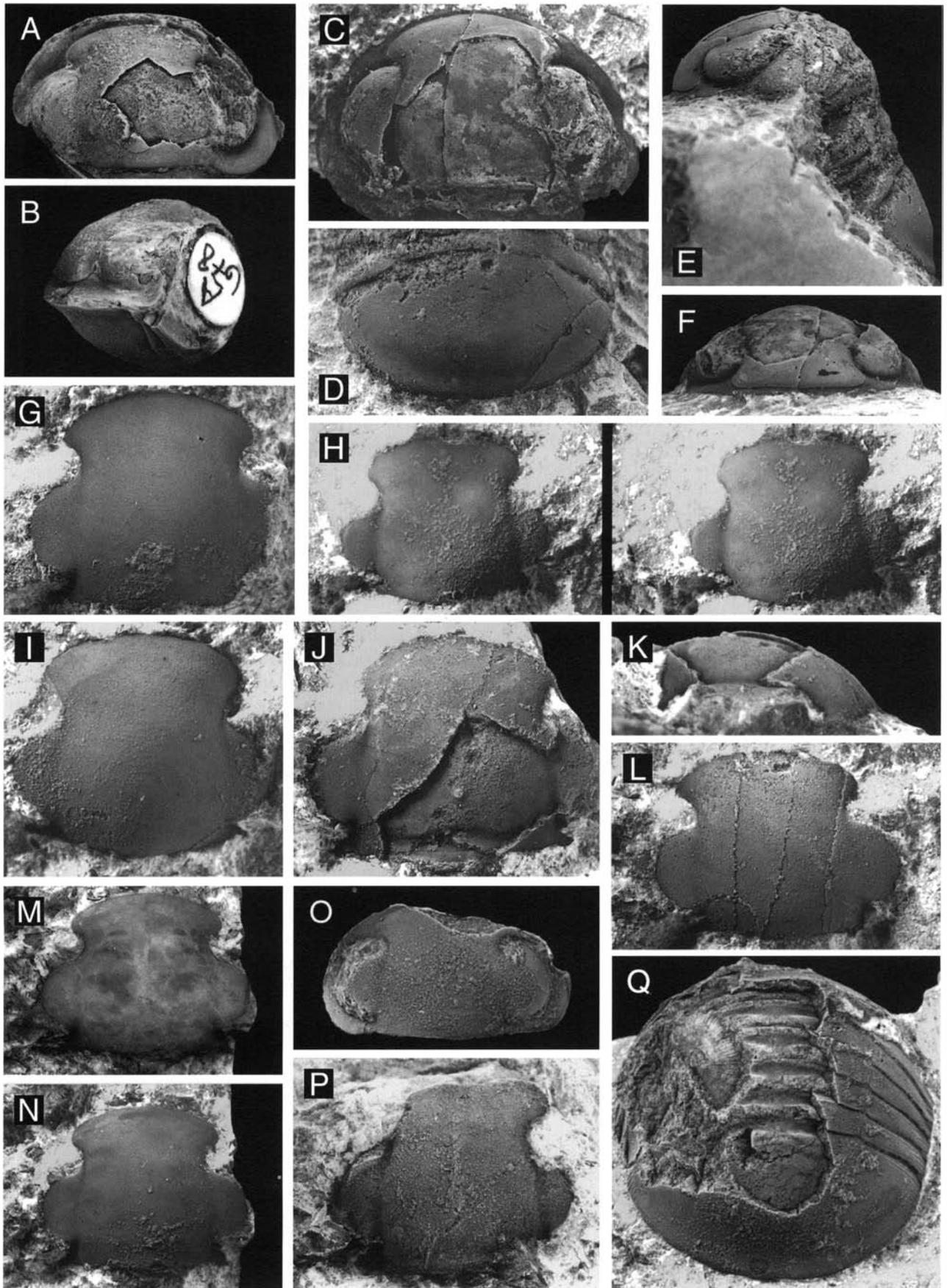
Fig. 187. *Nileus depressus glazialis* (closed symbols) and *Nileus depressus* subsp. A (open symbols). Stated number of specimens refers to *N. d. glazialis* plus *N. d.* subsp. A. Maximum width plotted against sagittal length.

Tjernvik (1980, p. 203). In my opinion the original estimate is probably not far off; the holotype seems most likely to originate either from the latest *M. estonica* Zone or from the *M. polyphemus* Zone.

Material. – Five complete specimens, 4 cephalia, 30 cranidia, 8 juvenile cranidia, 23 pygidia and 30 juvenile pygidia.

List of material. – □ Complete specimens A 670? (c), A 678 (t) [MGUH 22.791], A 688a (pim) [MGUH 22.792], A 731 (t), A 733 (t) □ Cephalia A 13 (pim), A 684 (im), A 686 (t) [MGUH 22.799], A 734 (t). □ Cranidia A 4 (c), A 5 (im), A 11 (pim), A 14 (im), A 16a (pim) [MGUH 22.796], A 16b (pim), A 616 (t), A 628b (im), A 632 (im), A 638a (im), A 642 (im) [MGUH 22.800], A 646 (pim), A 652 (t) [MGUH 22.798], A 654 (t), A 665 (im), A 681 (im), A 682 (t), A 696 (im), A 697c (t) [MGUH 22.795], A 700 (t), A 704

Fig. 188. *Nileus depressus glazialis* Schrank, 1973. □ A–B. Corroded cephalon, dorsal and side views, $\times 3$. Complete specimen MGUH 22.791 (A 678), bed M-4, Slemmestad. Pygidium shown on 190G. □ C–F. Complete specimen MGUH 22.792 (A 688a), bed M-4, Slemmestad, dorsal ($\times 4$), frontal ($\times 3$) and side ($\times 3$) views. The stance resembles life position, but is skew with respect to bed boundaries and is probably a death posture. □ G. Small cranidium, $\times 9$. MGUH 22.793 (A 653), bed M-2, Slemmestad. □ H. Corroded cranidium, stereo-pair, $\times 5$. MGUH 22.794 (A 726), bed M-5, Slemmestad. □ I. Small cranidium, $\times 9$. MGUH 22.795 (A 697c), bed M-4, Slemmestad. □ J–K. Partly exfoliated cranidium, dorsal and side views, $\times 6$. MGUH 22.796 (A 16a), bed M-3, Slemmestad. □ L. Small, slightly compacted cranidium, $\times 9$. MGUH 22.797 (A 650), bed M-2, Slemmestad. □ M–N. Small cranidium with transparent cuticle. M non-whitened, showing coloured muscle insertion sites, $\times 6$. MGUH 22.798 (A 652), bed M-2, Slemmestad. □ O. Corroded, slightly damaged cephalon, $\times 4$. MGUH 22.799 (A 686), bed M-4, Slemmestad. □ P. Internal mould of early cranidium, showing rather elongate glabella, $\times 6$. MGUH 22.800 (A 642), bed M-1, Slemmestad. □ Q. Partly exfoliated thorax and pygidium; the somewhat corroded cuticle shows terrace-line sculpture, $\times 4$. MGUH 22.801 (A 759), bed M-6, Slemmestad.



(t), A 706 (im), A 710b (im), A 715 (pim), A 726 (t) [MGUH 22.793], A 767 (im), A 769 (t), A 779 (t), A 782 (t), A 784 (t). □ Juvenile cranidia A 630a (im), A 650 (t) [MGUH 22.797], A 653 (t) [MGUH 22.793], A 693 (t), A 703 (t), A 708a (t), A 708d (t), A 723 (t). □ Pygidia A 581 (im), A 592? (im), A 593 (pim), A 594 (t), A 614a (t) [MGUH 22.806], A 627 (im) [MGUH 22.804], A 628a (im) [MGUH 22.805], A 629 (im), A 638b? (im), A 639 (im), A 640? (im), A 641? (im), A 644? (im), A 648 (pim) [MGUH 22.803], A 687? (is), 697a (pim), A 697b (pim), A 714 (pim) [MGUH 22.802], A 720? (im), A 738 (pim), A 739a? (pim), A 742 (pim), A 759 (t) with thoracic segments [MGUH 22.801]. □ Juvenile pygidia (all tentatively identified) A 7 (im), A 601 (t), A 611 (t) [MGUH 22.808], A 614b (t), A 615 (t) [MGUH 22.811], A 619a (t), A 619b (t), A 622 (t) [MGUH 22.810], A 623 (t) [MGUH 22.809], A 626a (c), A 630b (im), A 633 (im), A 638c (im), A 651 (im), A 655 (t), A 660 (t), A 662 (t), A 667 (t), A 688b (t), A 689 (t), A 691 (c), A 701 (t), A 708b (t) [MGUH 22.807], A 708c (t) [MGUH 22.812], A 708e (t), A 708f (t), A 710a (im), A 728 (c), A 739b (c), A 762 (t).

Occurrence. – *N. depressus glazialis* is frequent in bed interval M-1 to M-5 (Hukodden Limestone) at Slemmestad, representing the upper part of the *M. polyphemus* Zone and the bulk of the *M. simon* Zone. It also occurs sparsely in bed M-6, mainly in the lower half; bed M-6 constitutes the uppermost part of the *M. simon* Zone. The subspecies, or a close relative, also occurs in the Herramb Member at Ringsaker, Norway (see remarks below), which represents either the top of the *M. estonica* Zone or the lower part of the *M. polyphemus* Zone, or both.

N. depressus glazialis is believed to match *N. glazialis* subsp. 1 Tjernvik (1980), reported from the *M. polyphemus* Zone of Sweden. The range of subsp. 1 depends, however, on subspecies definition (see remarks below).

The isolated pygidial doublure, tentatively assigned to *N. glazialis glazialis* by Fortey (1975a, p. 42; Pl. 10:17) cannot be confidently assigned to subspecies.

Diagnosis. – Small form; cephalon moderately convex (sag.), glabella slightly rounded between palpebral lobes, anterior

cranial margin gently rounded, librigenae moderately convex (tr.) posterolaterally, and cephalic test surface smooth or, rarely, with some terrace lines, in particular anterolaterally on cranidium. Pygidium covered with 'depressus-type' terrace-line pattern; pygidial border narrow and often rather steep. [Emended from Schrank 1972.]

Description. – Small for a *Nileus*, largest cranidium 9.4 mm long, largest pygidium 8.7 mm long. Length ratios between cephalon, thorax and pygidium of complete specimens are about 28:50:22 ($N = 3$; dorsal projection). In articulated specimens, the length and width of pygidium average, respectively, 0.82 and 0.87 of the cephalic length and width ($N = 3$; standard maximum measures). Cephalon subsemicircular in outline, L:W ratio varies between 0.56 and 0.63 (mean 0.60; $N = 7$). Glabella elongate (Table 25), with a trend towards a relatively broader glabella in the latest specimens (Table 24 and Fig. 179B), caused by a stronger sagittal convexity of cranidium. Axial furrows, delimiting palpebral areas from glabella, are shallow on testaceous material, but augmented by a decrease of slope from glabella to palpebral areas. The furrows are gently arcuate, and the central portion of glabella assumes a roundness, best seen on internal moulds. However, the degree of roundness is variable and a few specimens show almost straight axial furrows, and, consequently, a more rectangular glabella. No systematic stratigraphical distribution of this variation is evident. Anterior branches of facial suture diverge in front of eyes at an angle of about 35–45° to sagittal line. The anterior cranial margin is gently rounded (dorsal view). Transverse glabellar convexity rather small, sagittal convexity moderate, but somewhat variable. Cranidia from bed M-1 and some from bed M-2 are clearly less convex (sag.) than later specimens. Mesial glabellar tubercle, as seen on internal moulds, moderately sized; it tends to be situated slightly further forwards in late specimens, presumably in response to the stronger sagittal cranial convexity (Fig. 179D). In addition to the low sagittal keel usually seen on internal moulds, running forwards from the tubercle, some specimens have a vague short keel behind the tubercle as well. Occipital furrow wide, fairly impressed on internal moulds, effaced on testaceous material, or with a nebulous external expression. Posterior branch of facial suture sigmoidal, curving outward-backwards from eye. Ex-sagittal length of posterior fixigena averages 0.16 ($N = 41$).

Table 24. Mean glabella width:length ratio in adult specimens of *Nileus depressus glazialis* from bed M-1 to M-6, Slemmestad.

Bed	Mean	N
M-6	0.93	3
M-5	0.88	5
M-4u	0.88	4
M-4l	0.84	5
M-3	0.87	2
M-2	0.85	1
M-1	0.84	4

Table 25. *Nileus depressus glazialis*. Ranges for variation of cranidia, expressed as ratios of cranial length.

Size (mm)	Maximum width of cranidium			Glabella width			Palpebral lobe length (exsag.)			Glabellar tubercle, distance to post. margin		
	Range	Mean	N	Range	Mean	N	Range	Mean	N	Range	Mean	N
2.7–2.8	1.22–1.25	1.24	2	0.78–0.79	0.78	2	0.44–0.46	0.45	2	0.29–0.33	0.31	2
3.4–5.3	1.18–1.31	1.26	9	0.80–0.85	0.82	10	0.43–0.48	0.45	10	0.29–0.34	0.32	9
>5.7	1.20–1.33	1.27	23	0.80–0.94	0.87	23	0.40–0.47	0.44	23	0.30–0.35	0.32	19

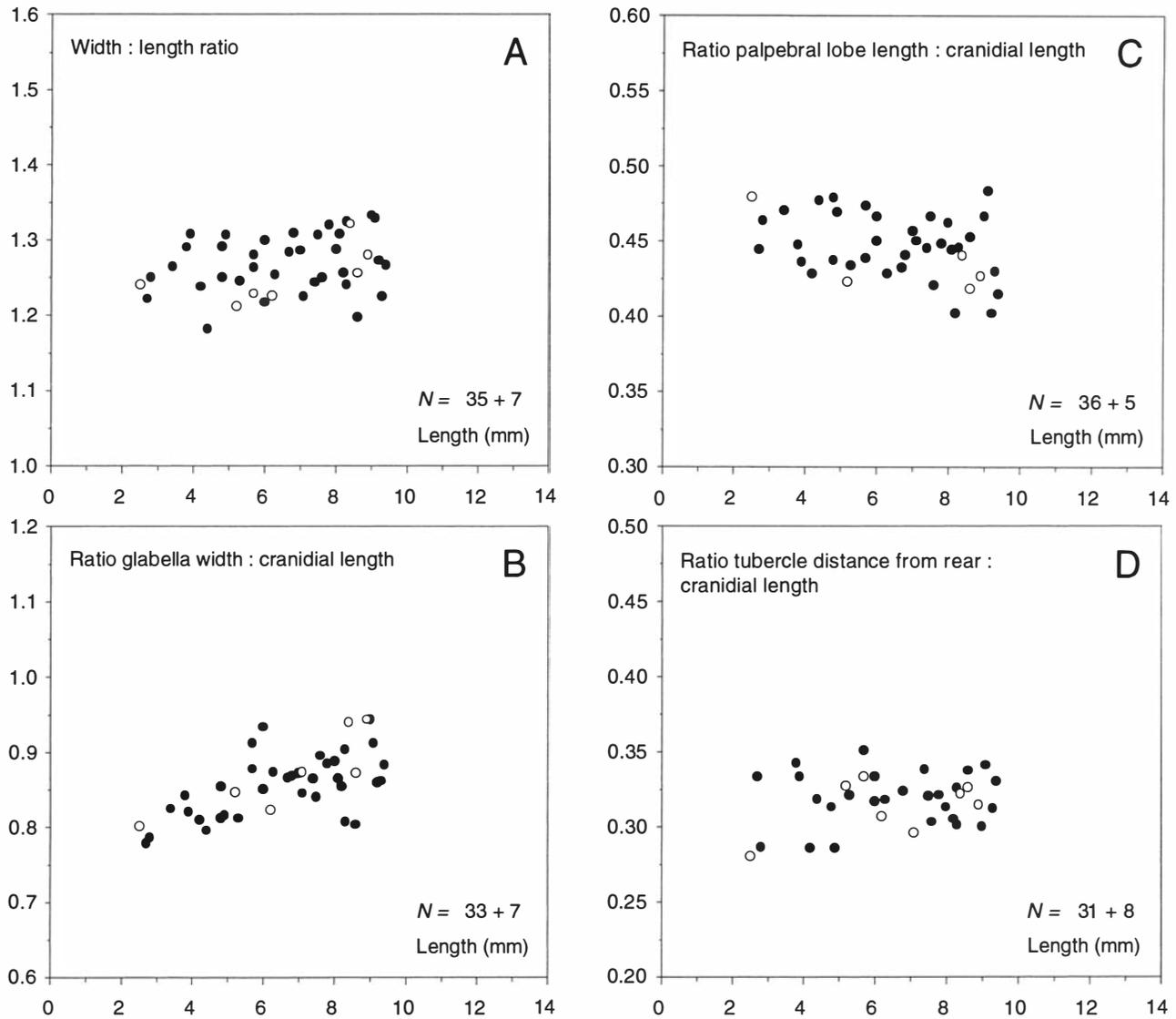


Fig. 189. Cranidia of *Nileus depressus glazialis* (closed symbols) and *N. d.* subsp. A (open symbols). Stated number of specimens refers to these subspecies, respectively. □A. Maximum width across palpebral lobes plotted against sagittal length. □B. Ratio between glabella width (measured between posterior corners of palpebral lobes) and cranial length plotted against cranial length. □C. Ratio between palpebral lobe length (exsag.) and cranial length plotted against cranial length. □D. Ratio between the distance from posterior cranial margin to glabellar tubercle and cranial length (sag.) plotted against cranial length.

The angle from palpebral lobe to sutural intersection with posterior margin is about 30° to sagittal line. Lateral border of cephalon moderately broad at eye level, then tapers to disappear short off genal angle; posterior convex part of librigena slopes moderately strongly outwards.

Most specimens with intact test are smooth except for the usual 'wrinkled' pattern along sagittal line. A few longitudinal terrace lines are present anterolaterally on glabella in early specimens from bed M-2 (no cranidia/cephala with intact test are available from bed M-1), and in one third of the

cranidia from bed M-5; two thirds of the cephalon from bed M-5 show transverse terrace lines posteriorly on librigenae.

Hypostome unknown

Thoracic segments decrease gently in size backwards; posterior segment slightly less than 0.9 times as wide (tr.) as the anterior segment, and usually about 0.7 times as long ($N = 3$), one specimen shows a L:L ratio of 0.8. Axis occupies on average 0.53 (tr.; $N = 3$) of the segmental width (tr.) on anterior segment; it is parallel-sided anteriorly, then tapers behind the third segment, and its width on posterior segment

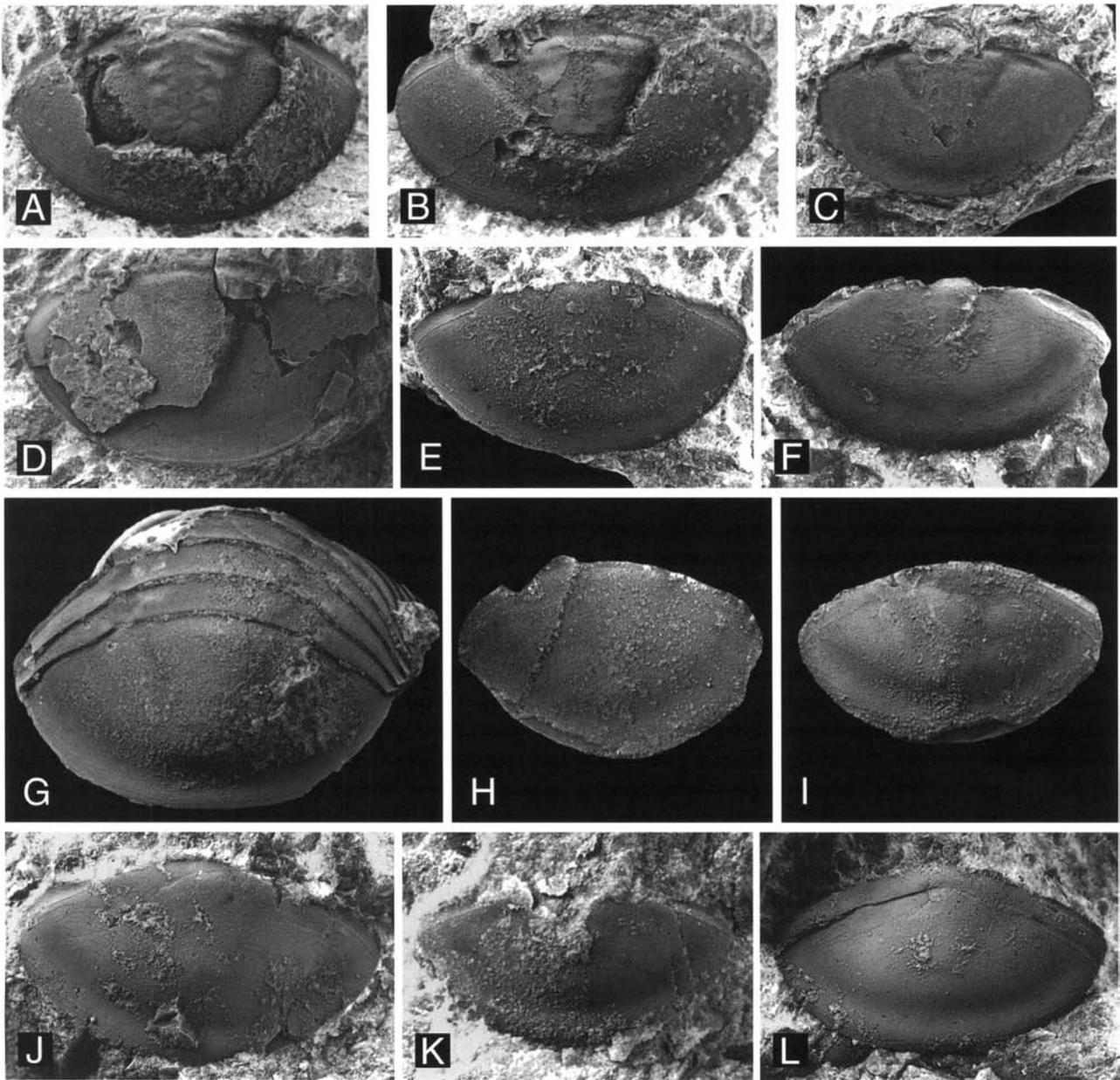


Fig. 190. *Nileus depressus glazialis* Schrank, 1973. □A. Partly exfoliated pygidium showing axis, $\times 4$. MGUH 22.802 (A 714), bed M-5, Slemmestad. □B. Partly exfoliated pygidium showing axis, $\times 4$. MGUH 22.803 (A 648), bed M-2, Slemmestad. □C. Internal mould of pygidium, $\times 3$. MGUH 22.804 (A 627), bed M-1, Slemmestad. □D. Internal mould of pygidium showing part of doublure, $\times 4$. MGUH 22.805 (A 628), bed M-1, Slemmestad. □E. Somewhat corroded pygidium, $\times 4$. MGUH 22.806 (A 614a), bed M-2, Slemmestad. □F. Small pygidium showing a not fully developed external terrace-line pattern, $\times 8$. MGUH 22.807 (A 708a), bed M-4, Slemmestad. □G. Somewhat corroded pygidium and thorax of enrolled specimen, $\times 4$. MGUH 22.791 (A 678), bed M-4, Slemmestad. See also 188A–B. □H. Badly preserved transitory pygidium, stage C, $\times 14$. MGUH 22.808 (A 611), bed M-2, Slemmestad. □I. Transitory pygidium, stage E; $\times 9$. MGUH 22.809 (A 623), bed M-2, Slemmestad. □J. Small pygidium showing a not fully developed terrace-line pattern ('*orbiculatoides-type*'), $\times 6$. MGUH 22.810 (A 622), bed M-2, Slemmestad. □K. Corroded small holaspid pygidium, $\times 8$. MGUH 22.811 (A 615), bed M-2, Slemmestad. □L. Juvenile pygidium with almost detached anterior segment, $\times 8$. The specimen apparently represents the smallest holaspid instar, but with failed detachment of the thoracic segment. MGUH 22.812 (A 708c), bed M-4, Slemmestad.

averages 0.81 ($N = 3$) of the anterior width. Each segment carry several, closely spaced transverse terrace lines on axis and pleura; articulating facet show eleven to thirteen less closely spaced lines running obliquely downward-outward. The terrace lines are irregular close to the articulating processes/sockets. Doublure not exposed.

Pygidium fairly vaulted. Axis triangular in outline, confluent with the pleural fields on testaceous material, or the anterior part may be barely raised. Hence it is almost impossible to discern, if not outlined by the lack of terrace lines and/or by colour differences. It is better defined on internal moulds, raising above the pleural fields; axial furrows very

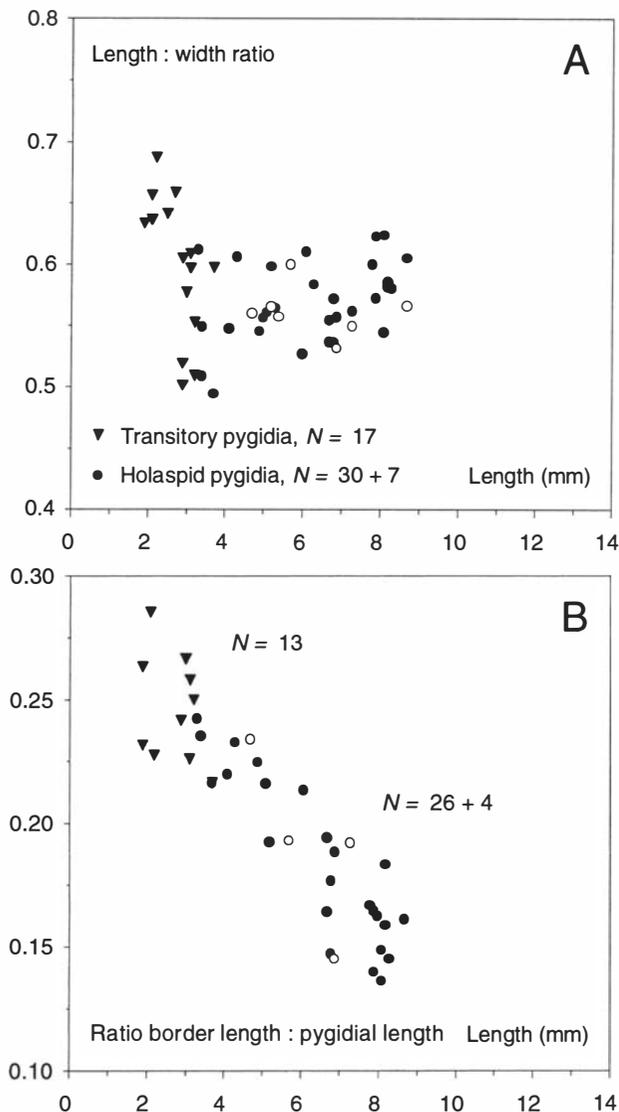


Fig. 191. Pygidia of *Nileus depressus glazialis* (●) and *N. d. subsp. A* (○); transitory pygidia cannot be differentiated. Stated number of specimens refer to these subspecies, respectively. □A. Ratio between sagittal length and maximum width plotted against sagittal length. □B. Ratio between border length (sag.) and pygidial length plotted against pygidial length.

shallow and wide. Anterior half-ring well-defined; posterior segmentation normally vestigial. Four axial segments in addition to the small terminal piece are defined by lateral swellings in a few, relatively well-preserved specimens; the mesial part of axis is smooth, and slightly depressed. The anterior pair of axial swellings may be divided by a transverse furrow, the succeeding pairs occasionally show such a furrow in the adaxial half; a narrow band across sagittal area join the posterior part of the first pair of lateral swellings. Articulating facets comparatively narrow, almost elongate subrectangular in outline; posterior edge rounded, smooth on internal moulds. Concave border slopes rather steeply outwards, and

is almost of the same width all the way. Border width seems to be constant throughout the range of *N. d. glazialis* in the Slemmestad section. Adult pygidia are covered with a 'depressus-type' terrace-line pattern; the lines are less dense and slightly coarser close to outer margin. Counts of line density on the pleural fields gave 8–10 lines/mm in two pygidia from bed M-1, 8 lines/mm in a pygidium from bed M-2, 8–9 lines/mm in a pygidium from bed M-4, and 12 lines/mm in two pygidia from bed M-6; all specimens are 7–8 mm long. Two smaller specimens, about 5 mm long, from beds M-4 and M-5, have, respectively, 12–13 lines/mm and 14–15 lines/mm. Accordingly, an overall trend towards a greater density of terrace lines on the pygidium is apparent, but this probably reflects environment rather than evolution. Only three specimens, A 594 from bed M-1, and A 697 and A 688, from bed M-4, show uncorroded, or only slightly corroded test in the axial region, and the two first mentioned specimens clearly have closely spaced terrace lines on axis, whereas the central part of axis in specimen A 688 seems to be smooth. Internal moulds occasionally exhibit vague impressions of terrace lines. Articulating facets show 5–7 terrace lines, running from the upper margin and obliquely downwards-outwards. Pygidium A 592 (from bed M-1) shows 11–12 terrace lines on the doublure, whereas pygidium A 687 (bed M-4) shows 15–16 doublural lines. It may be noted that pygidium A 745c (bed M-6), assigned to *N. depressus* subsp. A, shows 18–19 lines on the doublure.

Juveniles. – *N. exarmatus* occurs rarely in parts of the interval from which the material originates, and some of the transitory pygidia may theoretically belong to that species.

Crania 2.7–5 mm long differ from larger crania by the same features as stated for *N. d. depressus* juveniles; no specimen show dorsal terrace lines.

A poorly preserved transitory pygidium of stage B has a pronouncedly concave border, a narrow doublure, and a smooth test surface. Two C-stage pygidia, 2.1–2.5 mm long, three D-stage pygidia, 1.9–2.3 mm long, and thirteen E-stage pygidia, 2.7–3.3 mm long, are of usual outline (see description pp. 243–245). A large E-stage pygidium, 3.7 mm long, has a partly detached anterior thoracic segment, which is still fused in the left part (Fig. 190L), and it clearly represents the smallest holaspid stage. Seven out of ten E-stage specimens investigated with intact test have a smooth surface, except for isolated lines on the outer part of border demarcating the attached segment, whereas the remaining three specimens show an 'orbiculatoides-type' terrace-line pattern with short, openly spaced lines on the pleural fields, in addition to the lines on the border and the fixed segment.

Eleven pygidia, 3.4–5.1 mm long, are holaspides, but lack the characteristic 'depressus-type' terrace-line pattern. All testaceous specimens show an 'orbiculatoides-type' terrace-line pattern on the pleural fields, but the line density varies. Apart from that the material resemble adults, although showing a somewhat wider border (Table 26).

Table 26. *Nileus depressus glazialis*. Ranges for variation of pygidia, expressed as ratios.

Size (mm)	Pygidial L:W ratio			Axial width : pygidial width			Axial length : pygidial length			Border length (sag.) : pygidial length		
	Range	Mean	N	Range	Mean	N	Range	Mean	N	Range	Mean	N
1.9–2.5 [Stage C]	0.63–0.64	0.64	3	–	0.33	1	–	–	0	0.23–0.29	0.26	2
1.9–2.2 [Stage D]	0.63–0.69	0.66	3	–	–	0	–	–	0	0.23–0.29	0.26	3
2.7–3.3 [Stage E*]	0.50–0.66	0.57	9	0.38–0.42	0.40	2	–	–	0	0.23–0.27	0.25	6
3.3–5.1 [Hol.]	0.49–0.61	0.55	10	0.33–0.49	0.41	2	–	–	0	0.22–0.24	0.23	8
>5.2 [Hol.]	0.53–0.62	0.58	20	0.36–0.41	0.38	10	–	–	0	0.14–0.21	0.17	18

* An unusually large E-stage pygidium, 3.7 mm long, is not included.

Affinities. – Distinguishing characters between *N. d. depressus* and *N. d. glazialis* are listed in the section on the former subspecies (see Fig. 186).

N. d. glazialis is distinguished from *N. depressus serotinus* n.subsp. by the lesser cephalic convexity (sag.), the more rounded cranial margin, the narrower glabella, the shorter palpebral lobes, and by the presence of a pygidial border.

N. d. glazialis is separated from *N. depressus* subsp. A by the absence of terrace lines on the cranidium, glabella is but slightly narrower, the pygidium has less dense and better impressed terrace lines, a slightly higher relief and a marginally better defined border. The pygidial doublure also appears to carry fewer terrace lines. The relations between *N. d. glazialis* and subsp. A are discussed below.

Remarks. – *Nileus glazialis* was defined by Schrank (1972, 1973) as a subspecies of *N. exarmatus* [= *N. exarmatus lineatus* Schrank, 1972], distinguished by the characteristic dense pygidial terrace-line pattern; the matching cranidium was not identified. *N. glazialis*, elevated to species rank by Fortey (1975a, pp. 40–41), was divided into three subspecies by Tjernvik (1980), viz. *N. glazialis* subsp. 1, *N. glazialis glazialis*, and *N. glazialis* subsp. 2 (in order of stratigraphical appearance). These subspecies were differentiated by the following features (Tjernvik 1980, and personal communication, 1983):

- 1 *N. glazialis* subsp. 1 shows none or only a few terrace lines on the cranidium, especially concentrated on the palpebral lobes, but rarely occurring on other parts of the cranidium as well. Its pygidium has a concave border and is covered with a 'depressus-type' terrace-line pattern, axis exclusive.
- 2 *N. glazialis glazialis* has a cranidium entirely covered with densely spaced terrace lines, late specimens show a punctate test, and the glabella is somewhat rounded. Pygidium, including axis or at least the posterior part of it, is covered with a 'depressus-type' terrace-line pattern (less dense on axis); border concave.
- 3 *N. glazialis* subsp. 2 has a finely punctate cranial surface, the glabella is rounded between the palpebral lobes. Pygidium as in *N. glazialis glazialis*, but without concave border.

The vertical distribution and assumed relationships of these subspecies, according to Tjernvik, are shown Fig. 146. The transitions from *N. glazialis* subsp. 1 to *N. glazialis glazialis*, and from *N. g. glazialis* to *N. glazialis* subsp. 2 are in Tjernvik's interpretation intergradational (Tjernvik, personal communication, 1983); Tjernvik (1980) did not discuss this intricate problem, and he accommodated all 'intermediate' specimens above the *M. polyphemus* Zone within *N. glazialis glazialis*.

The prime diagnostic feature of *N. glazialis* (s.l.) is the dense terrace-line sculpture covering the pygidium (cf. Schrank 1972; Fortey 1975a; Tjernvik 1980), but this feature is also characteristic of *Nileus depressus*. Accordingly, all subspecies, previously attributed to *N. glazialis*, are here transferred to the senior taxon *N. depressus*. *N. depressus glazialis*, as I conceive it, is believed to match *N. glazialis* subsp. 1 *sensu* Tjernvik (1980); the Norwegian equivalent to *N. glazialis glazialis sensu* Tjernvik is referred to as *N. depressus* subsp. A, while *N. d. depressus* is considered identical to *N. glazialis* subsp. 2 *sensu* Tjernvik. This changed interpretation of *N. glazialis* is based on the circumstance that pygidia with terrace-line covered axis and concave border (*N. glazialis glazialis sensu* Tjernvik), occur down to the very base of the Hukodden Limestone at Slemmestad, but are associated with smooth or nearly smooth cranidia (*N. glazialis* subsp. 1 *sensu* Tjernvik). These specimens would presumably be ranked as 'intermediate' in Tjernvik's classification, but the presence or absence of terrace lines on the pygidial axis seems to be a variable feature, which should not be given taxonomic significance. It also appears that the pygidia, associated with the slightly later terrace-line covered cranidia (*N. glazialis glazialis sensu* Tjernvik), carry a very fine, dense terrace-line pattern (see description of *N. depressus* subsp. A below), but the holotype pygidium of *N. glazialis* has a terrace-line density of only about 9–10 lines/mm on the pleural fields (cf. Schrank 1972, Pl. 5:3). It is noted that the axial area of the slightly corroded holotype specimen (which has been examined) originally was smooth, despite claims to the opposite by Schrank (1972), and this feature, in combination with its well-developed border, leads to an identification with *N. glazialis* subsp. 1 *sensu* Tjernvik according to Tjernvik's own definition of this subspecies.

At Slemmestad *N. depressus glazialis* dominates from the *M. polyphemus* Zone and almost to the top of the *M. simon* Zone, whereas *N. depressus* subsp. A occurs solely at the very top of the *M. simon* Zone, with a single tentatively assigned specimen from bed M-4 as a possible exception. Except for the latter uncertain occurrence, the two subspecies overlap only in bed M-6, where they, however, are largely isolated, occurring almost exclusively in the lower and the upper half of the bed. The distinction between them is reasonably objective, although intermediate specimens *sensu* Tjernvik, that is, with terrace lines on parts of the cranium, occur throughout the range of *N. depressus glazialis*. In the Lanna section the two subspecies overlap from the upper part of the *M. polyphemus* Zone and through the *M. simon* Zone (Fig. 146), and the different distribution, compared to the Slemmestad section, indicates that the nominal chronosubspecies occur contemporaneously, but spatially separated. It is possible, and regarded most likely, that the two forms simply should be regarded as ecophenotypes. For further discussion, see section on autecology.

Complete specimen A 678 (Fig. 188A–B) from bed M-4 is tentatively assigned to *N. depressus glazialis*. Compared to the associated specimens of *N. d. glazialis* the glabella is broader (W:L ratio 0.91), more quadratic and the anterior margin is straighter, the cephalic border is wider, the eye socle is higher and more prominent, and the eye itself seems slightly larger; the posterior branch of the facial suture appears to be more oblique, running further outwards. Thorax is almost smooth with only 1–2 terrace lines crossing each segment. The pygidial border is unusually well-defined, although narrow, being strongly concave. The presence of a pygidial ‘*depressus*-type’ terrace-line pattern places the specimen within the *N. depressus* group, and it presumably belongs to *N. depressus glazialis*, indicating a much higher variability of this subspecies than evident from the remaining material.

The complete specimen assigned to *N. armadillo* by Skjeth (1952, Pl. 2:7) is certainly a *N. depressus*, and may belong to *N. d. glazialis*, but an assignment to subspecies is not possible.

Nileus depressus schranki n.subsp.

Figs. 192–198

Synonymy. – □v 1919 *Nileus Armadillo* Dalm. [*partim*] – Funkquist, Pl. 2:1 (illustrations of cranium [not seen!]). □1965 *Nileus exarmatus* Tjernvik, 1956 [*partim*] – V. Poulsen, p. 75 (described specimens include a pygidium of *N. depressus schranki* n.subsp.).

Derivation of name. – In honour of Dr. Eckart Schrank, Germany, who was one of the first to realize the high diversity among the Baltoscandian nileids.

Holotype. – Cranium MGUH 22.817 (K 246) (Fig. 193E–F) from 2 cm below top of bed +9, Killeröd (*M. limbata* Zone).

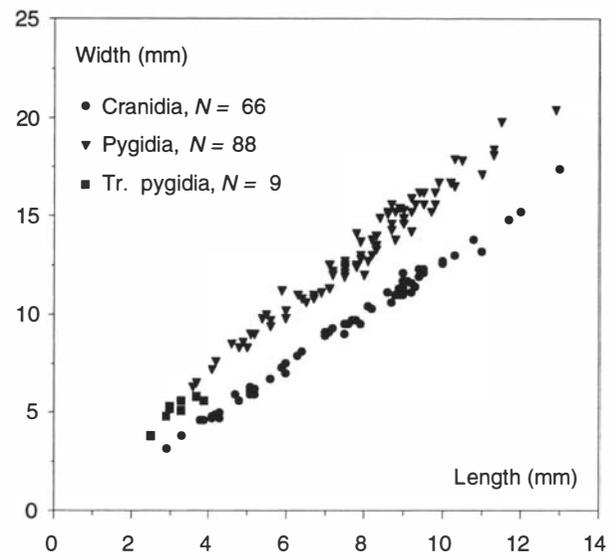


Fig. 192. Cranidia and pygidia of *Nileus depressus schranki* n.subsp. Maximum width plotted against sagittal length.

Paratypes. – Complete specimen LO 7067 (LU 9a) (Fig. 194G) from a loose boulder at Andrarum (level unknown); pygidium MGUH 22.836 (S 1075) (Fig. 196D) from 1 cm below top of bed 0, Skelbro (*M. limbata* Zone).

Additional material. – Six complete specimens, 6 cephalae including 4 with articulated thoracic segments, 59 cranidia, 19 juvenile cranidia, 102 pygidia, and 10 additional juvenile pygidia.

List of additional material. – (Early representatives marked by *). □ Complete specimens *S 285 (t), S 1230 (t), S 1263 (t), DGU 1-4 (t), GM 1884.1620c (t, pc), *K 463 (pc). □ Cephalae *S 549 (t) [MGUH 22.822], S 1228 (t) with thoracic segments, LU 9b (t) with thoracic segments, K 235 (c) with thoracic segments, *K 467 (c) with thoracic segments, K 494a (pc). □ Isolated cephalic doublure S 1177c (t). □ Cranidia *S 243 (im), *S 288b (im), *S 295e (im), *S 295f (pim), *S 443a (t) [MGUH 22.825], *S 501b (pim), *S 601 (im), *S 677c (im), *S 801 (c), *S 816? (t), S 1082 (t), S 1119 (t) [MGUH 22.831], S 1138 (im), S 1147 (im) [MGUH 22.816], S 1151? (im), S 1157 (pim), S 1158 (im), S 1160 (pim), S 1161 (im), S 1164a? (c), S 1177b (c), S 1187 (pim), S 1201 (t) [MGUH 22.823], S 1236? (im), S 1251 (pim), S 1269a (t), S 1269b (t), S 1274 (t), S 1312b (t), S 1315 (t), S 1320 (t), S 1323a (pim), S 1333 (c), S 1345 (c), S 1354 (c), S 1371 (t), S 1402a (pim) [MGUH 22.824], S 1403 (t), S 1408 (pim), S 1443 (pim), S 1653a (t), DGU 1-1 (im) [MGUH 22.815], MGUH 9434b (im), K 164 (t), K 168a (t), K 168c (t), K 180 (pim), K 219 (im), K 225a (t), K 242 (t), K 248 (im), K 402 (im), K 536 (t), K 575 (c), K 637 (t), K 978 (t), K 1348 (t) [MGUH 22.813], LU 20b (im) [LO 7075], F 11? (pim). □ Juvenile cranidia *S 443b (t) [MGUH 22.829], *S 445 (t), *S 452b? (t), *S 676 (t), *S 828 (t) [MGUH 22.814], S 1100 (pim), S 1139b (t), S 1189 (im) [MGUH 22.827], S 1209? (t), S 1273 (t) [MGUH 22.832], S 1299 (t), S 1423 (t) [MGUH 22.821], S 1439 (t), S 1644 (t) [MGUH 22.830], K 253 (t) [MGUH 22.826] K 256 (t), K 258 (t) [MGUH 22.828], K 680? (t), K 989 (t). □ Pygidia (including juvenile specimens with developed terrace-line pattern, which are marked by #) *S 274b (im) [MGUH 22.835], *S 288a (im), *S 289b (im), *S 295b (t), *S 306c (im), *S 318 (im) [MGUH 22.834], *S 348 (im), *S 350 (pim), *S 351 (im), *S 613 (c), *S 614 (pim), #*S 664b (t) [MGUH 22.845], *S 680 (t), #*S 750 (t) [MGUH 22.846], *S 788b (t), S 834b (t), #S 1065a (t) [MGUH 22.844], #S 1065b (t) [MGUH 22.847], S 1066 (t), S 1067 (t), S 1070 (t) [MGUH 22.838], S 1073 (t), S 1093? (t), S 1099 (c), S 1106 (t), S 1112 (t) with thoracic

segments, S 1139a (c), S 1142 (pim), S 1164b? (c), S 1166a (c), S 1168 (c), S 1177a (t), #S 1198 (t) [MGUH 22.837], S 1211 (t), S 1222a (t), S 1222b (c), S 1242 (t), S 1248 (c), S 1250 (im), #S 1253 (t), S 1271 (t), S 1280 (t), S 1284? (im), S 1289 (im), S 1295a (t), #S 1295b (t), S 1300 (c), S 1312a (c), S 1313 (pim), S 1316 (is), S 1317 (im), S 1319 (c), S 1322? (t) [MGUH 22.841], S 1323 (c), S 1326 (is), S 1328 (t) [MGUH 22.842], S 1335a (im), #S 1335b (im), #S 1335c (im), S 1335d (im), S 1340 (c), S 1346 (im), S 1349 (t), S 1355 (t), S 1363 (c), S 1367 (t) [MGUH 22.833], S 1370a (im) [MGUH 22.819], S 1370b (c), S 1378 (pim), S 1397 (c), S 1402b (im), #S 1409 (t), S 1415a (c), S 1415b (c), S 1648 (t), S 1653c (im), S 1663a (c), S 1691 (pim), K 145 (d) [MGUH 22.820], K 168b (t), K 173 (t), #K 178 (t) [MGUH 22.840], K 200 (t), #K 203 (t), K 233 (t), K 244a (t), K 247 (t), #K 254 (t), K 265 (im), K 548 (c), K 748 (im) [MGUH 22.818], K 754 (t) [MGUH 22.848], K 776 (im), K 969 (t), #K 971 (t), #K 974 (t) [MGUH 22.839], K 977 (c), K 982 (c), #K 1344 (t), LU 50-4 (t), GM 1987.20 (im), F 13 (t). □ Additional juvenile pygidia [the material comprises juveniles lacking a 'depressus-type' terrace-line pattern, but originating from limestone intervals in which only *N. depressus schranki* n.subsp. has been found] S 1109 (t) [MGUH 22.849], S 1113 (t), S 1174 (t), S 1295c (is), S 1369 (t) [MGUH 22.843], K 225b (t), K 244b (t), K 416 (t), K 994? (t), LU 16a (t).

Occurrence. – *N. depressus schranki* n.subsp. occurs in two intervals of the Komstad Limestone at Skelbro. The lower interval includes the major part of the *M. polyphemus* Zone (beds –20 to –13) and the lower part of the *M. simon* Zone (beds –12 to –10). The upper interval (beds 0 to +12) comprises the bulk of the *M. limbata* Zone. A few specimens were found in the Komstad Limestone at Gårdlösa-1 and Flagabro (lower part of the *M. simon* Zone) and in bed interval 1 to 12 at Gårdlösa-4a (upper part of the *M. simon* Zone). The new subspecies is fairly frequent in bed interval +1 to +12 at Killeröd, i.e. the lower to middle part of the *M. limbata* Zone; a few specimens were also found in beds +14 to +18 at this locality (upper part of the *M. limbata* Zone). Two badly preserved specimens from bed 1 at Fågelsång (Zone of *M. limbata*) seem to belong to *N. depressus schranki* n.subsp. The material listed from various collections cannot be assigned to precise level.

N. depressus schranki n.subsp. is currently unknown outside the Komstad Limestone domain.

Diagnosis. – Large for a *N. depressus*. Cephalic convexity (sag.) small; central part of glabella typically with a slight degree of roundness; anterolateral expansion of glabella strong. Lateral cephalic border extends almost to genal angle. Test surface of cranidium finely punctate, mostly without terrace lines. Pygidium has well-defined wide border; articulating facets narrow, elongate triangular; dorsal surface, axis exclusive, covered with densely spaced terrace lines.

Description. – 'Early specimens' and 'late specimens' refer to material from the lower, respectively upper interval of the Komstad Limestone (see 'Occurrence' above).

Large for a *N. depressus*, largest cranidium about 13–13.5 mm long, largest pygidium about 13 mm long (both specimens slightly damaged). Ratios between cephalon, thorax and pygidium of articulated specimens 28:48:24 ($N = 2$; dorsal projection); pygidial length and width correspond, respectively, to about 0.9 and 0.8 of the cephalic length and width in complete specimens ($N = 2$) [standard maximum measures].

Cephalon semicircular to parabolic in outline, moderately convex (both ways); L:W ratio 0.63–0.64 ($N = 4$). Axial furrows very shallow on testaceous material, but accentuated by the change of slope between glabella and palpebral areas. Late specimens in particular show gently arcuate axial furrows, and the central part of glabella, therefore, attains a more or less pronounced degree of roundness, whereas most early specimens have almost straight, gently forward-converging furrows and a subrectangular glabella. The identical relative glabellar width of early and late specimens (Tables 27–28) reflects that the width is measured between hind corners of palpebral lobes. Anterior branches of facial suture diverge rather strongly in front of the eyes, at an angle of about 45–55° to sagittal line; they meet smoothly at sagittal line. The anterior cranial margin is gently rounded in early specimens (dorsal view), as well as in juveniles, whereas adult late cranidia typically have a fairly straight anterior margin, which is also gently arched (frontal view). Transverse glabellar convexity low, sagittal convexity moderate; early specimens exhibit a but slightly higher glabellar convexity (tr.), and a lower sagittal convexity, compared to late specimens. Palpebral lobes moderately long, with no differences in relative length between early and late specimens (Tables 27–28). Mesial glabellar tubercle of modest size on internal moulds. Occipital furrow moderately impressed, defined only on internal moulds. The mesial expansion is flanked by a pair of muscle insertion sites as in *N. d. glazialis*, but which by comparison are less distinct. Posterior branches of facial suture gently sigmoidal in most specimens, thereby resembling *N. d. glazialis*, but some specimens seem to have straight posterior sutures. Exsagittal length of posterior fixigena varies between 0.12 and 0.17 of the cranial length (mean 0.15; $N = 42$). Anterior continuation of librigena rather wide compared to other subspecies of *N. depressus*. The border widens level with the eye into a fairly broad lateral border, which tapers in posterior direction to disappear close to genal angle; only the genal angle is without lateral border. Posterior convex part of librigena slopes moderately. Test

Fig. 193. Nileus depressus schranki n.subsp. □A. Well-preserved cranidium showing 'wrinkled' cuticle, stereo-pair, $\times 4$. MGUH 22.813 (K 1348), bed +9, Killeröd. □B. Small cranidium, stereo-pair, $\times 6$. MGUH 22.814 (S 828), bed –10, Skelbro. □C. Internal mould of cranidium, stereo-pair, $\times 4$. MGUH 22.815 (DGU 1-1), Skelbro. □D. Internal mould of cranidium showing traces of paired lateral-muscle-insertion sites, stereo-pair, $\times 2$. MGUH 22.816 (S 1147), bed +3, Skelbro. □E–F. Holotype. Cranidium, frontal (stereo-pair, $\times 3$) and dorsal ($\times 4$) views. MGUH 22.817 (K 246), bed +9, Killeröd. □G. Internal mould of pygidium showing doublure, $\times 4$. MGUH 22.818 (K 748), bed 11, Gårdlösa-4a. □H. Internal mould of pygidium showing doublure, $\times 4$. MGUH 22.819 (S 1370), bed +9, Skelbro. □I. Latex cast of internal mould of pygidium showing doublure, $\times 4$. MGUH 22.820 (K 145), bed –3, Killeröd. □J. Internal mould of cranidium showing paired lateral muscle insertion sites, $\times 3$. LO 7075 (LU 20b), Andrarum. □K. Juvenile cranidium, $\times 6$. MGUH 22.821 (S 1423), bed +10, Skelbro. □L–N. Damaged small cephalon, side, dorsal and frontal views, $\times 5$. MGUH 22.822 (S 549), bed –18, Skelbro.

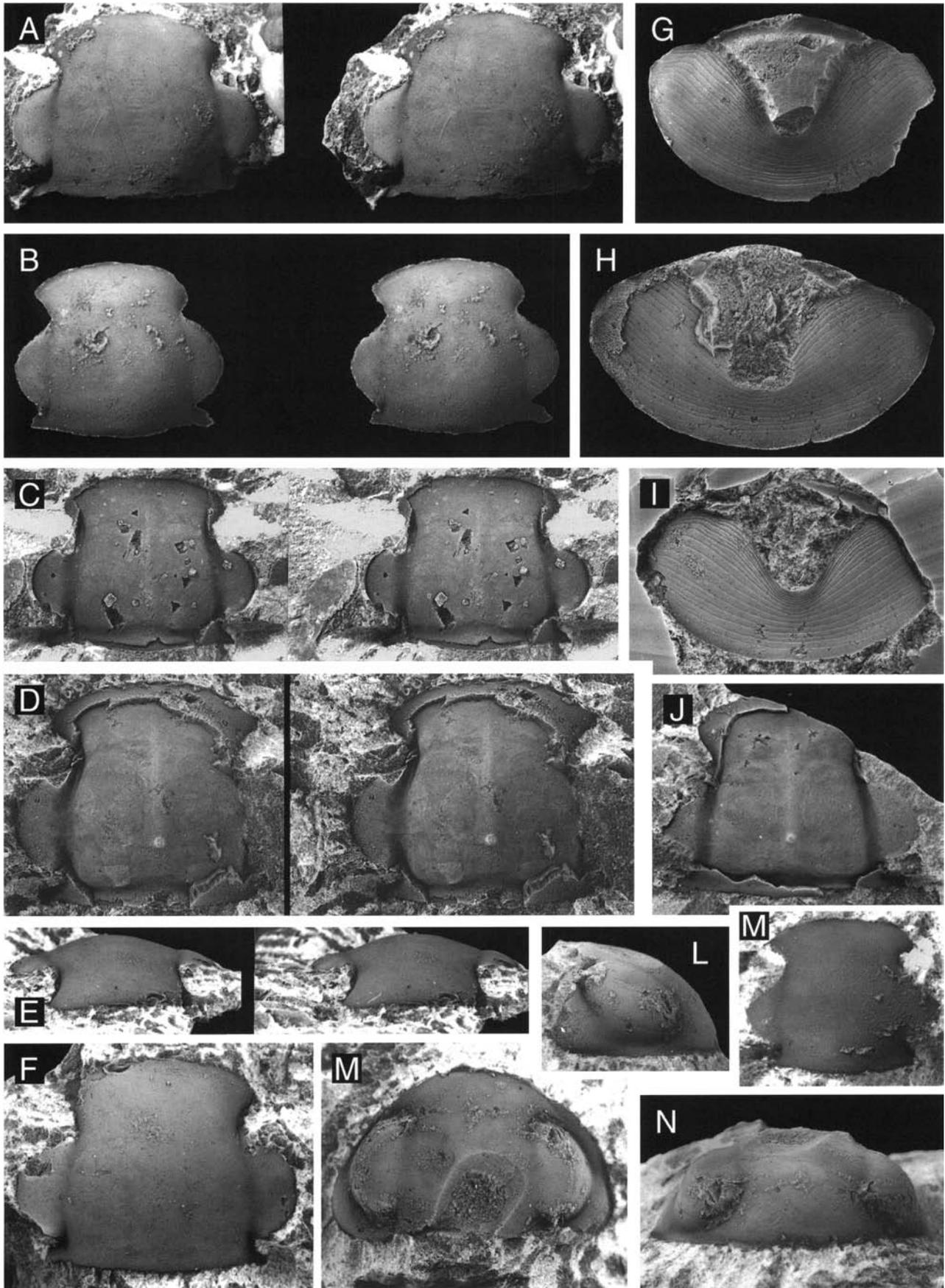


Table 27. *Nileus depressus schranki* n.subsp.. Ranges for variation of early cranidia, expressed as ratios of cranial length.

Size (mm)	Maximum width of cranium			Glabella width			Palpebral lobe length (exsag.)			Glabellar tubercle, distance to post. margin		
	Range	Mean	N	Range	Mean	N	Range	Mean	N	Range	Mean	N
3.3–5.6	1.09–1.20	1.15	5	0.75–0.84	0.77	5	0.42–0.51	0.45	5	0.30–0.34	0.32	5
≥5.9	1.24–1.26	1.25	5	0.81–0.88	0.84	5	0.41–0.47	0.45	5	0.31–0.36	0.33	5

Table 28. *Nileus depressus schranki* n.subsp.. Ranges for variation of late cranidia, expressed as ratios of cranial length.

Size (mm)	Maximum width of cranium			Glabella width			Palpebral lobe length (exsag.)			Glabellar tubercle, distance to post. margin		
	Range	Mean	N	Range	Mean	N	Range	Mean	N	Range	Mean	N
2.9	–	1.07	1	–	0.69	1	–	0.52	1	–	0.31	1
3.3–5.2	1.15–1.26	1.19	13	0.74–0.82	0.79	13	0.45–0.50	0.48	13	0.29–0.34	0.32	11
>6.0	1.17–1.34	1.26	42	0.80–0.89	0.85	45	0.41–0.51	0.46	43	0.28–0.35	0.32	31

Table 29. *Nileus depressus schranki* n.subsp. Ranges for variation of pygidia, expressed as ratios.

Size (mm)	Pygidial L:W ratio			Axial width : pygidial width			Axial length : pygidial length			Border length (sag.) : pygidial length		
	Range	Mean	N	Range	Mean	N	Range	Mean	N	Range	Mean	N
2.5–3.3 [Stage D]	0.65–0.66	0.65	2	0.39–0.42	0.41	2	0.55–0.64	0.59	2	0.21–0.24	0.23	2
2.9–3.9 [Stage E*]	0.57–0.70	0.61	7	0.38–0.41	0.40	5	0.57–0.62	0.60	4	0.23–0.28	0.25	6
3.5–5.6 [Hol.]	0.54–0.60	0.57	15	0.30–0.41	0.37	14	0.50–0.63	0.57	12	0.20–0.27	0.23	15
>5.9 [Hol.]	0.53–0.65	0.60	63	0.31–0.43**	0.37	24	0.49–0.63	0.57	16	0.13–0.22	0.18	54

* Including two groups, 2.9–3.3 mm long ($N=5$) and 3.7–3.9 mm long ($N=2$).

** Early pygidia show 0.31–0.38 (mean 0.36; $N=5$), late pygidia show 0.34–0.43 (mean 0.38; $N=19$).

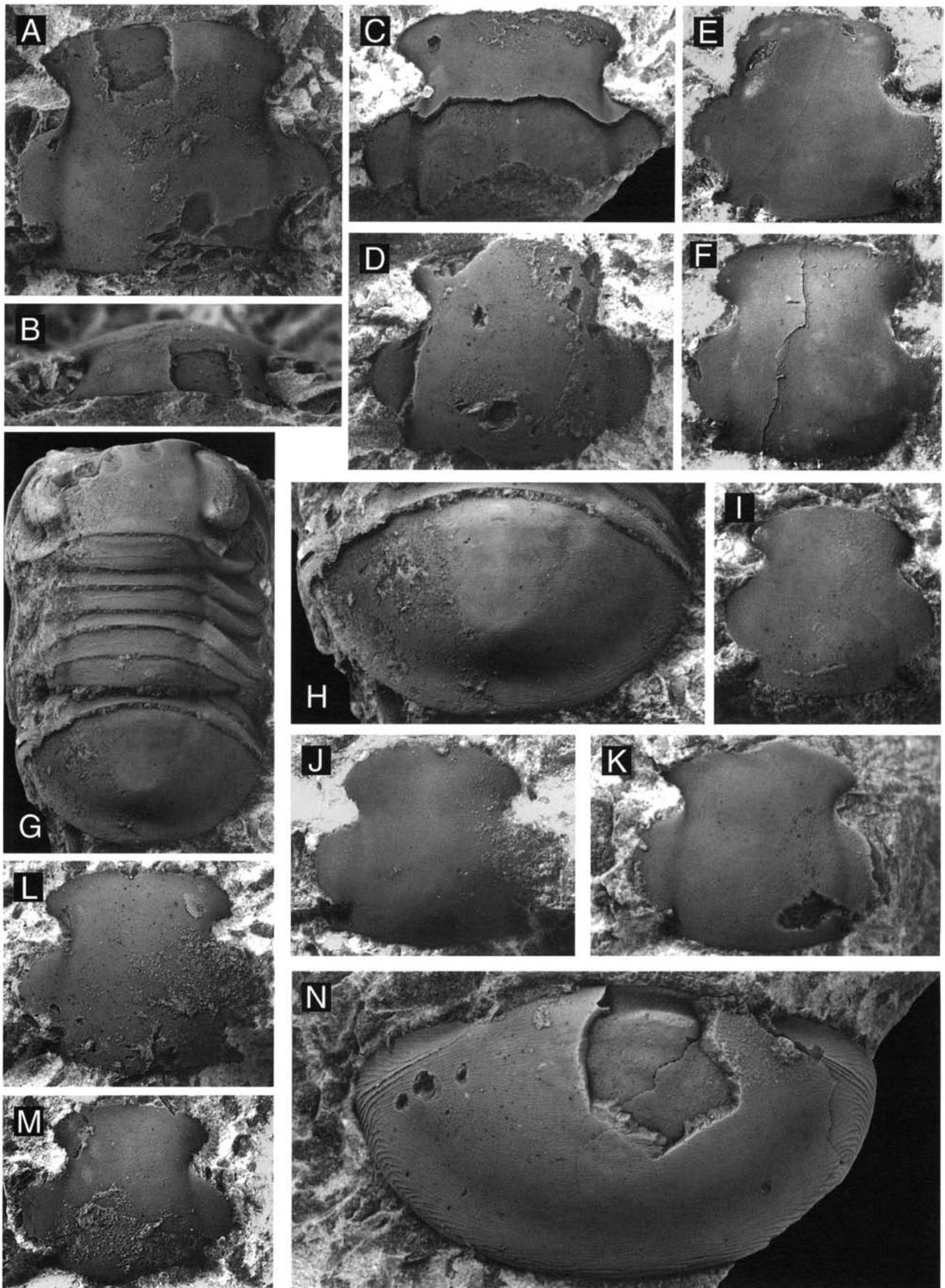
surface of cranium finely pitted in all well-preserved specimens ($N=21$). Pitting has not been seen on the librigena, which, however, are corroded in all complete specimens and cephalae available. A single, less corroded specimen fails to show pits, and the librigenae are probably genuinely smooth. Three cephalae exhibit scattered terrace lines along the posterior margin of librigena, while four specimens certainly lack terrace lines on librigenae. All but two of the cranidia lack terrace lines. Specimen S 285 is impaired, and the cephalon is largely missing, but a patch of occipital region shows terrace lines along posterior margin. Cranium K 1348 has terrace lines in the lateral part of the occipital 'furrow', and a few lines on glabella inside palpebral area. Relative dimensions of cephalic doublure as in *N. depressus glazialis*. It is provided with at least eighteen terrace lines, counted just anterior to eye level. Posterior part of doublure not exposed in the material at hand.

Hypostome not yet identified.

Thoracic segments diminish gradually in posterior direction; posterior segment is about 0.9 times as wide as the anterior segment and about 0.7 times as long. Thoracic axis only moderately vaulted; it is bounded by fairly distinct 'pseudo' axial furrows, formed by the moderately impressed, oblique, short pleural furrows. Axis is widest on the third segment, occupying about 0.55 of the segmental width (tr.),

to taper in both directions, most so posteriorly, and it occupies 0.50 of the segmental width (tr.) on the rear segment. The axis of each segment typically show several vaguely impressed, short, irregular lines laterally, and a single transverse terrace line across. Four to six coarse, continuous, transverse terrace lines occur on the pleurae, often separated by faint second order lines. Articulating facets generally covered with about 10–12 lines. Specimen S 285 from bed

Fig. 194. *Nileus depressus schranki* n.subsp. □A–B. Corroded late cranium showing gently arched, truncate anterior margin, dorsal and frontal views, ×4. MGUH 22.823 (S 1201), bed +5, Skelbro. □C. Partly exfoliated late cranium showing truncate anterior margin, ×4. MGUH 22.824 (S 1402), bed +10, Skelbro. □D. Early cranium showing proportionally long glabella, ×5. MGUH 22.825 (S 443a), bed –19, Skelbro. □E. Juvenile cranium, ×9. MGUH 22.826 (K 253), bed +12, Killeröd. □F. Juvenile cranium, ×9. MGUH 22.827 (S 1189), bed +7, Skelbro. □G–H. Paratype. Slightly damaged complete specimen, ×3, and close-up of pygidium, ×5, showing 'depressus-type' terrace-line pattern. LO 7066 (LU 9a), Andrarum. □I. Small juvenile cranium, ×12. MGUH 22.828 (K 258), bed +12, Killeröd. □J. Early juvenile cranium, ×9. MGUH 22.829 (S 443b), bed –19, Skelbro. □K. Late juvenile cranium, ×9. MGUH 22.830 (S 1644), bed 0, Skelbro. □L. Late juvenile cranium, ×6. MGUH 22.831 (S 1119), bed +3, Skelbro. □M. Late juvenile cranium, ×6. MGUH 22.832 (S 1273), bed +7, Skelbro. □N. Well-preserved pygidium showing dense 'depressus-type' terrace-line pattern, ×8. MGUH 22.833 (S 1367), bed +9, Skelbro.



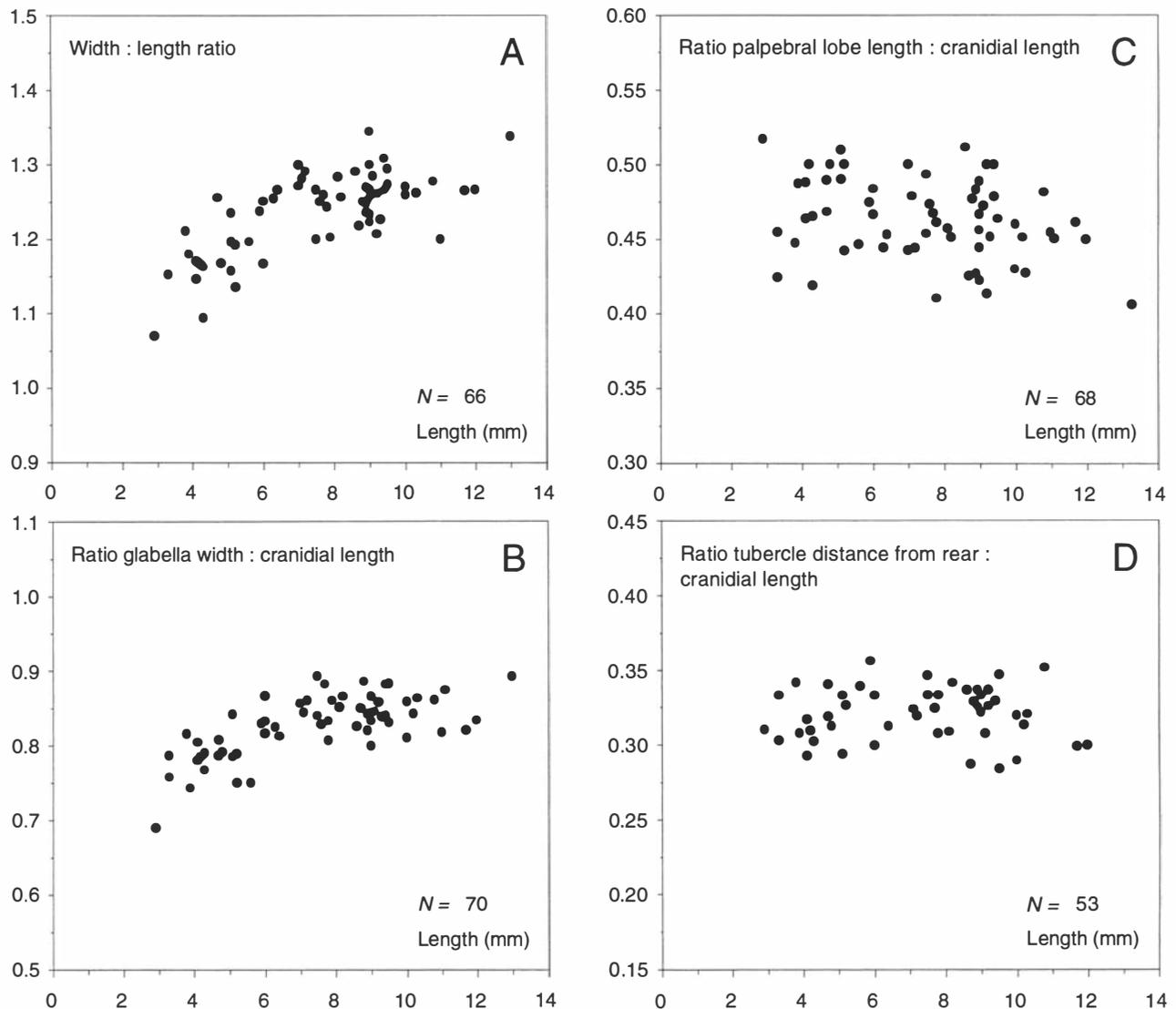
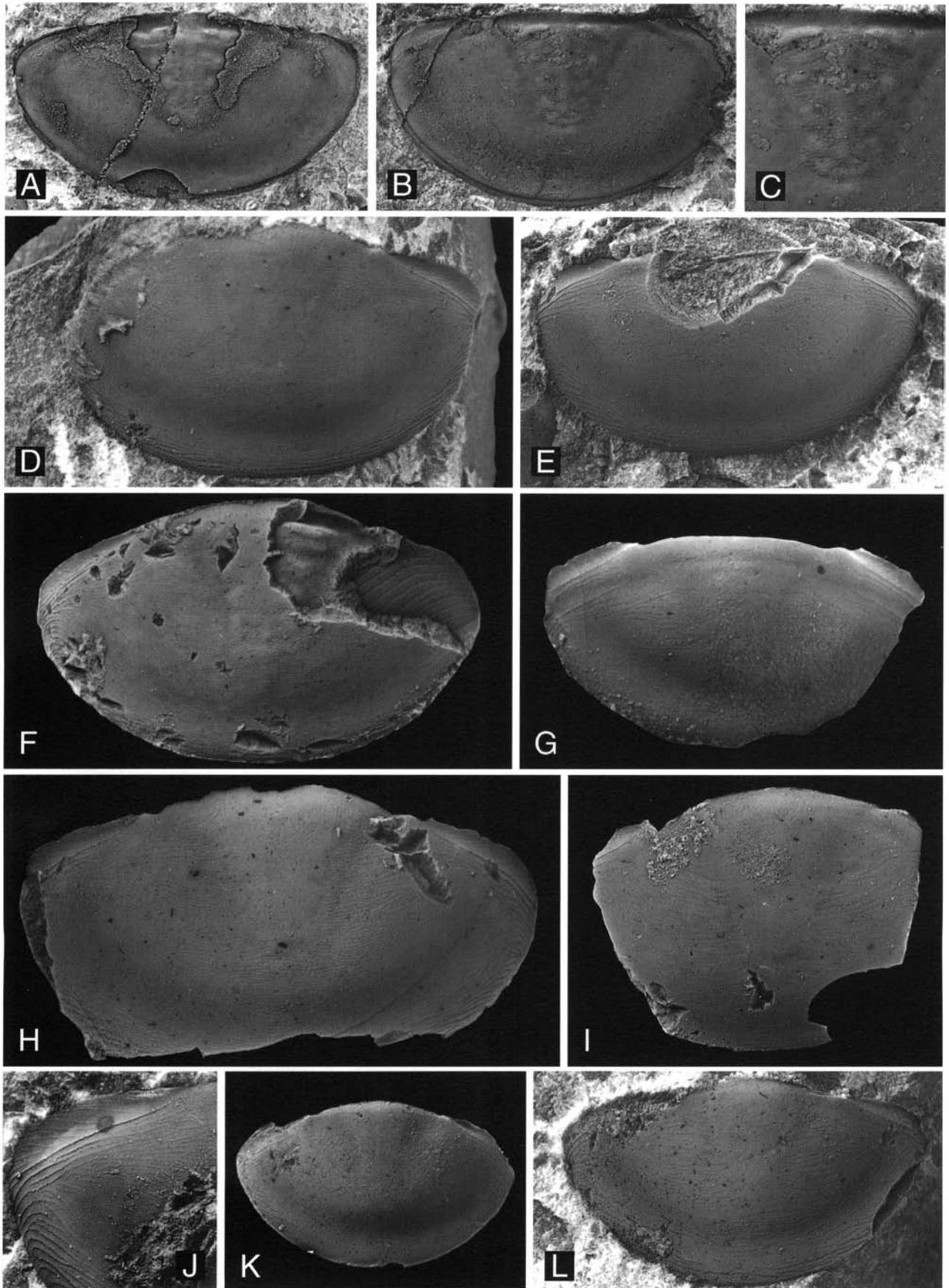


Fig. 195. Crania of *Nileus depressus schranki* n. subsp. □A. Ratio between maximum width across palpebral lobes and cranial length plotted against sagittal length. □B. Ratio between glabella width (measured between posterior corners of palpebral lobes) and cranial length plotted against cranial length. □C. Ratio between palpebral lobe length (exsag.) and cranial length plotted against cranial length. □D. Relative position of glabellar tubercle plotted against cranial length.

–20 at Skelbro is rather damaged, but a minute patch of intact test on the posterior thoracic segment reveals the presence of densely spaced transverse terrace lines across the segment. Specimen K 467 from bed F at Gårdlösa-1 is corroded, but also appears to have numerous terrace lines on the axial region of thorax.

Pygidium quite strongly vaulted. The axis, as seen on internal moulds, quickly tapers in posterior direction, and stretches for about 0.6 of the pygidial length. The proportionally narrower axis of early specimens compared to late (Table 29) is particularly evident on internal moulds. Axial furrows very shallow and wide on internal moulds, and axis is defined mainly by having a slightly higher relief than the pleural fields, and a more uneven mould surface. On testaceous material the axis may be barely raised above the pleural

Fig. 196. *Nileus depressus schranki* n. subsp. □A. Internal mould of pygidium, $\times 4$. MGUH 22.834 (S 318), bed –20, Skelbro. □B–C. Internal mould of pygidium showing axis, $\times 4$; close-up showing impressions of terrace lines on axial region, $\times 6$. MGUH 22.835 (S 274b), bed –20, Skelbro. □D. Paratype. Pygidium showing 'depressus-type' terrace-line pattern, $\times 6$. MGUH 22.836 (S 1075), bed 0, Skelbro. □E. Pygidium showing 'depressus-type' terrace-line pattern, $\times 9$. MGUH 22.837 (S 1198), bed +5, Skelbro. □F. Pygidium showing 'depressus-type' terrace-line pattern, $\times 5$. MGUH 22.838 (S 1070), bed 0, Skelbro. □G. Transitory pygidium, stage E, showing partially developed 'depressus-type' terrace-line pattern on pleural fields, $\times 12$. MGUH 22.839 (K 974), bed +16, Killeröd. □H. Damaged pygidium showing 'depressus-type' terrace-line pattern, $\times 9$. MGUH 22.840 (K 178), bed +2, Killeröd. □I. Tentatively assigned fragmentary pygidium showing very openly spaced terrace lines, $\times 6$. MGUH 22.841 (S 1322), bed +7, Skelbro. □J. Pygidium, close-up of articulating facet, $\times 9$. MGUH 22.842 (S 1328), bed +7, Skelbro. □K. Small holaspid pygidium without 'depressus-type' terrace-line pattern, $\times 6$. MGUH 22.843 (S 1369), bed +9, Skelbro. □L. Small holaspid pygidium showing dense 'orbiculatoides-type' terrace-line pattern, $\times 9$. MGUH 22.844 (S 1065a), bed 0, Skelbro.



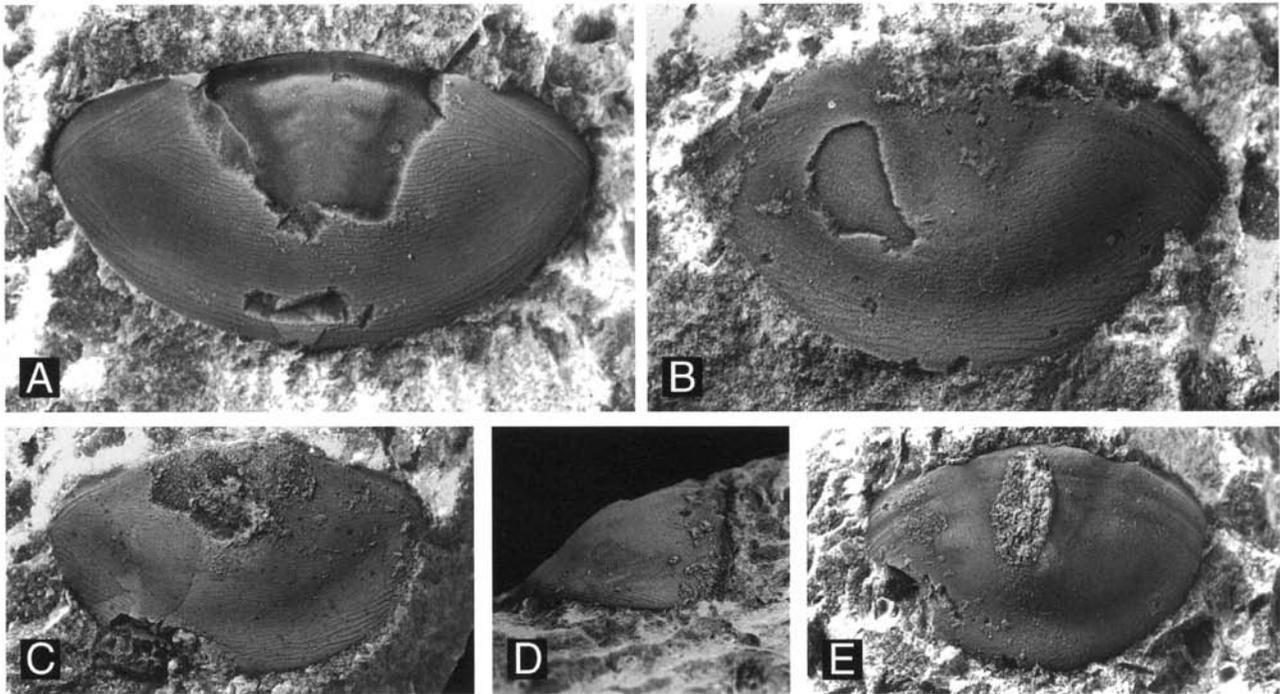


Fig. 197. *Nileus depressus schranki* n. subsp. □A. Partly exfoliated small pygidium showing axis, $\times 12$. MGUH 22.845 (S 664b), bed -18, Skelbro. □B. Transitory pygidium, stage E, showing unusually extensive, dense terrace-line pattern, $\times 12$. MGUH 22.846 (S 750), bed -14, Skelbro. □C. Small holaspid pygidium showing extensive terrace-line pattern and proportionally broad border, $\times 6$. MGUH 22.847 (S 1065b), bed 0, Skelbro. □D. Side view of pygidium showing the steepness of border, $\times 4$. MGUH 22.848 (K 754), bed 11, Gårdlösa-4a. □E. Transitory pygidium, stage D, $\times 9$. MGUH 22.849 (S 1109), bed +2, Skelbro.

fields, but mostly has no relief at all. Axial outline is then roughly indicated by the lack of terrace lines. Axial segmentation as in *N. d. glazialis*, but on the average marginally better defined. Internal moulds show four axial rings, an anterior half-ring, well set off by a deep, but comparatively narrow (sag.) transverse furrow, and a terminal piece, fused with the last axial ring. The usual pleural furrow, seen anteriorly on internal moulds, is less impressed than in *N. d. glazialis*. Articulating facets narrow, elongate triangular, slanting moderately forwards. Inner edge of facet slightly raised on internal moulds, forming a low, rounded crest. The concave border is narrowest postaxially (Table 29), but almost of the same width throughout. It is comparatively well-defined; the largest specimens tend to show a steeper border. The test is thickened in the flexure between pleural fields and border, hence internal moulds exhibit a more pronounced border concavity. Adult pygidia are covered with the characteristic 'depressus-type' terrace-line pattern; the configuration is shown in Figs. 194N, 196D-H. The line density varies independently of specimen size (Fig. 198C, Table 30), and pygidia from the same horizon have roughly the same line densities, regardless of size. The line densities varies between 7 and 19 lines/mm on the pleural fields (mean 13 lines/mm; $N=52$); the density is predominantly between 9 and 16 lines/mm (Fig. 198C, Table 30). The smallest pygidium showing terrace lines is 3.6 mm long. It is characteristic that terrace-

line bearing juvenile pygidia show short, irregular lines, different from the more continuous lines of adults. Axial region smooth in most pygidia; only a few specimens have very short, irregular, single lines in the axial region. Pygidium S 274 is an internal mould, but rather densely spaced terrace lines are impressed across the entire axial region, which is not seen in any specimen with preserved test. Internal moulds as a rule show faint impressions of terrace lines on the pleural fields. Doublure strongly concave, and provided with 17-20

Table 30. *N. depressus schranki* n. subsp., Killeröd area, SE Scania. Densities of terrace lines on pleural fields of pygidia.

Pygidium	Bed	Length (mm)	Lines per mm
K 969	+16	5.2	10
K 254	+12	5.6	16
K 233	+7	6.0	13
K 203	+4	~9	17
K 178	+2	5.5	15
K 173	+2	8.1	17
K 168	+1	10.3	10
K 776	-9	~4	11
K 754	-9	7.5	10
K 748	-9	7.8	12
K 463	E	8.3	10

lines ($N = 4$, late specimens). An indistinct, shallow depression posterior to axis is present in a few specimens.

Juveniles. – Cranidia 2.9 to 6.0 mm long show a more rounded anterior margin than larger specimens. Late juvenile cranidia have clearly less rounded margins, compared to early juveniles (Fig. 194J–M); in fact, a trend towards a more truncate anterior margin is apparent even among the late juvenile cranidia. Cranidial W:L ratios are significantly below adult values (Tables 27–28), and juveniles also show a narrower glabella. Late juvenile cranidia typically have straight, gently forward-converging axial furrows, so the glabella is sub-rectangular, not rounded like in the contemporaneous adults.

Two D-stage pygidia, 2.5 and 3.3 mm long, and five E-stage pygidia, 2.9–3.3 mm long, plus two specimens, 3.7 mm and 3.9 mm long, are comparatively broad (Table 29), but otherwise resemble the material described on pp. 244–245. Of the smaller E-stage pygidia, a single specimen, 3.0 mm long, has a smooth test, except for a few transverse terrace lines, outlining the anterior segment, whereas the remaining specimens, 2.9–3.3 mm long, show short, openly spaced terrace lines on the pleural fields arranged in a ‘*orbiculatoides*-type’ pattern in addition to transverse lines outlining the anterior segment. The largest specimens, 3.7 mm and 3.9 mm long, are covered with a typical ‘*depressus*-type’ terrace-line pattern, axis exclusive.

Seventeen pygidia, 3.5–5.6 mm long, are holaspides. They match the description on p. 245. The majority of specimens, even the smaller ones, show a dense terrace-line pattern of the ‘*depressus*-type’, covering the entire surface of test, except for the axial area. A few specimens even show sparse lines on the axis. Three specimens do not show the ‘*depressus*-type’ terrace-line pattern. Two of those are smooth, except for a few transverse lines along the anterior margin and along the posterior margin (‘*exarmatus*-type’ terrace-line pattern). The third specimen has short, openly spaced lines on the pleural fields in addition to the lines along the margins (‘*orbiculatoides*-type’ terrace-line pattern).

Additional juvenile pygidia of *N. depressus schranki* n.subsp. are undoubtedly included in the material described as ‘Juvenile pygidia of *Nileus exarmatus*, *N. sp. B*, *N. orbiculatoides* and *N. depressus schranki* n.subsp.’.

Affinities. – *N. depressus schranki* n.subsp. is larger than other *depressus* subspecies, from which it is distinguished

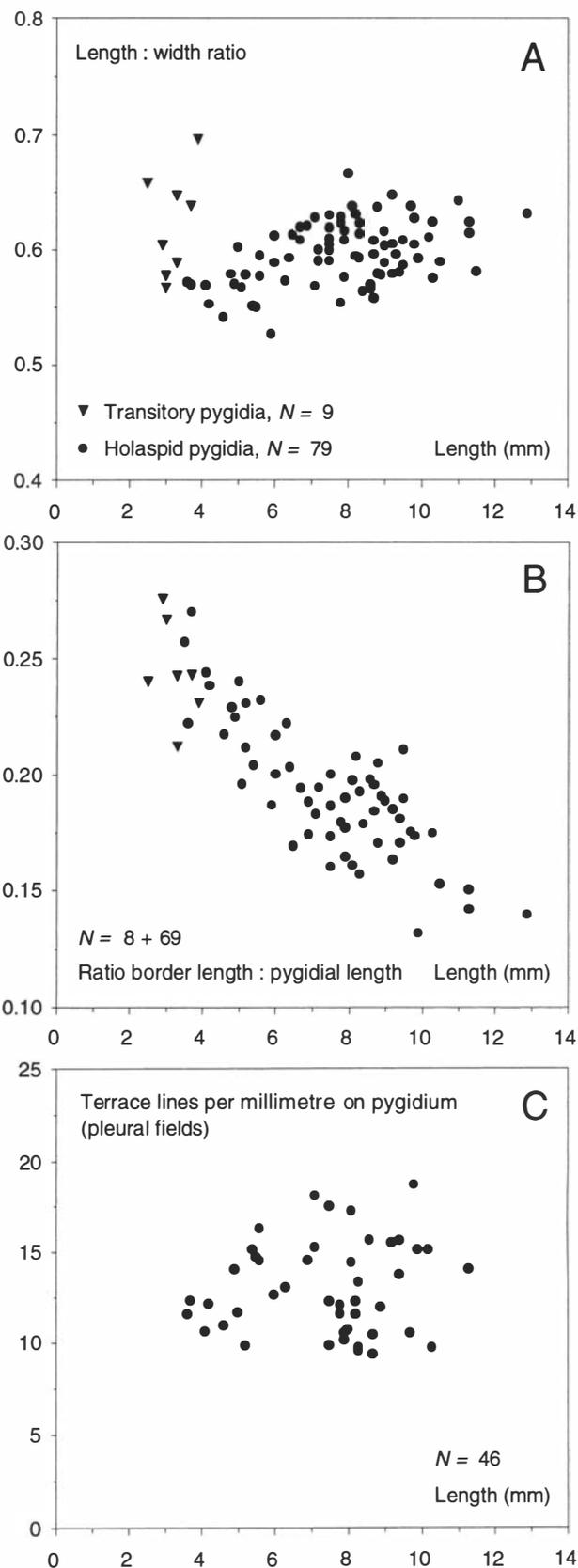


Fig. 198. Pygidia of *Nileus depressus schranki* n.subsp. □A. Ratio between sagittal length and maximum width plotted against sagittal length. □B. Ratio between border length (sag.) and pygidial length plotted against pygidial length. □C. Number of terrace lines per millimetre on pleural fields plotted against sagittal length of pygidium.

by the less convex cephalon (both ways, but most pronounced sagittally), which is semicircular, not subreniform in outline, with larger eyes, a relatively elongate glabella, less vaulted librigenae, and a lateral border extending almost to genal angle. The pygidium also has a comparatively distinct border.

Compared to *N. depressus glazialis*, *N. d. schranki* n.subsp. also differs by having a more truncate cranial margin, a strong anterolateral expansion of glabella, a pitted cranial test, a relatively longer pygidium with elongate triangular articulating facets, not narrow subrectangular as in *N. depressus glazialis*, the inner edge of articulating facet is slightly raised on internal moulds, and the pygidial doublure typically bears more terrace lines. The respective pygidia are, however, most easily separated by the different border morphology.

An enigmatic nileid, informally called *Nileus* sp. B, occurs in bed -21 and, very sparsely, in bed -20 at Skelbro; the first representatives of *N. d. schranki* n.subsp. appear in bed -20. *Nileus* sp. B attains slightly larger maximum sizes than *N. d. schranki* n.subsp., but otherwise the respective cranidia are virtually identical. The only recognized difference is the distribution of external pitting, which in sp. B is limited to the palpebral lobes, whereas the entire cranidium of *N. d. schranki* n.subsp. is pitted. The thorax and pygidium of *N. sp. B* are, on the contrary, quite different from those of *N. d. schranki* n.subsp. and more comparable to *N. orbiculatoides*. *Nileus* sp. B either represents an early transitional form or is a shallow-water ecophenotype of *N. depressus schranki* n.subsp. The latter interpretation, which entails a profound reassessment of the intraspecific variation of *Nileus*, is regarded most likely.

N. depressus schranki n.subsp. is coeval with *N. exarmatus*, *N. orbiculatoides* and *N. planiceps* n.sp. *N. exarmatus* has, compared to *N. depressus schranki* n.subsp., a more elongate glabella, and the external ornamentation, of both cephalon and pygidium, differs significantly. *N. orbiculatoides* is larger than *N. depressus schranki* n.subsp., the cephalic convexity (both ways, most pronounced sagittally) is stronger, the cranial anterior margin is provided with a small obtuse mesial boss, and the external ornamentation (both cephalon and pygidium) differs markedly. *N. planiceps* n.sp. has a cranidium of low convexity (sag.) with a characteristic flattened anterior margin, and its pygidium is separated from *N. depressus schranki* n.subsp. by the much denser terrace-line pattern, the comparatively ill-defined border, the better defined axis, and the higher number of terrace lines on the doublure.

Remarks. – The ‘early’ and ‘late’ *N. depressus schranki* n.subsp. should perhaps be separated as individual subspecies, but the differences are for the time being considered within the range of intraspecific variation. The *M. simon* Zone of SE Scania is currently being sampled in great detail, and an analysis of *N. d. schranki* n.subsp. from this interval

will show whether the transition from early to late types are gradational or abrupt.

Pygidium S 1322 (Fig. 196T) from bed +7, Skelbro, is tentatively assigned to *N. depressus schranki* n.subsp.. The specimen is unusual in showing a very low terrace-line density, 7 lines/mm, and the posterior border is ill-defined, narrow, sagittally occupying only 0.1 of the pygidial length.

Some of the SE Scanian material assigned to *N. armadillo* by Funkquist (1919) belongs to *N. depressus schranki* n.subsp. (part of LU material listed above), probably including one of the figured cranidia (Funkquist 1919, Pl. 2:1), which, however, has not been examined.

V. Poulsen (1965, p. 75) stated in his description of *Nileus exarmatus* that the pygidium is covered with terrace lines. The material was obviously mixed with *N. depressus schranki* n.subsp., but it has not been possible to locate the specimen in question.

Nileus depressus serotinus n.subsp.

Figs. 199–203

Derivation of name. – Latin *serotinus* = arrive too late. The new subspecies is frequent only in a few beds in the middle of the *M. limbata* Zone at Killeröd, but is believed closely related to *Nileus depressus depressus*, which occurs from the base of the *M. limbata* Zone in southern Norway and central Sweden.

Holotype. – Cranidium MGUH 22.850 (K 932) (Fig. 200A) from 1 cm above base of bed +15, Killeröd, *M. limbata* Zone.

Paratype. – Pygidium MGUH 22.863 (K 914a) (Fig. 200Q), horizon (2 cm above base) and locality as holotype.

Additional material. – Twenty-two cranidia and 24 pygidia including 7 juvenile cranidia and 19 juvenile pygidia.

List of additional material. – □Cranidia K 199 (t), K 251 (t) [MGUH 22.854], K 279 (t), K 285a (t), K 403a (t), K 403b (t), K 541 (t) [MGUH 22.856], K 545 (c), K 547? (c), K 910 (t), K 911a (t) [MGUH 22.851], K 911b (t) [MGUH 22.853], K 918b (t) [MGUH 22.855], K 935 (c), K 946 (pim), K 950 (t), K 951 (t), K 953a (pim), K 959 (t) [MGUH 22.852], K 967 (t), K 999a (pim), LU 156a (pim). □Pygidia K 185b (t) [MGUH 22.870], K 185c (t), K 263 (pim) [MGUH 22.859], K 266 (im), K 280 (t), K 285b (t), K 291 (t), K 393 (t), K 401 (t), K 549 (t) [MGUH 22.871], K 914b [MGUH 22.865], K 917 (t), K 918a (t) [MGUH 22.861], K 925 (t), K 929 (t), K 931a (d) [MGUH 22.860], K 931b (t) [MGUH 22.864], K 945 (t) [MGUH 22.857], K 952 (t) [MGUH 22.869], K 953b (t) [MGUH 22.868], K 956 (t) [MGUH 22.858], K 963 (t) [MGUH 22.862], K 999b (t) [MGUH 22.866], K 1003 (t) [MGUH 22.867].

Occurrence. – *Nileus depressus serotinus* n.subsp. occurs sparsely in bed 3 at Gårdlösa-4a and the equivalent beds -2 and -3 at Killeröd; this narrow interval belongs to the upper part of the *M. simon* Zone. The subspecies is frequent in beds +14 and +15 at Killeröd, and single specimens were found in beds +11 and +18, which all belong to the middle of the *M. limbata* Zone (upper subzone).

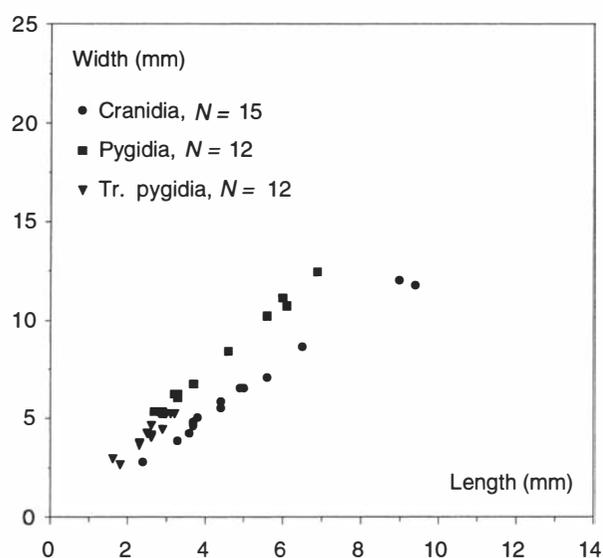


Fig. 199. Cranidia and pygidia of *Nileus depressus serotinus* n.subsp. Maximum width plotted against sagittal length.

N. serotinus n.subsp. strongly resembles *N. depressus depressus*, occurring in the *M. limbata* Zone of Sweden and Norway, and may be an ecophenotype of that subspecies.

Diagnosis. – Small subspecies. Glabella wide (tr.) with slightly rounded central portion and short, quite convex (sag.) anterior part; anterior cranial margin straight; palpebral lobes long (exsag.). Adult pygidia without border, and covered with ‘*depressus*-type’ terrace-line pattern, axis inclusive.

Description. – Small for a *Nileus*, largest cranidium 9.4 mm long, largest pygidium 6.9 mm long (Fig. 199). Cranidium rather convex sagittally, only slightly so transversely. Glabella

quite wide (Table 31), most so in the larger cranidia. Axial furrows ill-defined on testaceous material, but accentuated by a small change of slope between glabella and palpebral lobes; internal moulds show fairly impressed axial furrows, which are somewhat arcuate, and the central part of glabella thereby gets a slightly rounded appearance. Anterior cranial margin almost straight (dorsal view) and gently arched (frontal view). Palpebral lobes comparatively long (exsag.) (Table 31). Mesial glabellar tubercle fairly conspicuous on internal moulds, it is situated closer to posterior cranial margin in the material from the middle part of the *M. limbata* Zone (0.29–0.34 of the cranial length from posterior margin; mean 0.32; $N = 7$), than in the specimens from the top of the *M. simon* Zone (corresponding values 0.36–0.38; mean 0.37; $N = 3$). Anterior branches of facial suture diverge from middle of eye at an angle of about 40° to sagittal line. Posterior branch of facial suture slightly sigmoidal; the angle from corner of palpebral lobe to sutural intersection with posterior margin is about 40° to sagittal line. Test of cranidium seems to be thicker than in most other nileid species described here. Dorsal surface smooth, even the ‘wrinkled’ pattern on sagittal line, present in most nileids, is uncommon, which perhaps relates to the thick test. The holotype has, however, a few oblique ‘wrinkles’ laterally on glabella (Fig. 200A).

Librigena, hypostome and thorax unknown.

Pygidium short, moderately vaulted, characterized in adult state (≥ 3.7 mm) by the lack of a concave border (ratios listed in Table 32). Axis is outlined on testaceous material only by the terrace-line pattern, or by changes of test colour. Because of the vague contour, precise axial dimensions are difficult to obtain, but the length slightly exceeds half of the pygidial length. The single internal mould available shows a slightly inflated triangular axis, delimited by shallow, wide

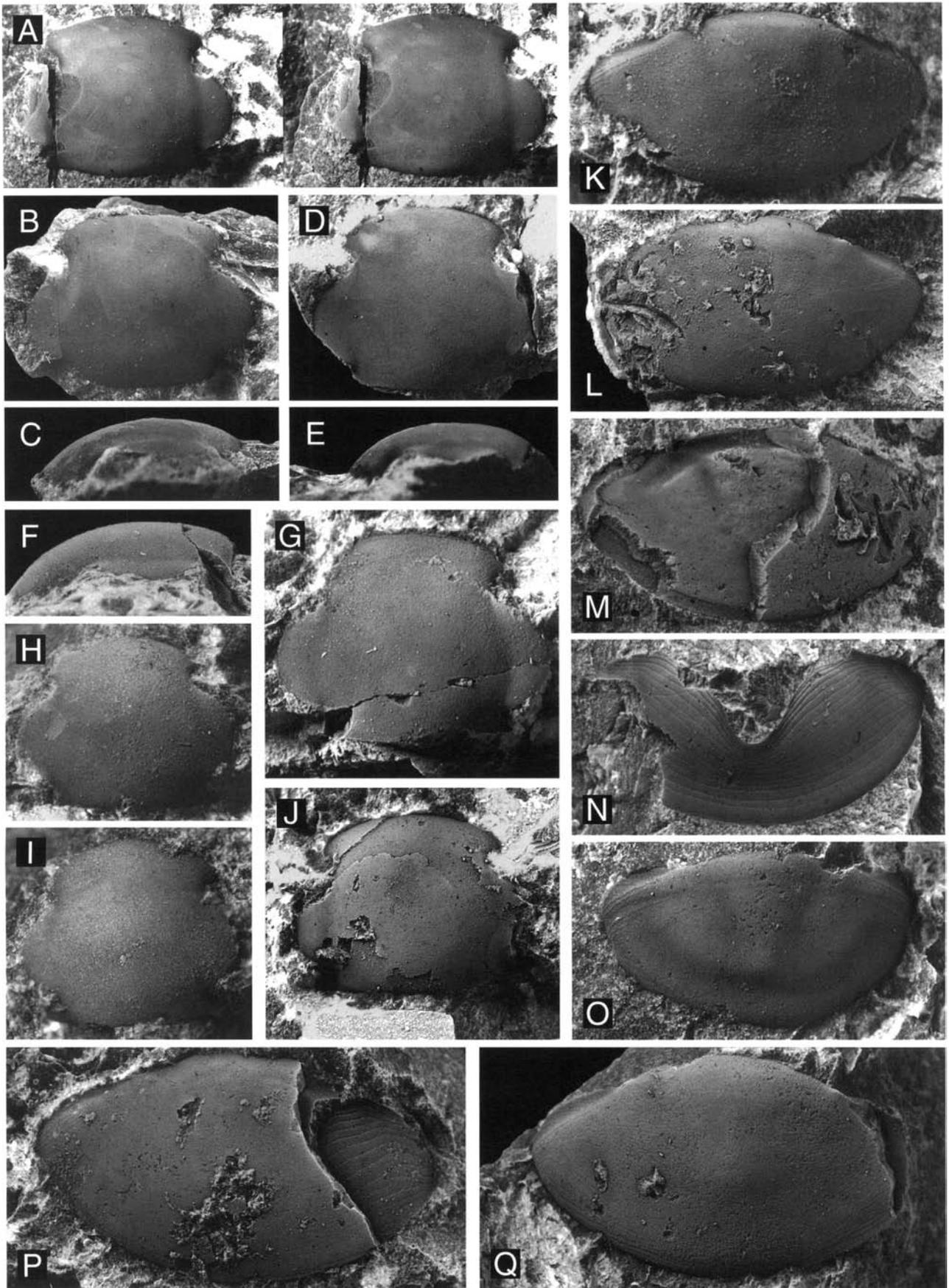
Table 31. *Nileus depressus serotinus* n.subsp.. Ranges for variation of cranidia, expressed as ratios of cranial length.

Size (mm)	Maximum width of cranidium			Glabella width			Palpebral lobe length (exsag.)			Glabellar tubercle, distance to post. margin		
	Range	Mean	<i>N</i>	Range	Mean	<i>N</i>	Range	Mean	<i>N</i>	Range	Mean	<i>N</i>
2.4–3.7	1.13–1.30	1.21	6	0.75–0.84	0.80	6	0.48–0.54	0.51	6	0.30–0.38	0.33	5
≥ 3.8	1.24–1.33	1.29	8	0.84–0.92	0.88	10	0.48–0.55	0.52	10	0.29–0.38	0.33	9

Table 32. *Nileus depressus serotinus* n.subsp. Ranges for variation of pygidia, expressed as ratios.

Size (mm)	Pygidial L:W ratio			Axial width : pygidial width			Axial length : pygidial length			Border length (sag.) : pygidial length		
	Range	Mean	<i>N</i>	Range	Mean	<i>N</i>	Range	Mean	<i>N</i>	Range	Mean	<i>N</i>
1.6–1.8 [Stage B]	0.55–0.69	0.62	2	0.31–0.35	0.33	2	–	–	0	0.19–0.22	0.20	2
2.3–2.9 [Stage D]	0.60–0.66	0.63	6	0.33–0.35	0.34	4	–	–	0	0.23–0.28	0.26	4
2.6–3.2 [Stage E]	0.57–0.62	0.59	4	0.37–0.44	0.41	3	–	–	0	0.22–0.23	0.22	2
2.7–3.3 [Hol.]	0.51–0.56	0.54	8	0.37–0.42	0.40	3	–	–	0	0.21–0.27*	0.24*	3*
≥ 3.7 mm / Hol.	0.54–0.57	0.55	6	–	–	0	–	–	0	–	0.00	7

* Including only specimens with a border.



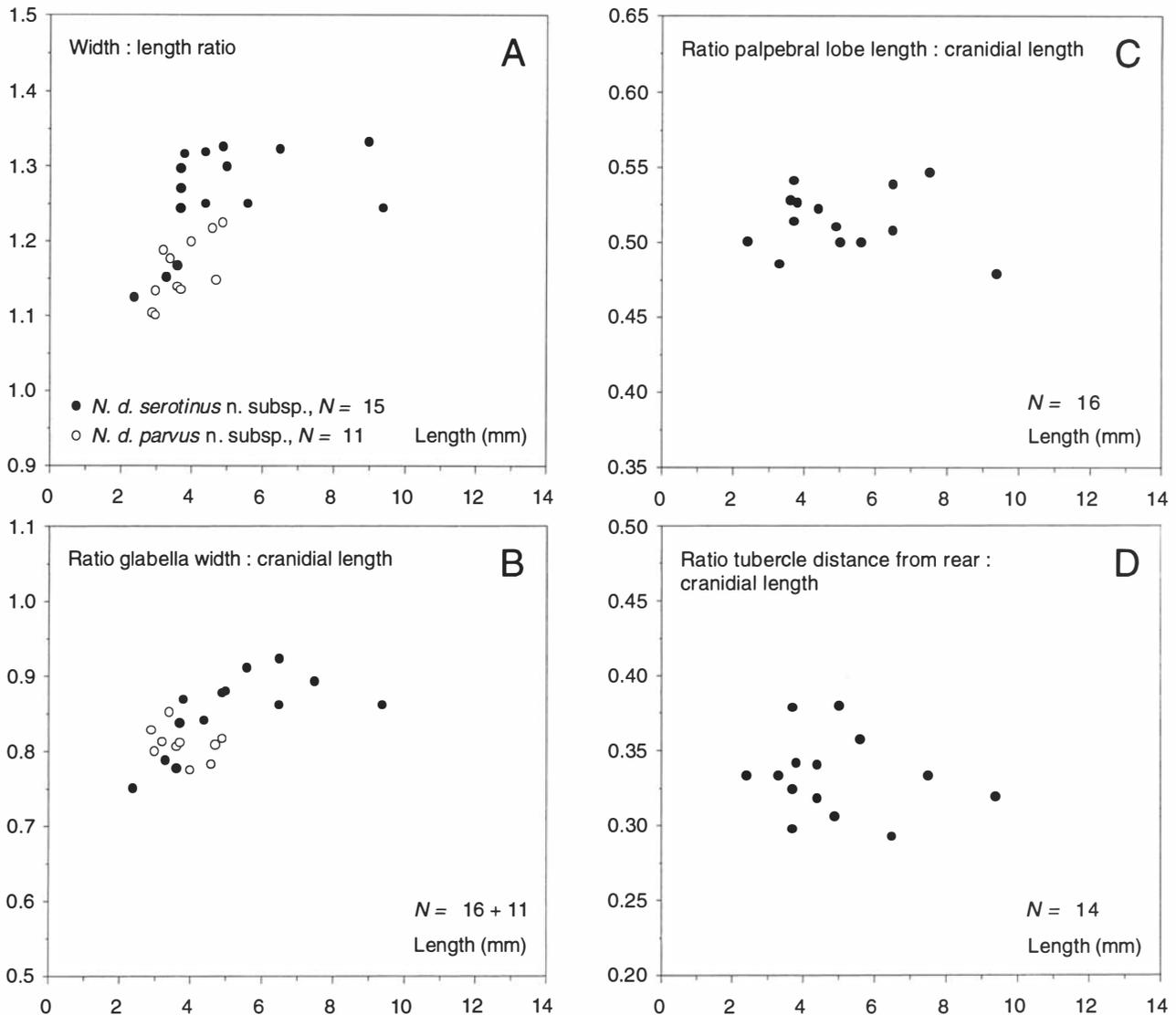


Fig. 201. Cranidia of *Nileus depressus serotinus* n.subsp. (●) and *N. d. parvus* n.subsp. (○). □A. Ratio between maximum width across palpebral lobes and cranial length plotted against sagittal length. □B. Ratio between glabella width (measured between posterior corners of palpebral lobes) and cranial length plotted against cranial length. □C. Ratio between palpebral lobe length (exsag.) and cranial length plotted against cranial length. □D. Ratio between the distance from posterior cranial margin to glabellar tubercle and cranial length (sag.) plotted against cranial length.

Fig. 200. *Nileus depressus serotinus* n. subsp. □A. Holotype. Cranidium, stereo-pair, $\times 6$. MGUH 22.850 (K 932), bed +15, Killeröd. □B–C. Cranidium, dorsal and side views, $\times 8$. MGUH 22.851 (K 911a), bed +15, Killeröd. □D–E. Cranidium, dorsal and side views, $\times 9$. MGUH 22.852 (K 959), bed +15, Killeröd. □F–G. Cranidium, side and dorsal views, $\times 9$. MGUH 22.853 (K 911b), bed +15, Killeröd. □H. Cranidium, $\times 9$. MGUH 22.854 (K 251), bed +11, Killeröd. □I. Juvenile cranidium, $\times 15$. MGUH 22.855 (K 918b), bed +15, Killeröd. □J. Early cranidium, $\times 6$. MGUH 22.856 (K 541), bed 3, Gårdlösa-4a. □K. Pygidium showing 'depressus-type' terrace-line pattern, $\times 9$. MGUH 22.857 (K 945), bed +15, Killeröd. □L. Pygidium, $\times 6$. MGUH 22.858 (K 956), bed +15, Killeröd. □M. Partly exfoliated pygidium showing axis, $\times 6$. MGUH 22.859 (K 263), bed +14, Killeröd. □N. Internal mould of pygidium showing doublure, $\times 5$. MGUH 22.860 (K 931a), bed +15, Killeröd. □O. Transitory pygidium, stage E, showing concave border, $\times 10$. MGUH 22.861 (K 918a), bed +15, Killeröd. □P. Pygidium showing 'depressus-type' terrace-line pattern, and no concave border, $\times 6$. MGUH 22.862 (K 963), bed +15, Killeröd. □Q. Paratype. Pygidium showing 'depressus-type' terrace-line pattern, $\times 9$. MGUH 22.863 (K 914a), bed +15, Killeröd.

axial furrows; three or four axial segments are faintly indicated in addition to the terminal piece and an anterior half-ring. The same specimen shows a well-impressed anterior pleural furrow; this furrow, as well as the axial segmentation, is effaced in all specimens with intact test. Adult pygidia are entirely covered with a very dense 'depressus-type' terrace-line pattern; 15–18 lines/mm were counted on the pleural fields in two pygidia 4.6 and 5.6 mm long. The terrace lines, which are very fine, are slightly less densely spaced in the axial area, and pygidia less than 5–5.5 mm long have a smooth axial area. Doublure strongly concave, so the distal part is flat. It is provided with a total of 15–16 moderately impressed terrace lines.

Juveniles. – Seven cranidia, less than 3.8 mm long, are comparatively elongate, with the smallest L:W ratio in a cra-

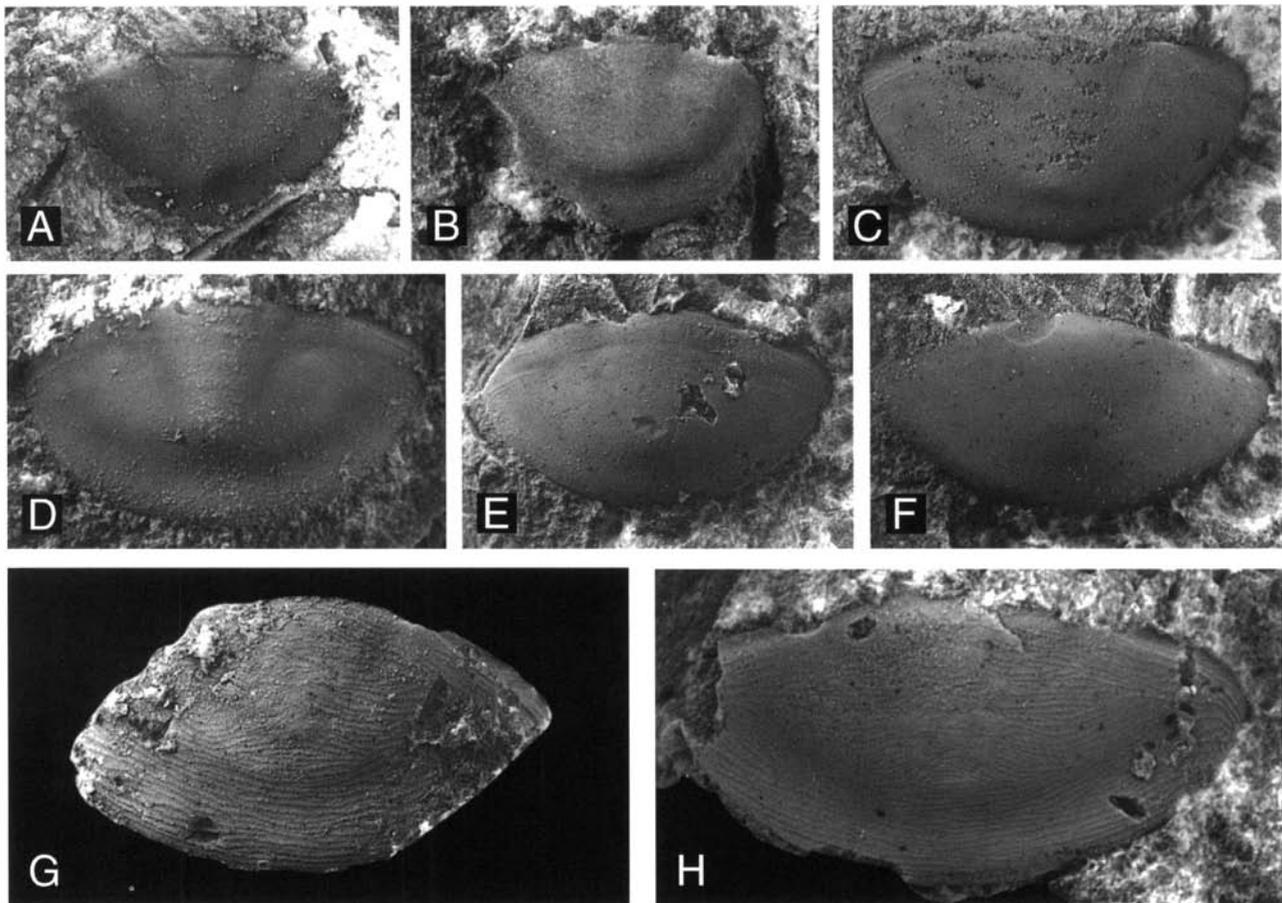


Fig. 202. *Nileus depressus serotinus* n. subsp. □A. Transitory pygidium, stage C, $\times 15$. MGUH 22.864 (K 931b), bed +15, Killeröd. □B. Transitory pygidium, stage C, $\times 15$. MGUH 22.865 (K 914b), bed +15, Killeröd. □C. Transitory pygidium, stage D, $\times 15$. MGUH 22.866 (K 999b), bed +18, Killeröd. □D. Transitory pygidium, stage E, $\times 12$. MGUH 22.867 (K 1003), bed +14, Killeröd. □E. Transitory pygidium, stage E, $\times 9$. MGUH 22.868 (K 953b), bed +15, Killeröd. □F. Small holaspid pygidium showing smooth cuticle surface, $\times 9$. MGUH 22.869 (K 952), bed +15, Killeröd. □G. Early pygidium showing border and 'depressus-type' terrace-line pattern, $\times 12$. MGUH 22.870 (K 185b), bed -3, Killeröd. □H. Early pygidium showing concave border, $\times 9$. MGUH 22.871 (K 549), bed 3, Gårdlösa-4a.

nidium 2.4 mm long, and the highest ratio in cranidia 3.7 mm long (Table 31). The elongation is also reflected by the glabellar W:L ratio, and again the smallest specimens have the most elongate glabella. Juvenile cranidia are also more strongly vaulted (tr.), and more evenly convex (sag.) in comparison to adults, in which the anterior part of glabella is steeply inclined, while its posterior main part exhibits a less strong curvature. Specimens less than 3 mm long have a slightly more rounded anterior cranidial margin. The juvenile cranidia overall clearly resemble the adults and are positively identified, e.g., by the long palpebral lobes (relative length as in adults).

Two transitory pygidia, less than 2 mm long, represent stage B and presumably have two unreleased thoracic segments, which, however, are not at all outlined (test is intact). These specimens show a comparatively wide, gently concave border sloping rather strongly in outwards direction, and

which occupies 0.3 of the pygidial length postaxially. Otherwise they match the description p. 243.

Six D-stage transitory pygidia, 2.3–2.9 mm long, and four E-stage transitory pygidia, 2.6–3.2 mm long, are comparatively small, but otherwise match the description pp. 244–245. However, one of the E-stage representatives apparently (it is slightly damaged) approaches the adult stage and lacks a border, which is most unusual for this growth stage.

The smallest holaspid pygidia, 2.7–3.3 mm long, are similar to the adult specimens in all but one feature: they lack the characteristic 'depressus-type' terrace-line pattern and instead have scattered terrace lines on the pleural fields arranged in a 'orbiculatoides-type' pattern; a single specimen is smooth. Two larger specimens, 3.7 and 4.6 mm long, show a 'depressus-type' pattern, but still have a smooth axis.

Only three small pygidia, 2.9, 3.2 and 3.3 mm long (all holaspides), were found in the upper part of the *M. simon*

Zone, in addition to several adult cranidia. These pygidia differ from the later juvenile pygidia of the same size by showing a dense 'depressus-type' terrace-line pattern. The specimens 3.2 and 3.3 mm long are the smallest nileid holaspidites recorded with terrace lines, which occur even on the axial area; the line density is 13–14 lines/mm on the pleural fields in both specimens (Fig. 202G–M). These three early pygidia also differ by the presence of a concave border, occupying 0.21–0.25 of the pygidial length, although the border is quite steep.

Affinities. – *N. d. serotinus* n. subsp. is coeval with *N. depressus schranki* n. subsp.; their spatial distribution within the Komstad Limestone is discussed below. *N. d. serotinus* n. subsp. is readily distinguished from *N. d. schranki* n. subsp. by the smaller size, the longer palpebral lobes, the more rounded glabella, the truncate appearance of the cranidium, and by the proportionally shorter pygidium without concave border in the adult stage, and also which carries fewer terrace lines on the doublure.

N. depressus serotinus n. subsp. strongly resembles *N. depressus depressus*, and may be an ecophenotype of that subspecies. Shared features are a rounded glabella, well-impressed furrows on internal moulds, a straight anterior cranial margin, a conspicuous glabellar tubercle on internal moulds and a pygidium with a comparatively prominent anterior pleural furrow, no concave border, virtually identical doublure, and an external surface covered with fine terrace lines; both subspecies are small. *N. depressus serotinus* n. subsp. is distinguished from *N. depressus depressus* by the slightly less rounded glabella, which is relatively narrower (see Fig. 203B), the cephalic axial furrows are more indistinct, the sagittal cranial convexity is slightly stronger, the transversal convexity is smaller, the palpebral lobes are comparatively longer (Fig. 203C) with correspondingly shorter posterior fixigenae (exsag.), the anterior and posterior branches of facial suture diverge more strongly, and the posterior branches are but slightly sigmoidal, not straight, there is apparently no pitting of the cranial test surface; the pygidium has a denser terrace-line pattern, and no border. The larger pygidia of *N. d. serotinus* n. subsp. all have terrace lines in the axial area, whereas *N. depressus depressus* shows variable conditions. *N. d. depressus* seems overall to attain larger sizes than *N. d. serotinus* n. subsp.

N. d. serotinus n. subsp. resembles the somewhat younger *N. depressus parvus* n. subsp.; see remarks on the latter.

N. orbiculatus Tjernvik has a rounded glabella and lacks a pygidial border and thus resembles *N. d. serotinus* n. subsp. with regard to size and general outline. *N. d. serotinus* n. subsp. is distinguished by the different course of the anterior branches of facial suture, which are diverging more strongly in front of the eyes and then run almost straight inwards, the palpebral lobes are relatively longer, the cranidium is not covered with terrace lines (the holotype of *N. orbiculatus* has been investigated) and the terrace-line pattern of the pygidium is different.

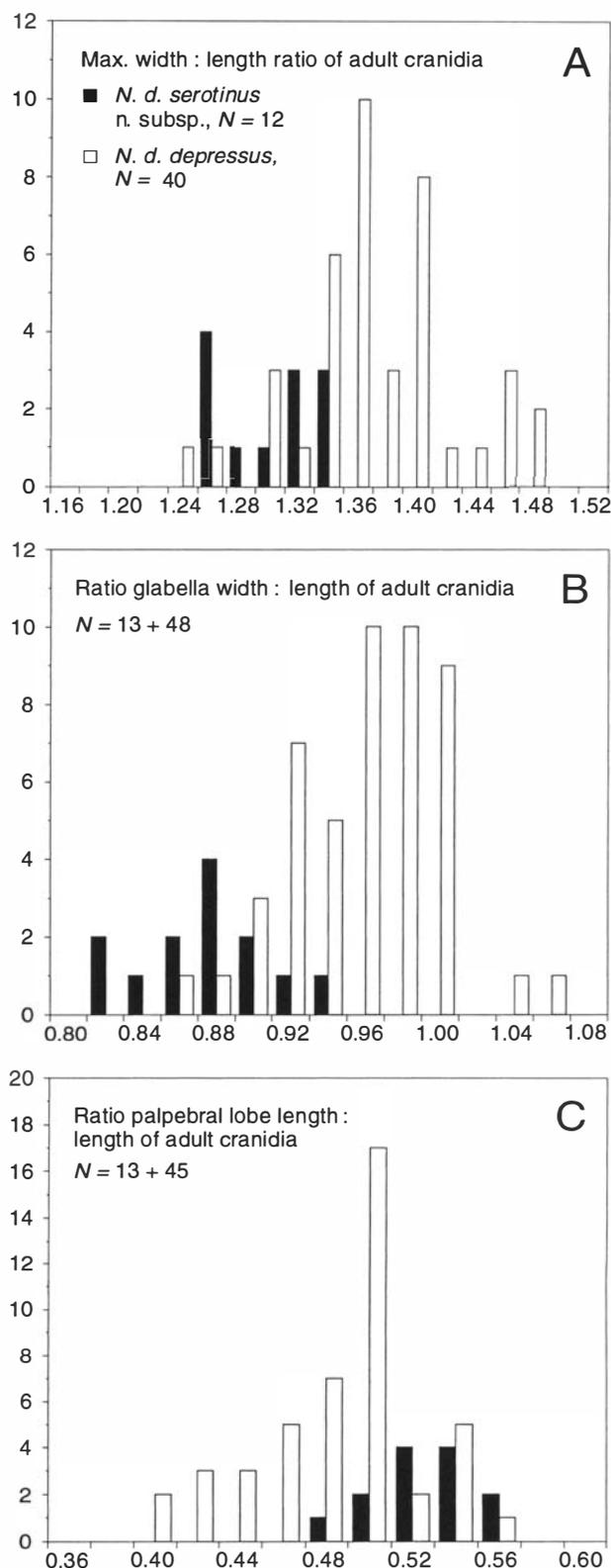


Fig. 203. *Nileus depressus serotinus* n. subsp. versus *N. d. depressus*, adult cranidia only (> 4 and 5 mm long, respectively). □A. Comparison of adult width:length ratios (measured across palpebral lobes). □B. Comparison of adult ratios between glabella width (measured between hind corners of palpebral lobes) and cranial length. □C. Comparison of adult ratios between palpebral lobe length (exsag.) and cranial length.

Remarks. – The distribution of *N. d. serotinus* n.subsp. and *N. d. schranki* n.subsp. is important for distinction of taxonomic rank, as subspecies of the same taxon by convention must not occur associated. It is immediately evident that the two subspecies are mutually exclusive in the section (Fig. 56), but they have actually been found together in bed 3 at Gårdlösa-4a and in beds +14, +16 and +18 at Killeröd. However, *N. depressus schranki* n.subsp. occurs only in the lower part of bed 3, 7–11 cm below top, whereas *N. d. serotinus* n.subsp. is confined to the upper part of the bed, 1–3 cm below top; in bed +16 a single specimen of *N. d. serotinus* n.subsp. was found 10 cm below top of bed, six specimens of *N. d. schranki* n.subsp. were found 2–5 cm below top; and in bed +18 three specimens of *N. d. serotinus* n.subsp. were found within the upper 0.5 cm of the bed, while a single pygidium of *N. d. schranki* n.subsp. was found 3 cm below top. It appears that the two subspecies intermingle only in bed +14, where two specimens of *N. d. schranki* n.subsp. were found together with five specimens of *N. d. serotinus* n.subsp.. As the two forms thus basically are isolated from each other, a separation at the subspecies level appears appropriate.

Nileus depressus parvus n.subsp.

Fig. 204

Synonymy. – □ v cf. 1984 *Nileus* sp. – Wandås, p. 232; Pl. 11A–B (short description, occurrence, illustrations of damaged cephalon).

Holotype. – Cranidium MGUH 22.873 (K 1188) (Fig. 204B) from 8 cm below top of bed 8, Killeröd site b (base of the *A. 'raniceps'* Zone).

Paratype. – Pygidium MGUH 22.879 (K 1206) (Fig. 204J) from 5 cm above base of bed 8, same locality.

Additional material. – Thirteen cranidia, 1 pygidium, and 4 transitory pygidia.

List of additional material. – □ Cranidia K 1163 (t), K 1168a (t) [MGUH 22.876], K 1168b (t), K 1174 b (t, c), K 1174d (t), K 1179a? (t), K 1201c (t), K 1205 (t) [MGUH 22.874], K 1208 (t) [MGUH 22.875], K 1209a (t) [MGUH 22.881], K 1209d (pim), K 1210a (t) [MGUH 22.872], K 1210b (t, fragment). □ Pygidia K 1173a (pim), K 1178 (im) [MGUH 22.877], K 1186? (t) [MGUH 22.880], K 1201b (t) [MGUH 22.878], K 1209e (t).

Occurrence. – All specimens are from bed 8 at Killeröd site b, basal part of the *A. 'raniceps'* Zone.

Diagnosis. – Minute subspecies. Cranidial convexity strong (sag.), anterior cranial margin rectilinear, glabella without anterolateral expansion and is confluent with palpebral areas; glabellar tubercle in relatively advanced position; palpebral lobes unusually long (exsag.); pygidium fully convex, and covered, exclusive of axis, with a '*depressus*-type' terrace-line pattern.

Description. – Largest cranidium 4.9 mm long, largest pygidium 3.8 mm long. Sagittal convexity of cranidium strong, transverse convexity fairly high for a *Nileus*; anterior margin almost rectilinear. Cranial L:W ratio varies from about 1.10 in specimens 2.9–3.0 mm long to about 1.22 in specimens 4.6–4.9 mm long (Table 33). Axial furrows effaced, and glabella is confluent with palpebral areas. Distance between posterior corners of palpebral lobes, i.e. 'glabellar' width, varies between 0.78 and 0.83 of the cranial length (mean 0.81; $N=11$). Anterior part of glabella parallel-sided without anterolateral expansion. Mesial glabellar tubercle usually visible as a dark spot on outside of test; no internal moulds are available. It is situated rather forwardly (Table 33). Palpebral lobes unusually long (see also Fig. 203C). Posterior fixigena acuminate triangular and rather long, stretching almost to outer level of the palpebral lobe; it is flexed somewhat downwards, but has no posterior declination, and posterior margin of cranidium is straight. Anterior branches of facial suture run straight forward from anterior inner corners of palpebral lobes, converging (!) at an angle of about 15° to sagittal line, then, halfway to anterior margin turn and diverge at an angle of about 10° to sagittal line to make a very sharp inwards bend and then run transversely, merging smoothly at sagittal line. Posterior branches of facial suture run straight backward-outward, diverging at an angle of about 50° to sagittal line. Test surface of cranidium appears smooth, but all specimens are slightly corroded.

Librigena, hypostome and thorax unknown.

Pygidium very like that of *N. d. serotinus* n.subsp., except for the broad axis; the two available holaspide specimens, ca. 3 and 3.8 mm long, lack any indications of a concave border. Pygidium slender (Table 34); axis only crudely outlined by the lack of terrace lines, but seems, nevertheless, to be unusually broad, approaching half the width of the pygidium. Dorsal surface covered with a dense terrace-line pattern of '*depressus*-type'; axial area smooth. Twelve lines/mm were counted on the pleural fields of the largest pygidium, 3.8 mm long. Doublure not exposed (see description of juveniles below).

Juveniles. – Apart from being a little elongate, small cranidia are alike larger specimens, and the entire cranial material is described jointly above.

Two D-stage transitory pygidia are only 1.9 and 2.3 mm long; the fixed segments are outlined by shallow furrows. The specimens are comparatively broad (Table 34), and provided with a remarkably broad axis. Both specimens are corroded, but appear smooth, except for a few anterolateral terrace lines; they are identified by their lack of a concave border, which is a unique feature for this growth stage.

Two E-stage transitory pygidia are only 2.1 and 2.5 mm long; they also show a slightly raised, broad axis, and no border. Specimens exfoliated, but a patch of test in pygidium K 1173a indicates that openly spaced terrace lines are present at least anterolaterally, and possibly the pleural fields are covered by an '*orbiculatoides*-type' terrace-line pattern.

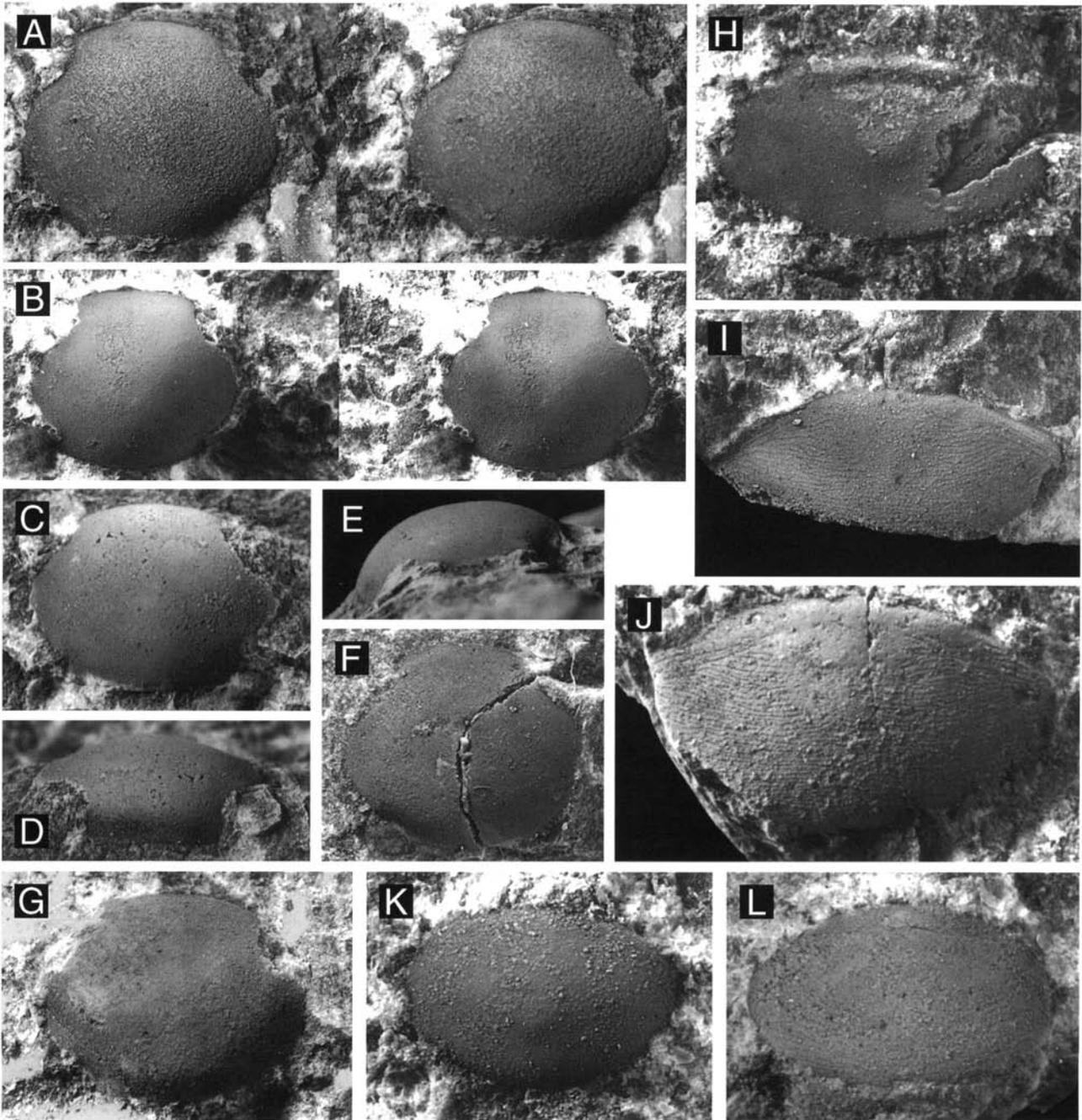


Fig. 204. *Nilæus depressus parvus* n. subsp. All specimens are from bed 8, Killeröd site b. □A. Cranidium, stereo-pair, $\times 9$, MGUH 22.872 (K 1210a). □B. Holotype. Cranidium, stereo-pair, $\times 6$, MGUH 22.873 (K 1188). □C–E. Cranidium, dorsal, frontal and side views, $\times 9$, MGUH 22.874 (K 1205). □F. Cranidium, $\times 9$, MGUH 22.875 (K 1208). □G. Slightly corroded cranidium, $\times 10$, MGUH 22.876 (K 1168a). □H. Internal mould of transitory pygidium, stage E, $\times 15$, MGUH 22.877 (K 1178). □I. Fragmentary pygidium showing 'depressus-type' terrace-line pattern, $\times 10$, MGUH 22.878 (K 1201). □J. Paratype. Pygidium showing 'depressus-type' terrace-line pattern, $\times 9$, MGUH 22.879 (K 1206). □K. Transitory pygidium, stage D, $\times 16$, MGUH 22.880 (K 1186). □L. Transitory pygidium, stage D, showing incipient 'depressus-type' terrace-line pattern, $\times 9$, MGUH 22.881 (K 1209a).

Doublure insignificantly concave, almost flat, steeply inclined, and provided with about 11–12 continuous terrace lines.

The D- and E-stage pygidia of *N. d. parvus* n. subsp. are unusually small.

Affinities. – *N. depressus parvus* n. subsp. resembles *N. d. serotinus* n. subsp. by being small, having a quite strongly convex cranidium (sag.), long palpebral lobes, straight anterior cranial margin, and an identical pygidium. The new subspecies is distinguished by the anterolaterally non-ex-

Table 33. *Nileus depressus parvus* n.subsp. Ranges for variation of cranidia, expressed as ratios of cranial length.

Size (mm)	Maximum width of cranidium			Glabella width			Palpebral lobe length (exsag.)			Glabellar tubercle, distance to post. margin		
	Range	Mean	N	Range	Mean	N	Range	Mean	N	Range	Mean	N
2.4–3.0	1.10–1.13	1.11	3	0.80–0.83	0.81	3	0.55–0.57	0.56	3	–	0.37	1
3.2–3.7	1.14–1.19	1.16	4	0.81–0.85	0.82	4	0.56–0.57	0.56	4	0.38–0.41	0.39	3
4.0–4.9	1.15–1.22	1.20	4	0.78–0.82	0.80	4	0.51–0.55	0.53	4	0.40–0.43	0.41	2

Table 34. *Nileus depressus parvus* n.subsp. Ranges for variation of pygidia, expressed as ratios.

Size (mm)	Pygidial L:W ratio			Axial width : pygidial width			Axial length : pygidial length			Border length (sag.) : pygidial length		
	Range	Mean	N	Range	Mean	N	Range	Mean	N	Range	Mean	N
1.9–2.3 [Stage D]	0.61–0.68	0.65	2	–	0.50	1	–	–	0	–	0	2
2.1–2.5 [Stage E]	0.54–0.57	0.56	2	–	0.46	1	–	0.62	1	–	0	2
3.8 [Hol.]	–	0.54	1	–	~0.45	1	–	–	0	–	0	1

panding glabella, by the lack of cephalic axial furrows, by the rather forwardly positioned glabellar tubercle, and by the proportionally longer palpebral lobes (see Fig. 203C). No differences have, so far, been established for the adult pygidia, but the doublure possibly differs, despite the external similarity, as a juvenile specimen of *N. d. parvus* n.subsp. shows a steep, only slightly concave doublure with 11–12 terrace lines; a strongly concave doublure with 15–16 terrace lines is typical for *N. d. serotinus* n.subsp. Transitory pygidia of *N. depressus parvus* n.subsp. differ by the absence of a concave border. The lack of terrace lines in the axial area in the largest pygidia of *N. d. parvus* n.subsp. is not significant, as the same phenomenon is seen in equal-sized pygidia of *N. d. serotinus* n.subsp.

N. depressus costatus Fortey (see Fortey 1975a) resembles *N. d. parvus* n.subsp. with regard to the undeveloped cephalic axial furrows, the lack of a pygidial border and the presence of a 'depressus-type' terrace-line pattern. However, *N. d. costatus* has a less convex (sag.) cranidium with smaller palpebral lobes, a more rounded anterior margin, an anterolaterally expanding glabella, and a pitted test surface; the pygidium of *N. d. costatus* is proportionally longer.

N. macrops Billings (see, e.g., Whittington 1965) has a very similar cranidium with long palpebral lobes, no axial furrows, strong sagittal convexity, no anterolateral glabellar expansion, a rather similarly shaped posterior fixigena, and the size is also approximately the same. No clear differences between the cranidia of *N. macrops* and *N. depressus parvus* n.subsp. are evident, but their pygidia are quite different, and presumably their thoraxes differ as well.

Remarks. – *Nileus depressus parvus* n.subsp. is, so far, known only from bed 8 at Killeröd site b, which is dominated by juveniles (*N. armadillo*, *N. implexus* n.sp. and *N. depressus parvus* n.subsp.). Hence it cannot be excluded that the described material contains only juveniles.

Wandås (1984, p. 232; Pl. 11A–B) briefly described an unnamed nileid with a short range in the uppermost part of

the Killingen Member at Furnes, Norway, i.e. considerably above the stratigraphical level of *N. d. parvus* n. subsp.. The slightly impaired 6.5 mm long cephalon figured by Wandås is strongly similar to *N. d. parvus* n.subsp., notably with regard to the long palpebral lobes, the absence of axial furrows, and the subparallel course of the anterior branches of facial suture. By comparison, the material from the Komstad Limestone has a slightly stronger convexity (sag.) of the anterior portion of glabella, which cannot be explained as due to size differences, as smaller nileid cranidia always are less strongly convex than larger ones. Besides, the furrows at the base of the eye socle in the Norwegian specimen impinge upon the anterolateral portions of the cranidium, which is a unique feature. The librigenae of *Nileus* sp. *sensu* Wandås are markedly vaulted, and suggests, like the pygidium of *N. d. parvus* n.subsp., that these new forms are members of the *N. depressus* group.

Nileus depressus subsp. A

Figs. 187, 189, 191, 205

Synonymy. – □1980 *Nileus glazialis glazialis* (Schrank) – Tjernvik & Johansson, pp. 178–179, 191, 192, 203 (short diagnosis, occurrence).

Material. – Nine cranidia, including 4 juvenile specimens, and 8 pygidia, including 2 juvenile specimens.

List of material. – □Cranidia A 744 (pim), A 745b? (t, juvenile), A 749 (pim) [MGUH 22.884], A 764a (pim) [MGUH 22.882], A 770? (im) [MGUH 22.883], A 772? (im), A 774? (t, juvenile) [MGUH 22.885], A 776? (im, juvenile), A 789? (t, juvenile). □Pygidia A 697d? (t, fragment), A 740 (pim), A 745a (im) [MGUH 22.888], A 745c? (t, juvenile), A 752 (pim), A 764b (pim) [MGUH 22.886], A 764c (pim) [MGUH 22.8878], A 790? (t, juvenile).

Occurrence. – *Nileus depressus* subsp. A is restricted to the upper half of bed M-6 at Slemmestad, which belongs to the uppermost part of the *M. simon* Zone. The fragmentary pygidium A 697d from bed M-4 is tentatively assigned.

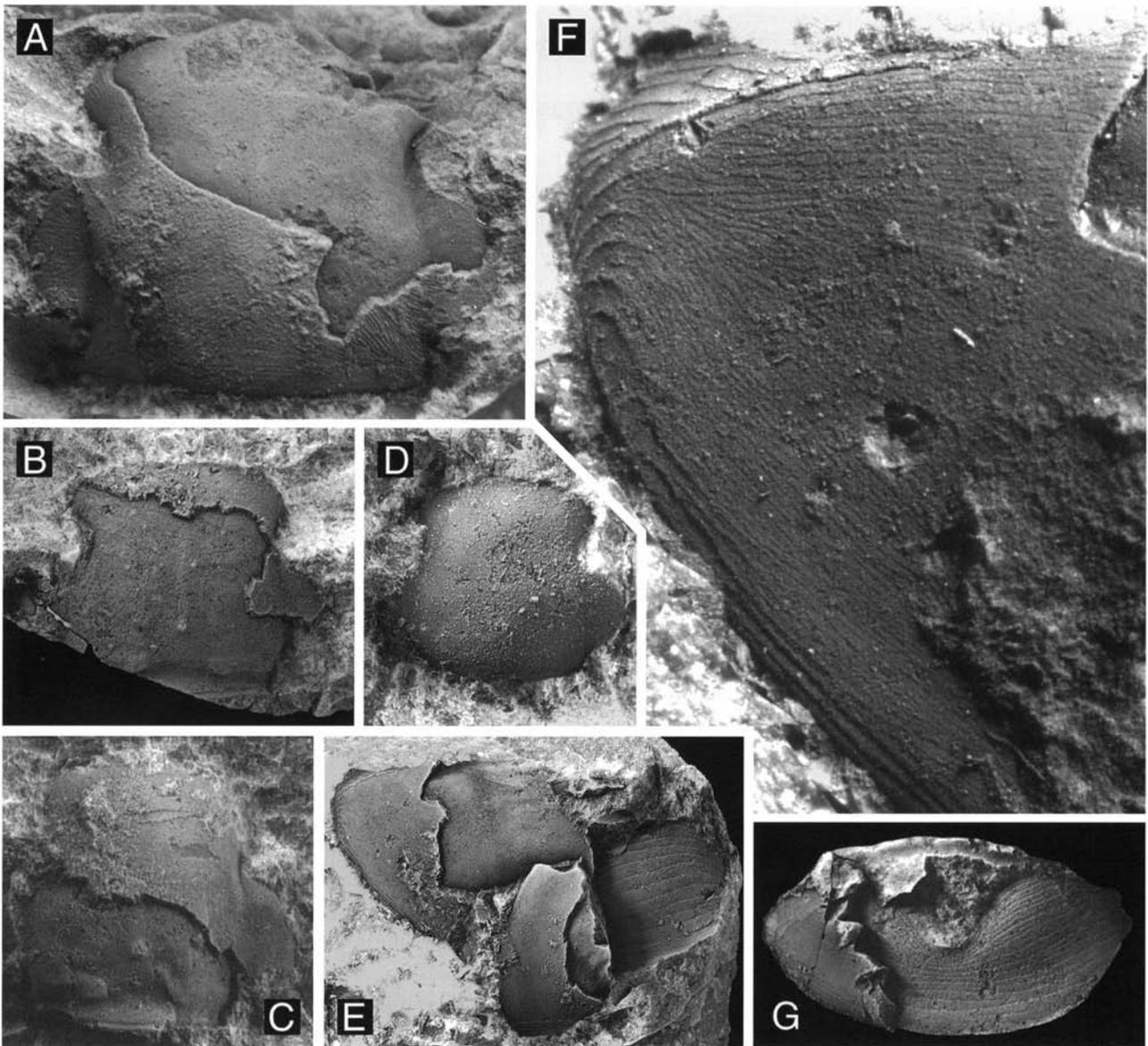


Fig. 205. *Nileus depressus* subsp. A. All specimens are from bed M-6, Slemmestad. □A. Partly exfoliated cranidium, showing cuticle terrace-line sculpture, $\times 6$. MGUH 22.882 (A 764a). □B. Exfoliated cranidium, $\times 4$. MGUH 22.883 (A 770). □C. Partly exfoliated cranidium, $\times 6$. MGUH 22.884 (A 749). □D. Small cranidium with smooth cuticle, $\times 6$. MGUH 22.885 (A 774). □E–F. Two partly exfoliated pygidia, $\times 4$. MGUH 22.886 (A 764b) and MGUH 22.887 (A 764c). Close-up (F) of pleural field showing fine terrace-line sculpture, $\times 20$. □G. Internal mould of pygidium showing doublure, $\times 6$. MGUH 22.888 (A 745a).

Nileus depressus subsp. A is considered identical to *Nileus glazialis glazialis sensu* Tjernvik (1980), which ranges from the top of the *M. polyphemus* Zone, through the entire *M. simon* and *M. limbata* Zones and into the basal part of the *A. expansus* Zone of Lanna, Sweden (Fig. 146).

Description. – Small for a *Nileus*, largest cranidium 9 mm long, largest pygidium 9 mm long (ratios in Table 35). Cranidium similar to late cranidia of *N. depressus glazialis*, except for the deviating terrace-line pattern. However, it is also the impression that the occipital ring, the adjoining pair of muscle insertion sites (see description of *N. depressus*

glazialis), as well as the mesial glabellar tubercle of internal moulds are slightly more conspicuous in subsp. A in comparison to *N. depressus glazialis*. The trend displayed by *N. depressus glazialis* towards a broader glabella seems to be followed by *N. depressus* subsp. A (Fig. 179B). Densely spaced terrace lines are present on the entire cranidium, except for the anterior part of glabella. The lines are gently undulating and roughly transverse. Ten lines/mm were counted posteriorly on glabella in a cranidium 8.6 mm long.

Available pygidia poorly preserved; in gross outline they are close to *N. depressus glazialis*. By comparison they appear less vaulted, and slightly elongate, although this is not con-

Table 35. *Nileus depressus* subsp. A. Ranges for variation of crania ≥ 5.7 mm long, expressed as ratios of cranial length. See also Fig. 189.

Feature	Range	Mean	N
Maximum cranial width	1.23–1.28	1.27	4
Glabellar width	0.82–0.94	0.89	5
Palpebral lobe length (exsag.)	0.42–0.44	0.43	3
Glabellar tubercle	0.30–0.33	0.31	5

firmed by the measured specimens, showing L:W ratios between 0.53 and 0.60 (mean 0.56; $N = 4$). The border is indicated only by a minimal change of slope, hence it is rather poorly defined. Axis seems to be relatively long and narrow; it occupies 0.34–0.35 (tr.) of the pygidial width at anterior margin in two specimens, which actually is at the lowest end and below the variation range demonstrated for *N. depressus glazialis*. The surface ornamentation consists of very fine, closely spaced terrace lines covering the entire pygidium (Fig. 205F). A total of 90–95 lines was counted from anterior to posterior margin in specimen A 740, about 8.5 mm long, but this figure must be regarded as a minimum, as the counting was not performed close to axis (test not preserved). Subsp. A thus seems to have 1.5 to 2 times as many lines as *N. depressus glazialis*. Three specimens, 5.7, 8.5 and 8.7 mm long, all show densities of about 14–15 terrace lines per millimetre on the pleural fields. Besides being more densely spaced, the terrace lines also differ from *N. d. glazialis* by being less impressed. Pygidial doublure shows 18–19 lines.

Juveniles. – A few juveniles from the upper half of bed M-6 presumably represent *N. depressus* subsp. A, but some of them may in fact belong to *N. depressus glazialis*, occurring sparsely at this level, too. Two crania, 2.5 mm and 3 mm long, have almost straight axial furrows, converging gently forwards; the subrectangular glabella is comparatively narrow, W:L ratio 0.8. The sagittal convexity is less pronounced and the anterior margin is presumably more rounded than in larger specimens. Test surface smooth.

Cranidium A 774, 5.2 mm long, resembles adult specimens with regard to morphology, but the test surface is smooth (the specimen perhaps belongs to *N. depressus glazialis*). The smallest cranium showing terrace lines is 6.2 mm long.

Two holaspid pygidia, 4.7 mm and 5.2 mm long, carries an 'orbiculatoides-type' terrace-line pattern, but are otherwise similar to adults; W:L ratio 0.57 ($N = 2$); border length (sag.) 0.23 of pygidial length ($N = 1$).

Remarks. – *Nileus depressus* subsp. A is believed to represent an ecophenotype of *N. d. glazialis*, but is readily separated from this subspecies, as well as from most other Nileids, by the highly characteristic dorsal terrace-line pattern. Subsp. A is inferred to correspond to *Nileus glazialis glazialis sensu* Tjernvik (1980); the relationship between *N. depressus glazi-*

alis (as defined here) and *N. depressus* subsp. A, and the possible shortcomings of separating them as subspecies, is discussed in the section on *N. depressus glazialis*. For the present material the separation appears fairly objective, but the distinction may be more arbitrary in central Sweden, as indicated by material demonstrated to me by Dr. Tjernvik in 1983. It is believed that *N. depressus glazialis* and *N. depressus* subsp. A represent end members in a continuous variation spectrum.

Nileus planiceps n.sp.

Figs. 206–207

Derivation of name. – Latin *planiceps* = flat-headed, alluding to the low cranial convexity (sag.) of the new species.

Holotype. – Cranidium MGUH 22.889 (S 785) (Fig. 206A), found 2 cm above base of bed –12 at Skelbro (lower part of *M. simon* Zone).

Paratype. – Pygidium MGUH 22.892 (K 610a) (Fig. 206H), found 1 cm above base of 6 at Gårdlösa-4a (*M. simon* Zone).

Additional material. – Five crania (including 1 juvenile specimen) and 15 pygidia.

List of additional material. – □Crania S 692 (im), S 784 (t) [MGUH 22.890], S 1153 (t), K 444 (pim), LU 21 (t) [LO 7076]. □Pygidia S 588 (c), S 591 (t), S 691 (partly c) [MGUH 22.891], S 944 (pim) [MGUH 22.895], S 1097 (t), S 1159a (im), K 43a (t) [MGUH 22.894], K 501b (t), K 510? (c), K 564 (im) [MGUH 22.896], K 698 (t), LU 49 (c), LU 50-9 (c), LU 112 (c), IK P-39 [MGUH 22.893].

Occurrence. – *Nileus planiceps* n.sp. occurs infrequently in the Komstad Limestone from the middle of the *M. polyphemus* Zone and into the lower part of the *M. limbata* Zone. It has been found in beds –18, –16 (middle part of the *M. polyphemus* Zone), –12, –4 (*M. simon* Zone), and +2, +3 (lower subzone of *M. limbata* Zone) at Skelbro. A few specimens were found in the *M. simon* Zone of SE Scania (bed K at Gårdlösa-1; beds 2, 4, 6 at Gårdlösa-4a; bed –9 at Killeröd); museum specimens LU 50 and LU 112 from Komstad originate from a similar level (corresponding to bed interval to –1 to –9 of Killeröd). Specimen LU 49 from Smedstorp is from the *M. simon* Zone. The fragmentary cranium LU 21 is from a loose boulder at Andrarum, level cannot be verified. The new species is, so far, not known from outside the Komstad Limestone domain.

Diagnosis. – Cranidium of low convexity (both ways), anterior margin evenly rounded and with flattened rim; antero-lateral expansion of glabella strong (tr.), but short (exsag.); axial furrows well-impressed; mesial glabellar tubercle situated relatively far back. Pygidium covered, axis inclusive, with extremely densely spaced, very fine terrace lines; axis slightly raised, moderately tapering; border very narrow and steep, ill-defined. Pygidial doublure show more than 25 terrace lines.

Description. – Medium-sized to large for a *Nileus*, largest cranidium 17.8 mm long, largest pygidium 17.8 mm long. Cranidium of low convexity (both ways) with subrectangular, fairly narrow glabella (Table 36). Axial furrows, separating palpebral area from glabella, wide and moderately shallow, but better defined than in most other Nileid species described here. The furrows are gently arcuate inwardly, with a gradually decreasing convergence in anterior direction. Anterior branch of facial suture runs almost straight forward in front of the eye, then, midway to anterior margin of cranidium, turns sharply outwards at an angle of about 70° to sagittal line. In consequence, glabella has a very pronounced, but short (exsag.) anterolateral expansion. Anterior margin of cranidium broadly and evenly rounded; a characteristic flattened narrow rim is present along anterior margin, occupying up to 0.05 of the total cranial length. The rim is almost flat in the material from Skelbro, and well set off from glabella, whereas specimen LU 21 from Andrarum has an ill-defined, rather steeply sloping rim. Palpebral lobes large (Table 36), quite wide (tr.), almost flat, presumably subhorizontal with only an insignificant outwards inclination. Mesial glabellar tubercle fairly prominent and even has a very slight relief on testaceous material; it is situated relatively rearwards on glabella (Table 36). An indistinct low sagittal keel is indicated anterior to the glabellar tubercle, but is poorly shown by the material; it is, however, unusual that the keel is visible on outside of test, and it is probably very distinct on internal moulds. A shallow occipital furrow is barely indicated laterally in the single internal mould available; it is effaced in the specimens with intact test. Posterior fixigena very slender (exsag.) and long (tr.), the tip almost level with outer edge of palpebral lobe. Posterior margin of cranidium nearly straight without rearwards deflection of fixigenae. A wide furrow or, more properly, depression crosses the proximal part of fixigena, extending from posterior margin and presumably to the furrow at base of the eye socle (no cephalon available). Posterior branches of facial suture run almost

straight from hind corner of palpebral lobe to posterior margin at an angle of about 40° to sagittal line. All specimens with intact test show a 'wrinkled' pattern along sagittal line, but the test surface otherwise appears smooth. However, the holotype cranidium S 785, which is the best preserved specimen, almost certainly has moderately densely spaced delicate pits at least on the central anterior part of glabella and along the margin of the palpebral lobes.

Librigena, hypostome, and thorax unknown.

Pygidia quite strongly vaulted (both ways); ratios are given in Table 37. Axis shows positive relief also on testaceous material; it is about as long as wide, and tapers only moderately in posterior direction, hence the terminal piece appears rather large; number of segments unknown. The anterior pleural furrow has a shallow expression even on outside of test, and is presumably deeply impressed on internal moulds. Posterior border narrow and steep, and because of its steepness it may be ill-defined posteriorly, whereas it is wider and more flattened laterally. Entire pygidium covered with extremely densely spaced terrace lines, showing a density on the pleural fields in the range of 16–22 lines/mm in the larger specimens, but precise counting is rendered difficult by the high density; the total number of lines exceeds 200 between anterior and posterior margins in the largest pygidia. The smallest specimen, 8.6 mm long, has 13–14 lines/mm on the pleural fields. The line density is occasionally slightly lower on axis. The terrace lines are gently anastomosing, and run roughly transversely to join the outer margin discordantly. They become coarser and less densely spaced immediately adjacent to the pygidial margin. Doublure gently concave, with only a narrow, flat, outer part. There is a shallow, poorly indicated postaxial depression. Doublure provided with at least 25–27 continuous terrace lines behind axis; the number is higher laterally, and may exceed 40.

Juveniles. – A badly preserved juvenile cranidium (S 784), 5.5 mm long, is about as wide as long (greatest width across palpebral lobes), and glabella is pronouncedly rectangular, showing a W:L ratio of 0.65. The specimen is identified by its flattened anterior rim.

Affinities. – *Nileus planiceps* n.sp. does not show obvious affinity to any known Scandinavian species. The pygidial terrace-line pattern may indicate a relation to the *N. depressus* group, but the resemblance is probably superficial. Isolated pygidia are distinguished from *N. depressus* subspp. by attaining larger sizes, the external terrace lines are very fine, and cover also the gently raised axis, and the doublure has an unusually high number of terrace lines. The cranidia are

Table 36. *Nileus planiceps* n.sp. Ranges for variation of cranidia >7 mm long, expressed as ratios of cranial length.

Feature	Range	Mean	N
Maximum cranial width	1.19–1.26	1.23	4
Glabellar width	0.77–0.83	0.79	4
Palpebral lobe length (exsag.)	0.41–0.49	0.44	4
Glabellar tubercle	0.26–0.30	0.28	4
Length of post. fixigenae (exsag.)	0.15–0.19	0.17	4

Table 37. *Nileus planiceps* n.sp. Ranges for variation of pygidia, expressed as ratios.

Size (mm)	Pygidial L:W ratio			Axial width : pygidial width			Axial length : pygidial length			Border length (sag.) : pygidial length		
	Range	Mean	N	Range	Mean	N	Range	Mean	N	Range	Mean	N
8.6–17.8	0.55–0.64	0.59	11	0.30–0.42	0.37	10	0.60–0.70	0.64	10	0.07–0.13	0.10	8

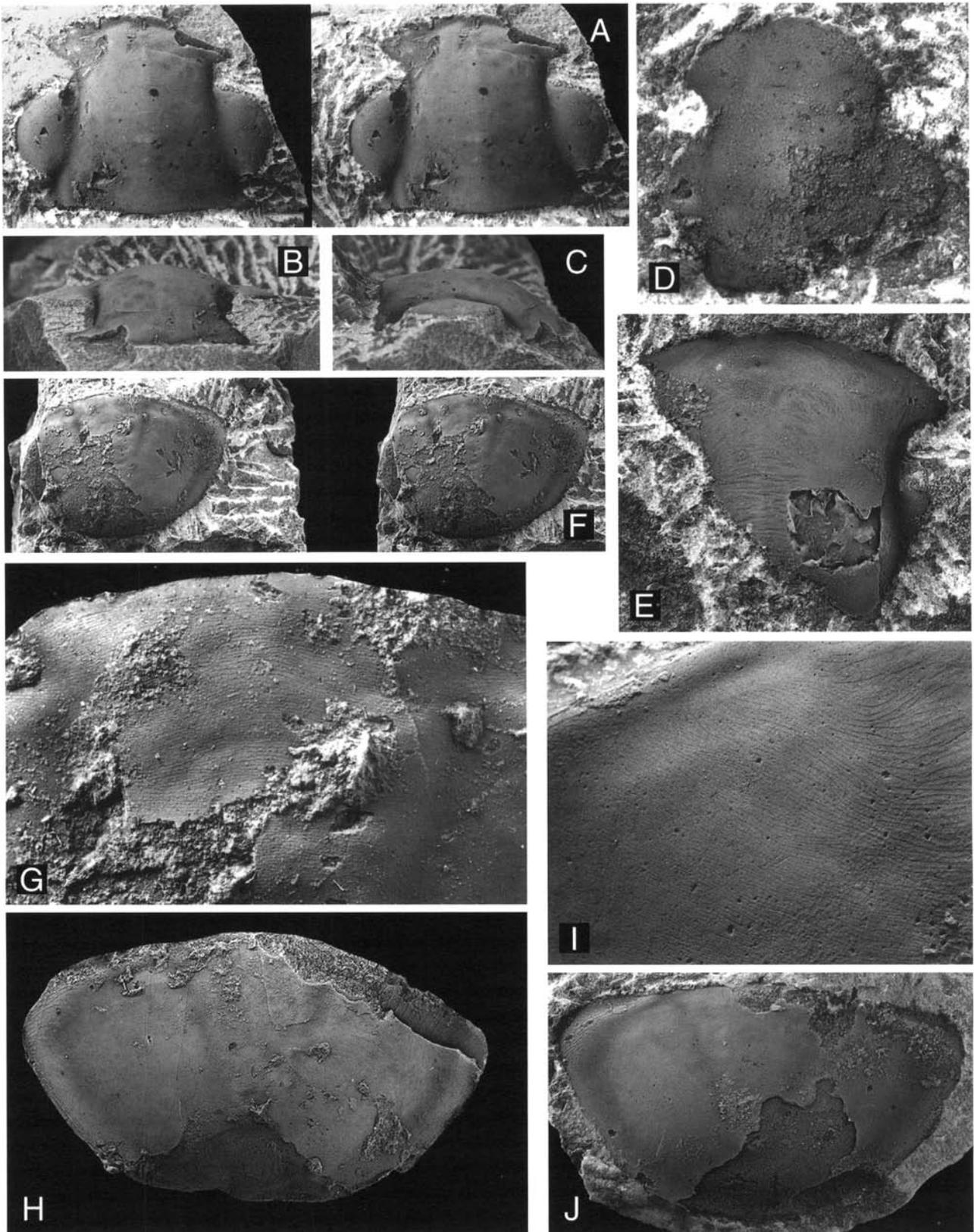


Fig. 206. *Nileus planiceps* n. sp. □A–C. Holotype. Cranium, dorsal view (stereo pair), frontal and side views, $\times 2$. MGUH 22.889 (S 785), bed –12, Skelbro. □D. Corroded juvenile cranium, $\times 9$. MGUH 22.890 (S 784), bed –12, Skelbro. □E. Fragment of cranium showing ‘wrinkled’ cuticle, $\times 4$. LO 7076 (LU 21), Andrarum. □F–G. Pygidium, stereo pair, $\times 1.5$, and close up of anterior part of axis showing fine terrace line sculpture, $\times 9$. MGUH 22.891 (S 691), bed –16, Skelbro. □H. Paratype. Pygidium, $\times 3$. MGUH 22.892 (K 610a), bed 6, Gårdlösa-4a. □I–J. Partially corroded pygidium, dorsal view, $\times 3$, and close up of anterior part of pygidial pleural field, showing fine terrace line sculpture, $\times 10$. MGUH 22.893 (IK P-39), Skelbro.

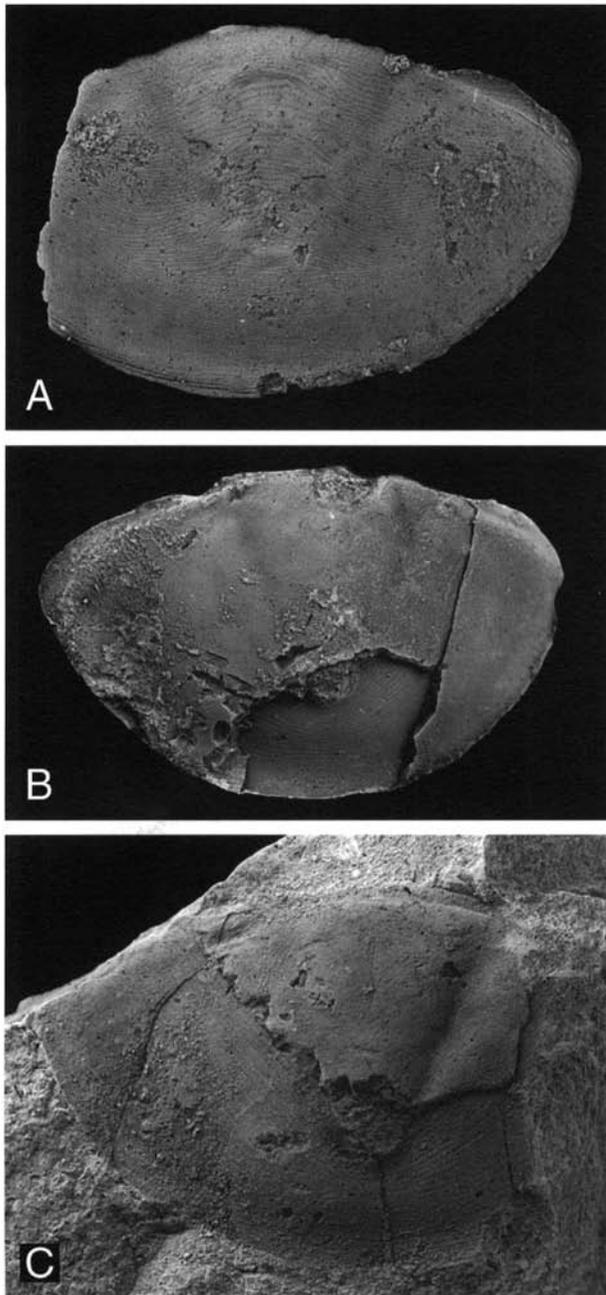


Fig. 207. *Nileus planiceps* n.sp. □A. Small pygidium showing coarser terrace lines on axis, $\times 4$. MGUH 22.894 (K 43), bed -9, Killeröd. □B. Somewhat corroded pygidium showing part of doublure, $\times 3$. MGUH 22.895 (S 944), bed -4, Skelbro. □C. Compacted internal of pygidium mould showing doublure, $\times 3$. MGUH 22.896 (K 564), bed 4, Gärdlösa-4a.

identified by the flattened anterior rim, the low convexity (particularly sagittally, but also transversely), the short (exsag.), but very strong anterolateral expansion of glabella, the large palpebral lobes, the relatively posterior position of the glabellar tubercle, and the larger maximum sizes. Several of these characters also separate *N. planiceps* n.sp. from the associated *N. orbiculatoides*.

A flattened anterior cranidial rim is occasionally seen also in *N. armadillo*, but that species has a much more convex (sag.) cranidium, typically provided with a mesial anterior boss, and the flattened rim is mostly narrower. *Nileus platys* Schrank, characterized by, among other things, a flattened rim along front of cranidium, differs from *N. planiceps* n.sp. in most other respects and is hardly closely related.

The Chinese species *N. huanxianensis* Zhou (see Zhou & Dean 1986) has a pygidium superficially resembling *N. planiceps* n.sp. with fine terrace lines and a narrow border. The cranidia are, however, much different, and the pygidium of *N. planiceps* n.sp. has possibly a much denser terrace-line pattern and a higher number of terrace lines on the doublure.

Peraspis obscura Zhou & Dean, 1986 is somewhat like *N. planiceps* n.sp., showing, e.g., a glabellar tubercle situated far back, distinct axial furrows, low cranidial convexity etc., and the pygidium has a rather long axis and an ill-defined border. The Chinese species has, however, no flattened anterior rim on the cranidium, the glabellar tubercle is positioned even further rearwards, and the pygidial surface is smooth. *P. obscura* appears closer to *Poronileus* than to *Peraspis* (cf. Fortey 1975a vs. Whittington 1965), although the cephalic surface is not punctate. *N. planiceps* n.sp., which obviously is not a typical representative of *Nileus* (s.str.), may also be compared to *Poronileus*.

Remarks. – The pygidium figured by Schmidt (1904, Pl. 8:17, 17a; see also Balashova 1976, Pl. 40:10) superficially resembles the pygidia described here with regard to outline, borderwidth (0.1 of length), and distribution of terrace lines. Schmidt (1904, p. 67), however, stated the density of terrace lines to be about 7–8 lines/mm, which agrees with counts made on the scaled figure in Balashova (1976, Pl. 40:10). This density is significantly below that of *Nileus planiceps* n.sp., and the eastern Baltic specimens more likely belong to the *N. depressus* group (see discussion of *N. depressus depressus*).

Nileus implexus n.sp.

Figs. 208–209

Synonymy. – □v 1937 *Nileus armadillo* Dalm. [partim] – Ekström, p. 15 (listed).

Derivation of name. – Latin *implexus* = interlaced, alluding to the characteristic terrace-line ornamentation of the new species.

Holotype. – Cranidium MGUH 22.897 (F 178) (Fig. 208A) from bed 20 at Fågelsång (lower part of the *A. expansus* Zone).

Paratype. – Pygidium MGUH 22.908 (K 1198a) (Fig. 209) from 4 cm below top of bed 8, Killeröd site b (lower part of the *A. raniceps*' Zone).

Additional material. – Three cranidia, 6 juvenile cranidia, 8 pygidia and 10 juvenile pygidia.

Table 38. *Nileus implexus* n.sp. Ranges for variation of crania, expressed as ratios of cranial length.

Size (mm)	Maximum width of cranium			Glabella width			Palpebral lobe length (exsag.)			Glabellar tubercle, distance to post. margin		
	Range	Mean	N	Range	Mean	N	Range	Mean	N	Range	Mean	N
2.9–4.8	1.00–1.02	1.00	5	0.64–0.71	0.66	5	0.42–0.45	0.43	5	–	0.31	1
5.4	–	–	0	–	0.76	1	–	0.43	1	–	0.30	1
>7.1	1.13–1.21	1.16	3	0.75–0.82	0.78	3	0.42–0.45	0.43	3	0.29–0.32	0.30	2

List of additional material. – □Crania F 185a (partly im), K 1176 (t) [MGUH 22.898], K 1200b (t). □Juvenile crania F 169b (t), K 1172a (t) [MGUH 22.901], K 1181a (t) [MGUH 22.899], K 1183 (t) [MGUH 22.900], K 1198d (t), K 1211b (t). □Pygidia F 240 (t) [MGUH 22.904], F 254 (t), F 271 (d), K 1172c (pim), K 1345 (t), LU 3b (t), LU 58 (t) [LO 7097], LU 60a (pim). □Juvenile pygidia K 1166? (t) [MGUH 22.906], K 1170 (pim) [MGUH 22.905], K 1172b (t), K 1173b? (t) [MGUH 22.907], K 1173c (t, is) [MGUH 22.903], K 1179b (t), K 1181b? (c), K 1200a (t) [MGUH 22.902], K 1202b (t), LU 72a (d) [LO 7104].

Occurrence. – *Nileus implexus* n.sp. is known only from the Komstad Limestone of Scania. At Fågelsång the species has been found in beds 19–20, representing the basal part of the *A. expansus* Zone, and in beds 27–28, belonging to the *A. 'raniceps'* Zone. Museum specimens LU 58, LU 60a, and LU 72a were collected by Ekström from bed I:k [= bed 7] at Fågelsång loc. E21a (see Ekström 1937, p. 15); this bed belongs to the upper part of the *M. limbata* Zone. Museum specimen LU 3b is from the Fågelsång area, level unknown.

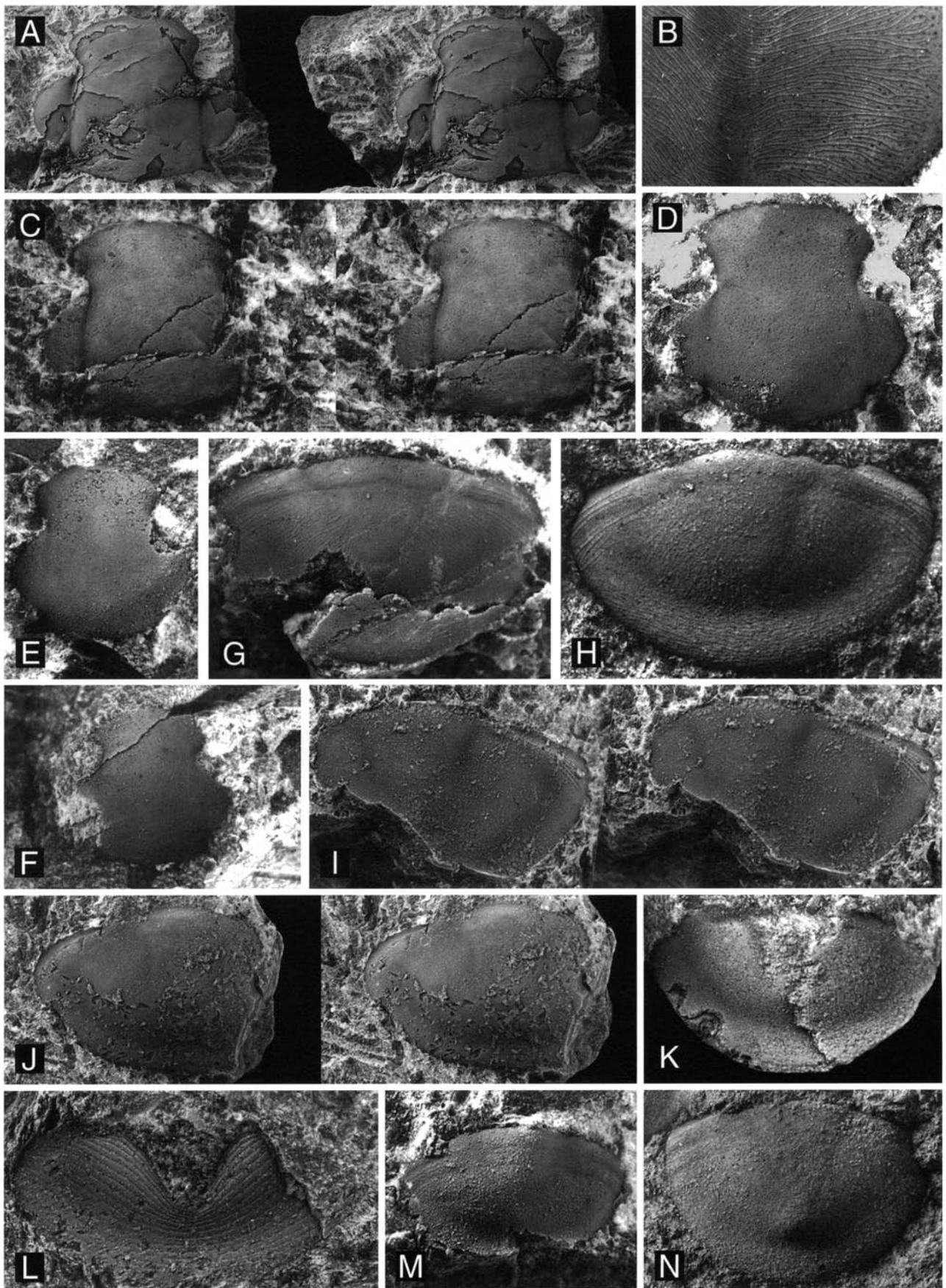
At Killeröd the species has been found in bed +35 near top of the *A. expansus* Zone, and, more abundantly, in bed 8 at site b, immediately above the base of the *Asaphus 'raniceps'* Zone.

Diagnosis. – Cranium comparatively strongly convex transversely; anterior margin quite convex (dorsal view), glabella subrectangular. Cranium almost entirely covered with densely spaced, fine terrace lines, and the surface of the palpebral lobes is punctate. Pygidium shows wide, well-defined border, and axis with positive relief in larger specimens. Densely spaced terrace lines cover entire pygidium, axis inclusive, and form a characteristic forward loop across main part of surface.

Description. – Medium-sized to large for a *Nileus*, largest cranium 20 mm long, largest pygidium 11 mm long. Only three adult crania, 7.1, 7.1 and 20.0 mm (holotype) are measurable. Cranium elongate, W:L ratio across palpebral lobes 1.13–1.14 in the two small specimens, and 1.21 in the holotype. Sagittal convexity moderate, transverse convexity fairly strong in the holotype, whereas the smaller specimens are less vaulted. Glabella subrectangular, W:L ratio 0.75–0.77 in the smaller specimens, and 0.81 in the holotype. Axial furrows virtually effaced even on internal moulds, but the boundary between glabella and palpebral lobes is well-defined owing to a marked change of slope. Anterior margin fairly and evenly rounded in dorsal view; a narrow fringe along margin is slightly less sloping, but still steep and a

pronounced flattened rim is not developed. Mesial glabellar tubercle relatively small (internal mould) and situated far back (Table 38). A shallow, indistinct occipital furrow is developed in the holotype specimen (test intact); it shallows up in abaxial direction. Occipital ring occupies (sag.) slightly less than 0.1 of the cranial length. Posterior fixigena short (tr.), and accounts for slightly less than 0.1 of the cranial width at posterior margin; exsagittal length averages 0.14 ($N = 5$) of the cranial length. Anterior branches of facial suture run straight forward from eye, then, one third the distance from anterior corner of palpebral lobe to anterior margin, turn outward at an angle of about 35° to sagittal line. Posterior branches of facial suture straight and run obliquely backward-outward from posterior corner of palpebral lobe, at an angle of about 35° to sagittal line. Holotype cranium covered with dense, very fine terrace lines; only a small sagittal area behind the glabellar tubercle is smooth. Terrace lines coarser and less dense on the smaller crania, and the main posterior part of glabella is smooth. Density of lines on glabella of holotype is 12 lines/mm posterolaterally and about 15 lines/mm on anterior part; one of the smaller crania has about 10 lines/mm anteriorly on glabella. Terrace lines are gently anastomosing, roughly transverse, but

Fig. 208. *Nileus implexus* n.sp. □A–B. Holotype. Large cranium, stereo-pair, ×1.5, and close-up of palpebral lobe and outer part of glabella, showing dense terrace-line pattern, ×6. MGUH 22.897 (F 178), bed 20, Fågelsång. □C. Small cranium showing terrace-line sculpture, stereo-pair, ×4. MGUH 22.898 (K 1176), bed 8, Killeröd site b. □D. Small cranium, ×9. The surface punctation is possibly secondary, ×9. MGUH 22.899 (K 1181a), bed 8, Killeröd site b. □E. Juvenile cranium, ×9. MGUH 22.900 (K 1183), bed 8, Killeröd site b. □F. Juvenile cranium, ×9. MGUH 22.901 (K 1172-1), bed 8, Killeröd site b. □G. Transitory pygidium, stage E, showing dense terrace-line sculpture, ×8. MGUH 22.902 (K 1200a), bed 8, Killeröd site b. □H. Latex cast of transitory pygidium, stage E, showing dense terrace-line sculpture, ×12. MGUH 22.903 (K 1173c), bed 8, Killeröd site b. □I. Fragmentary, corroded pygidium, showing faintly visible terrace-line pattern and raised axis, stereo-pair, ×4. MGUH 22.904 (F 240), bed 27, Fågelsång. □J. Corroded early pygidium, showing faintly visible terrace-line pattern and raised axis, stereo-pair, ×2. LO 7097 (LU 58), bed k [= 7], Fågelsång, loc. E21a. □K. Partly exfoliated small holaspid pygidium showing dense terrace-line sculpture, ×9. MGUH 22.905 (K 1170), bed 8, Killeröd site b. □L. Internal mould of early pygidium showing double, ×9. LO 7104 (LU 72a), bed k [= 7], Fågelsång, loc. E21a. □M. Slightly corroded transitory pygidium, stage D, ×9. MGUH 22.906 (K 1166), bed 8, Killeröd site b. □N. Latex cast of transitory pygidium, stage D, ×12. MGUH 22.907 (K 1173b), bed 8, Killeröd site b.



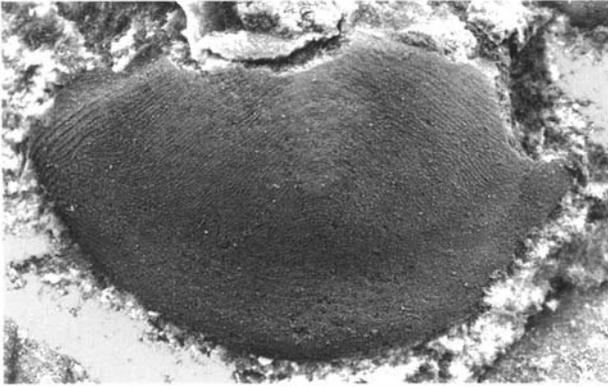


Fig. 209. *Nileus implexus* n.sp. Paratype. Small pygidium showing characteristic, dense terrace-line pattern, $\times 10$. MGUH 22.908 (K 1198a), bed 8, Killeröd site b.

laterally on glabella they run longitudinally, so anterior lines more or less follow the glabellar contour; posterolateral lines run obliquely backward-outwards to bend outwards onto the posterior fixigena. Outer brim of palpebral lobe devoid of terrace lines, but test surface is punctate (Fig. 208B). Holotype shows 5–6 ‘wrinkles’, up to 1.5 mm long, directed obliquely forwards-inwards, situated on the imaginary line connecting mesial tubercle with anterior inner corner of palpebral lobe.

Librigena, hypostome and thorax unknown.

Pygidium fairly vaulted and relatively long (Table 39). Axis occasionally slightly raised anteriorly, in particular in the larger specimens, but descends rearwards and is confluent with pleural fields posteriorly; it tapers only moderately. Pleural fields smooth, but no internal moulds are available to study the anterior pleural furrow. Posterior border well-developed, concave, almost flat, occupying 0.17–0.18 ($N = 3$) of the sagittal length in specimens more than 9 mm long; a specimen about 6.5 mm long has a border occupying 0.24 of the pygidial length. Dorsal terrace-line pattern most unusual, as the entire pygidium is covered with densely spaced terrace lines describing a large, forward loop across the main part of pygidium. A few lines immediately adjacent to anterior margin and on the border are roughly paralleling the pygidial margins. About 8–9 lines/mm were counted on the pleural fields in specimens 9–11 mm long and 10–11 lines/mm were counted in the paratype pygidium,

about 5 mm long. Doublure moderately to strongly concave, and provided with about 20 coarse, continuous terrace lines.

Juveniles. – Cranidia, 2.9–5.4 mm long, are of low convexity (both ways), and as long as wide (Table 38). Glabella pronouncedly elongate, delimited by very shallow axial furrows, and there is no change of slope between glabella and palpebral lobes, so glabella is almost confluent with palpebral area. Anterior margin of cranidium more rounded than in adults, and anterolateral expansion of glabella is stronger, as anterior branches of facial suture diverge immediately in front of palpebral lobes (at an angle of about 35° to sagittal line, as in adults). Some juveniles, but not all, have a slightly less steep fringe along the anterior margin of cranidium. Glabellar tubercle normally not visible on testaceous material. Juvenile cranidia ca. 4 mm long have a smooth test without terrace lines, whereas specimens 4.8 and 5.4 mm long show some terracelines on anterior part of glabella (because of corrosion of the test surface these terrace lines do not show on the photographed specimens).

Four D-stage transitory pygidia are tentatively assigned to *N. implexus* n.sp. By comparison to D-stage material described elsewhere (p. 244) the specimens are rather broad (Table 39) and show a wide border. Test surface smooth, except for some terrace lines outlining the unreleased segments anterolaterally and on the border along outer margin. The presence of terrace lines is unusual for D-stage juveniles, and in combination with the wide border this feature is taken to support the identification.

Seven juvenile pygidia are positively identified as *N. implexus* n.sp., because of their well-developed terrace-line pattern, rather similar to that of the adult pygidia. Five of them are E-stage transitory pygidia with one unreleased anterior segment, outlined by a shallow furrow. Axis is somewhat inflated and comparatively well set off, but it is also outlined by the terrace-line pattern. The well-defined border is comparatively wide for this growth stage (Table 39); relative border width decreases with size, and the border accounts on average for 0.30 ($N = 3$) of the pygidial length in specimens 3.2–3.3 mm long, and for 0.26 of the pygidial length in two specimens 3.5 and 4.6 mm long. The material shows an almost fully developed adult terrace-line pattern, which is very rare for transitory pygidia of this growth stage; the only difference from adults is the absence of terrace lines on the axial area.

Table 39. *Nileus implexus* n.sp. Ranges for variation of pygidia, expressed as ratios.

Size (mm)	Pygidial L:W ratio			Axial width : pygidial width			Axial length : pygidial length			Border length (sag.) : pygidial length		
	Range	Mean	<i>N</i>	Range	Mean	<i>N</i>	Range	Mean	<i>N</i>	Range	Mean	<i>N</i>
2.5–2.9 [Stage D]	0.63–0.68	0.65	4	0.37–0.41	0.38	4	0.57–0.68	0.62	4	0.24–0.32	0.29	4
3.2–4.6 [Stage E]	0.57–0.66	0.62	5	0.35–0.41	0.39	4	0.53–0.59	0.56	3	0.26–0.31	0.28	5
3.9–4.7 [Hol.]	0.57–0.59	0.58	2	–	–	0	–	–	0	–	0.28	1
≥ 5.2 [Hol.]	0.58–0.62	0.60	5	0.38–0.40	0.39	2	0.57–0.60	0.59	3	0.17–0.24	0.19	4

Two small holaspid pygidia, 3.9 and 4.7 mm long, differ from the larger adults by showing a very wide border (Table 39). The doublure is exposed in the smallest specimen (a small patch of test verifies the identification); the larger specimen, paratype K 1198a, exhibits a fully developed adult terrace-line pattern (Fig. 209). The paratype undoubtedly belongs to the smallest holaspid instar, and it is rare among nileids that this growth stage has a fully developed adult terrace-line pattern.

Affinities. – *Nileus implexus* n.sp. is perhaps related to the *N. depressus* group but is readily separated by the unique terrace-line pattern (both cranidium and pygidium), the subrectangular glabella, the well-developed pygidial border, and the larger maximum size. *N. depressus* subsp. A has a somewhat similar cranidium, but the terrace lines are coarser and less dense, and it is smaller, shows a rounded central part of glabella, a comparatively prominent mesial tubercle and a more truncate anterior cranial margin.

Nileus implexus n.sp. occurs associated with *N. armadillo*, *N. latifrons* n.sp. and *N. depressus parvus* n.subsp. Apart from the highly characteristic terrace-line pattern, *N. implexus* n.sp. differs from the two last mentioned species by having a less strong cephalic convexity (sag.), a markedly more elongate glabella, a glabellar tubercle situated relatively far back, and a rather elongate pygidium with a distinct border. Compared to *N. armadillo*, *N. implexus* n.sp. has a slightly less strong cephalic convexity, no flattened rim along anterior cranial margin, no mesial boss on the anterior cranial margin, and the pygidium has a slightly wider concave border. Juvenile cranidia of *N. armadillo* are markedly more convex (sag.) compared to *N. implexus*, and usually have a flattened rim along anterior margin, provided with a mesial boss.

Remarks. – The material from the *M. limbata* and lower *A. expansus* Zone should most likely be separated at the subspecies level from the younger material from the *A. 'raniceps'* Zone, but the total number of specimens is considered to small to formalize such a subdivision.

Nileus sp. B (aff. *schranksi* n.subsp.)

Figs. 210–213

Material. – Two complete specimens, 20 cranidia, 10 juvenile cranidia and 42 pygidia. Juvenile pygidia are described on pp. 241–245.

List of material. – □ Complete specimen GM 1885.40 (pim; slightly damaged) [MGUH 22.910], IK 8 (t) [MGUH 22.909]. □ Cranidia S 9 (t), S 16a (pim), S 27c (pim), S 34 (im), S 42? (pim), S 70f (im), S 98d (t), S 100 (im), S 106 (im), S 135g (im), S 158 (pim) [MGUH 22.911], S 167 (im), S 168b (pim), S 168d (im), S 168e (t), S 168g (t), S 174 (im) [MGUH 22.913], S 189b (im), S 192 (im), GM 1988.13 (t). □ Juvenile cranidia S 40 (im), S 54 (pim), S 70b (t) [MGUH 22.912], S 105b? (im), S 106c (t), S 140d (im), S 145 (im), S 187c (t), S 215c (t), S 216a (im). □ Pygidia S 36 (t), S 39a (pim), S 39b (d), S 41? (im), S 44 (pim), S 45 (pim), S 50b (t), S 51 (pim), S 54b

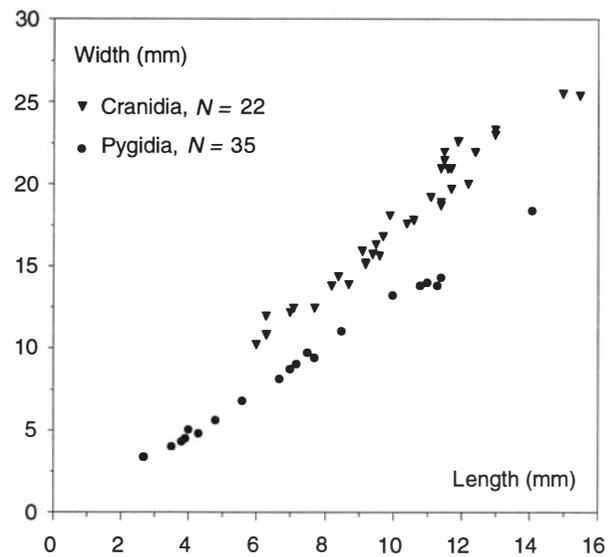


Fig. 210. Cranidia and pygidia of *Nileus* sp. B. Maximum width plotted against sagittal length.

(pim) [MGUH 22.917], S 54c (t), S 56b (im), S 70e (t), S 94 (t) [MGUH 22.916], S 97 (im), S 98a (t), S 99 (pim), S 100c (pim), S 107b (t) [MGUH 22.914], S 114 (im), S 120 (im), S 128c (im) [MGUH 22.915], S 131 (t), S 135e? (im), S 135f (im), S 140c (t), S 142 (pim), S 143 (im) [MGUH 22.920], S 166 (pim), S 168f (pim), S 169b (im), S 182 (t), S 187b (pim), S 194 (im), S 208b? (im), S 213 (im) [MGUH 22.921], S 216d? (im), S 216e? (im), S 358 (im), S 360 (t), S 362 (t) [MGUH 22.918], S 1678b (pim), DGU 1-3 (t) [MGUH 22.919].

Occurrence. – The material almost exclusively comes from bed –21 at Skelbro; three pygidia are from bed –20. Both beds belong to the basal part of the *M. polyphemus* Zone. The museum specimens studied originate from the same interval.

Description. – Largest cranidium 14.1 mm long, largest pygidium 15.5 mm long (Fig. 210). The cranidia are entirely similar to the early representatives of *N. depressus schranksi* n.subsp., except for having a more limited surface sculpture. Thus the cranial surface of *Nileus* sp. B is largely smooth, with pitting restricted to the palpebral lobes; even the common sagittal ‘wrinkled’ pattern is usually absent. Ranges for variation of various cranial ratios are shown in Table 40.

Thorax as in *N. orbiculatoides*. The transverse terrace line on axis is effaced mesially on the posterior two segments in the available specimens.

Pygidium fairly strongly vaulted. Axis is barely raised above the pleural fields on internal moulds, and has no positive relief on testaceous material, but is usually outlined by the lack of terrace lines and a lighter colour of test. It tapers moderately in posterior direction; segmentation normally effaced, but internal moulds may show half-ring, four axial segments, outlined by lateral swellings, and a terminal piece. Segmental outline as in *N. d. schranksi* n.subsp. The anterior

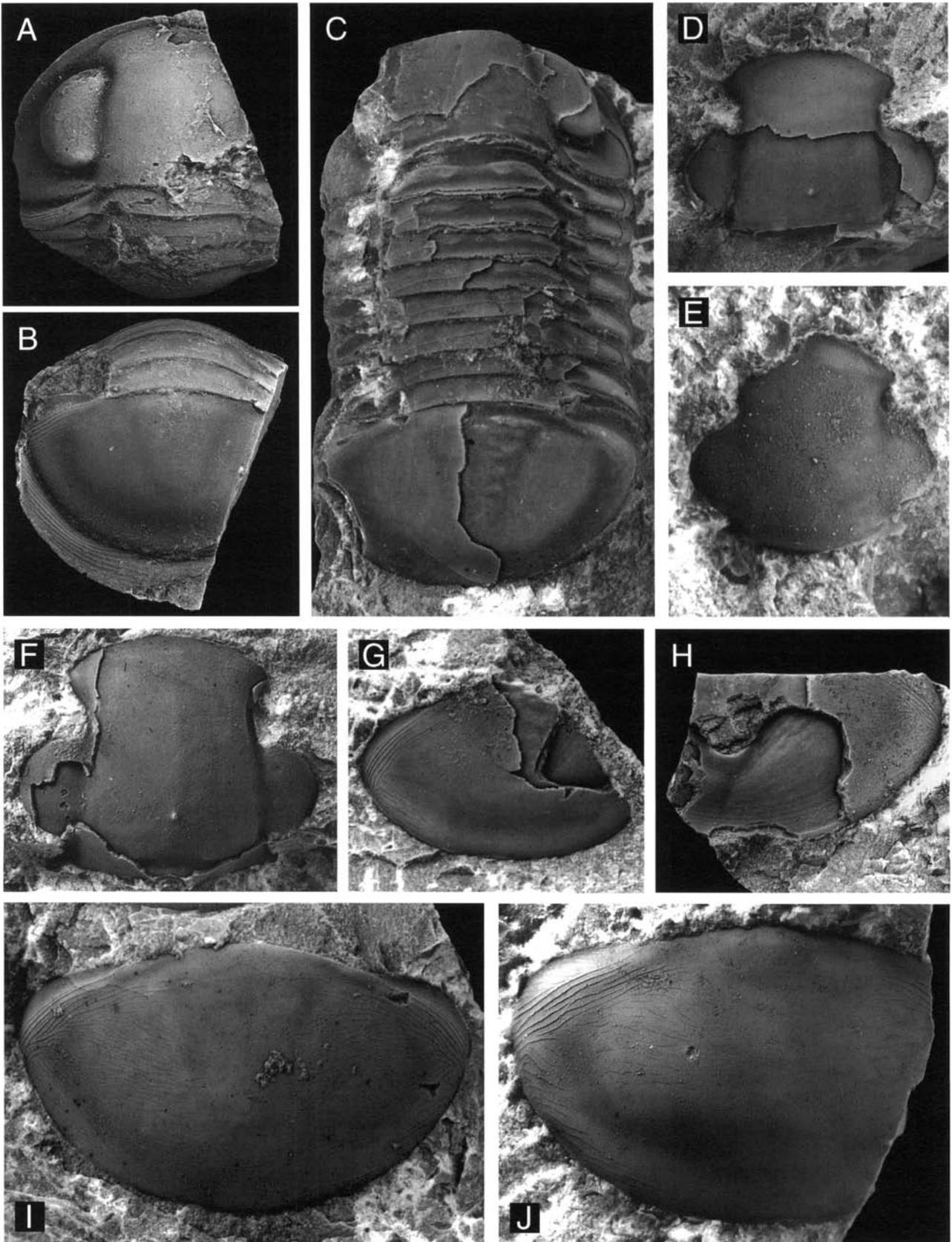


Table 40. *Nileus* sp. B cranidia ≥ 5.6 mm long, Skelbro. Range for variation of selected features, expressed as ratios of cranidial length; see also Fig. 212. Distances to the mesial tubercle and to the hind corner of palpebral lobe are measured from the posterior margin of cranidium.

Feature	Range	Mean	N
Maximum cranidial width	1.20–1.32	1.26	14
Glabellar width	0.77–0.85	0.81	14
Palpebral lobe length	0.41–0.49	0.45	14
Distance to mesial tubercle	0.29–0.32	0.31	11
Distance to palpebral lobe	0.13–0.17	0.15	9

Table 41. *Nileus* sp. B. Ranges for variation of pygidia ≥ 6 mm long, expressed as ratios.

Feature	Range	Mean	N
Pygidial length:width	0.53–0.63	0.58	33
Axial width : pyg. width	0.34–0.42	0.38	28
Axial length : pyg. length	0.55–0.69	0.61	28
Border length (sag.) : pyg. length	0.11–0.24	0.16	29

pleural furrow even has a very shallow expression on testaceous material. Posterior border narrow and steep (Table 41), widest in the smaller specimens. Pygidia covered with an 'orbiculatooides-type' terrace-line pattern; the line density on the pleural fields is rather variable (Fig. 211I vs. J), whereas the axial area always is devoid of lines, but show a fine pitting on axis and immediately behind in well-preserved specimens. Pygidial doublure only moderately concave, and covered with 19–22 coarse terrace lines, of which the innermost four or five are coarser than the remaining lines. The doublure has a shallow, but characteristic elongate postaxial depression (Fig. 211H).

Fig. 211. *Nileus* sp. B. □A–B. Enrolled, complete specimen, dorsal views of cephalon and pygidium, the latter showing 'orbiculatooides-type' terrace-line pattern, $\times 3$. MGUH 22.909 (IK 8), Skelbro beds, Skelbro. □C. Damaged, partly exfoliated, complete specimen showing thoracic and pygidial 'orbiculatooides-type' terrace-line pattern, $\times 3$. MGUH 22.910 (GM 1885.40), Skelbro beds, Duegård, Bornholm. □D. Partly exfoliated cranidium showing faintly indicated paired muscle impressions on glabella, $\times 4$. MGUH 22.911 (S 158), bed –21, Skelbro. □E. Juvenile cranidium, $\times 10$. MGUH 22.912 (S 70-2b), bed –21, Skelbro. □F. Exfoliated cranidium, oblique dorsal view, $\times 6$. MGUH 22.913 (S 174), bed –21, Skelbro. □G. Damaged pygidium showing open 'orbiculatooides-type' terrace-line pattern, $\times 4$. MGUH 22.914 (S 107b), bed –21, Skelbro. □H. Fragment of internal mould of pygidium showing postaxial depression in doublure, $\times 3$. MGUH 22.915 (S 128c), bed –21, Skelbro. □I. Pygidium showing terrace-line pattern intermediate between 'orbiculatooides-type' and 'depressus-type', $\times 4$. MGUH 22.916 (S 94), bed –21, Skelbro. □J. Small pygidium showing 'orbiculatooides-type' terrace-line pattern, $\times 9$. MGUH 22.917 (S 54b), bed –21, Skelbro.

Juveniles. – Cranidia less than 6 mm long have, compared to larger specimens, a more rounded front, and a narrower, relatively elongate glabella (Figs. 211E, 212B). Cranidial W:L ratios, measured across the palpebral lobes, are also markedly below adult ratios (Fig. 212A). Cranidial convexities, length (exsag.) of palpebral lobes, distances from posterior margin to the hind corner of palpebral lobe and to mesial glabellar tubercle are comparable to adults (Fig. 212C–D).

For discussion of transitory pygidia and small holaspides, see pp. 241–245. The smallest pygidium assigned to *Nileus* sp. B is 6.0 mm long. Pygidia 6 to 8 mm long tend to show a comparatively wider and well-defined border, stretching for about 0.2 of the pygidial length.

Affinities. – The relations between *Nileus* sp. B and *N. depressus schranki* n.subsp. are discussed below.

Cranidia of *Nileus* sp. B are readily separated from the associated *N. orbiculatooides* (differences the same as stated for *N. depressus schranki* n.subsp. versus *N. orbiculatooides*), while the quite *orbiculatooides*-like pygidia and thorax of sp. B are distinguished by having a less well-defined and narrower border, an indistinct, elongate postaxial depression in the doublure, coarser doublural terrace lines along the axis, and by exhibiting subtle differences in the dorsal test ornamentation. Thus sp. B always has 4–7 continuous transverse terrace lines along the anterior margin and several lines anterolaterally on the border, in addition to short lines on the pleural fields in some specimens. *N. orbiculatooides* shows fewer lines anteriorly and anterolaterally, but, in addition to the terrace lines, also has widely spaced small pits. Pitting is present only on the axis and immediately behind in *Nileus* sp. B.

The differences between the cranidia of *Nileus* sp. B and *N. exarmatus* are the same as stated for *N. depressus schranki* n.subsp. versus *N. exarmatus*. Pygidia of *N. exarmatus* are separated from *Nileus* sp. B by having a different terrace-line pattern and a much better defined border.

Nileus sp. B somewhat resembles *N. svalbardensis* (cf. Fortey 1975a, pp. 43–44; Pl. 11:1–13), e.g., regarding the glabellar outline, the course of the anterior branches of facial suture, the relative width of the lateral cephalic border, the type of cuticular ornamentation (cephalon and pygidium), and the lack of a pygidial border. By comparison, *Nileus* sp. B has better defined cephalic axial furrows, a less distinct punctuation of the cephalic test, generally fewer external pygidial terrace lines, more numerous terrace lines on the pygidial doublure, and commonly at least a faintly indicated pygidial border.

Remarks. – Three types of *Nileus* cranidia, *N. exarmatus* ($N = 24$), *N. orbiculatooides* ($N = 2$) and *N. 'd. schranki'* ($N = 29$), were found in bed –21 at Skelbro (stated number of specimens includes juveniles). Only two types of adult pygidia were recorded at first, *N. exarmatus* ($N = 16$) and *N.*

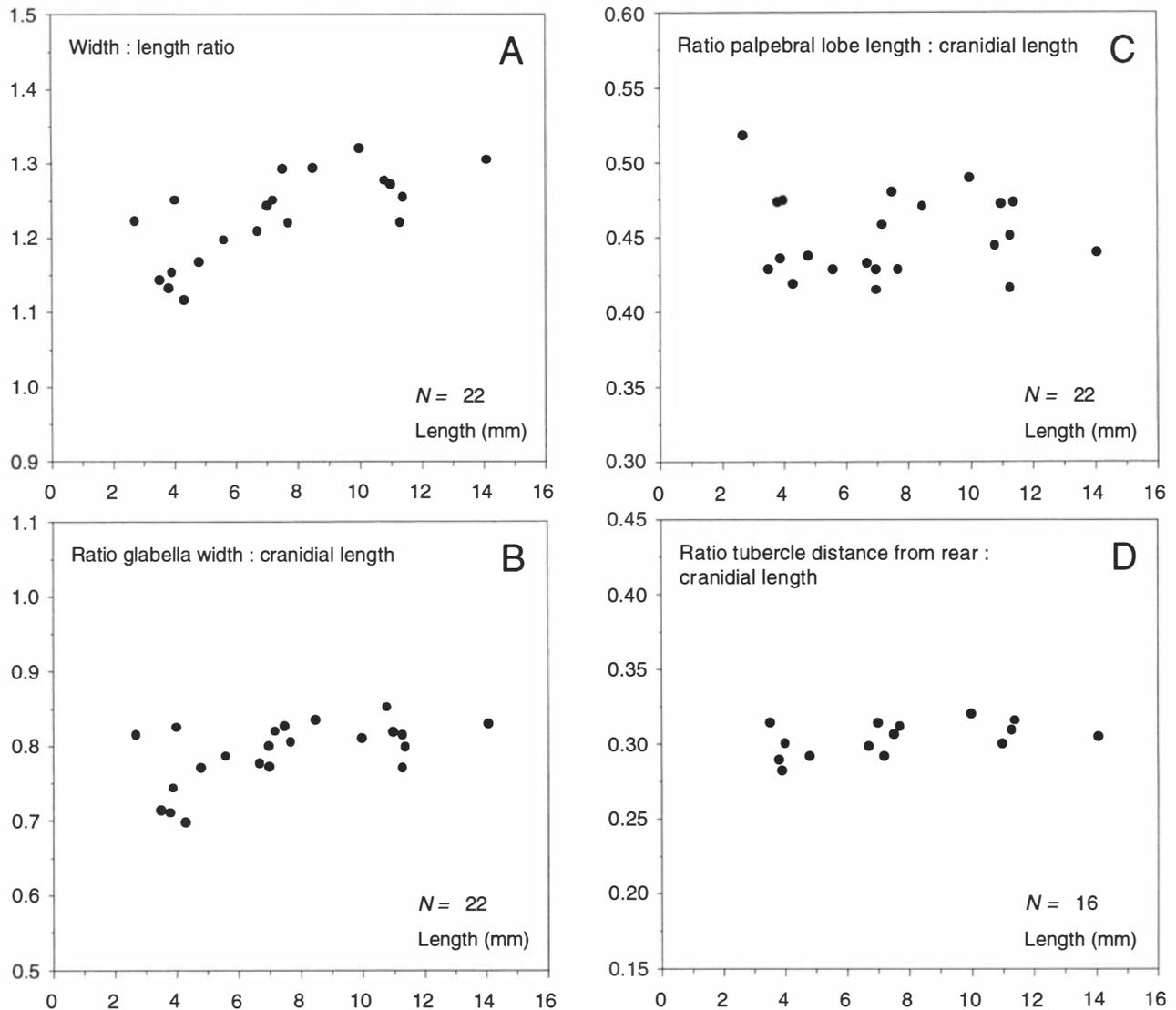


Fig. 212. Cranidia of *Nileus* sp. B. □A. Ratio between maximum width across palpebral lobes and cranial length plotted against sagittal length. □B. Ratio between glabella width (measured between posterior corners of palpebral lobes) and cranial length plotted against cranial length. □C. Ratio between palpebral lobe length (exsag.) and cranial length plotted against cranial length. □D. Relative position of glabellar tubercle plotted against cranial length.

'*orbiculatoides*' ($N = 45$); the associated juvenile pygidia cannot be identified. In fossil materials the ratio between adult nileid cranidia+cephala to pygidia is usually slightly below 1:1; in *N. orbiculatoides* and *N. depressus schranki* n.subsp. this ratio is identically 0.75:1 in the available collection. Hence the strong disparity between 2 cranidia to 45 pygidia shown by *N. 'orbiculatoides*' and 29 cranidia to 0 pygidia shown by *N. 'd. schranki*' from bed -21 was puzzling, and a reexamination revealed that the *N. 'orbiculatoides*' pygidia comprise two morphs, *N. orbiculatoides* (*s.str.*) ($N = 3$) and a much more common type, referred to as *Nileus* sp. B ($N = 42$). Judging from the proportional abundance, the sp. B pygidia must match the *N. 'd. schranki*' cranidia, although this causes bewilderment, as

cranidia, exceedingly similar to *N. d. schranki* n.subsp., thus appear to match pygidia similar to the central Swedish type of *N. orbiculatoides*. However, the inferred association was subsequently verified by the entire specimen IK-8 (Fig. 211A–B), which kindly was handed over to me for description by Mrs. Inga Krause, Germany (as apparent from Fig. 211C the cephalon of the second entire specimen at hand is damaged). It is stressed that no pygidia of *N. depressus schranki* n.subsp. (*s.str.*) have been found in bed -21. Typical pygidia of *N. d. schranki* n.subsp. turn up in bed -20, from which only three pygidia of sp. B have been collected, all from the lower half of the bed.

I am inclined to interpret *Nileus* sp. B as a shallow-water ecophenotype of *N. depressus schranki*. This entails that the

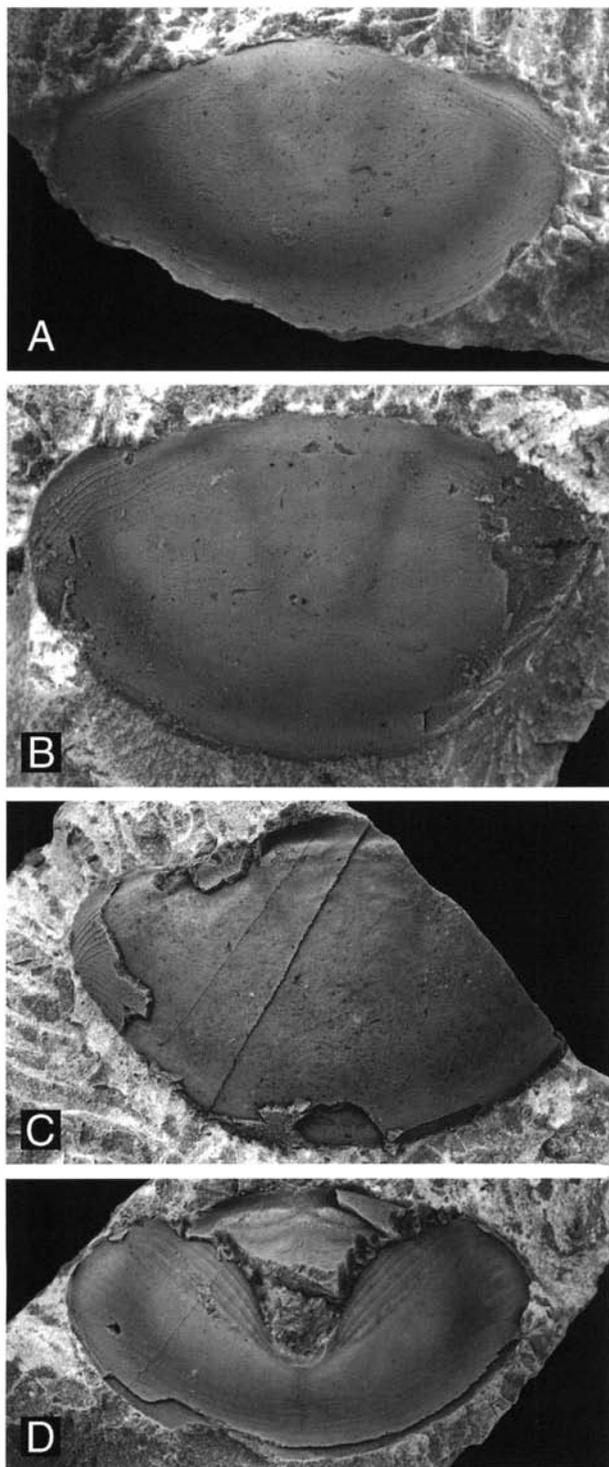


Fig. 213. *Nileus* sp. B. □ A. Pygidium showing terrace-line pattern intermediate between 'orbiculatoides-type' and 'depressus-type', $\times 6$, MGUH 22.918 (S 362), bed -20, Skelbro. □ B. Pygidium showing open 'orbiculatoides-type' terrace-line pattern, $\times 5$, MGUH 22.919 (DGU 1-3), Skelbro. □ C. Internal mould of pygidium showing axis, $\times 3$, MGUH 22.920 (S 143), bed -21, Skelbro. □ D. Internal mould of pygidium showing double furrows, $\times 3$, MGUH 22.921 (S 213), bed -21, Skelbro.

intraspecific variation of *N. depressus* (*s.l.*) is much more profound than hitherto assumed. *N. latifrons* n.sp. may be another example of a 'smooth' *N. depressus* shallow-water ecophenotype.

Family Styginidae Vogdes, 1890

Subfamily Stygininae Vogdes, 1890

Genus *Stygina* Salter, 1853

Type species. – *Asaphus latifrons* Portlock, 1843 (SD Vogdes 1890).

Remarks. – For a discussion of genus, see Warburg (1925), Whittington (1950) and Skjeseth (1955).

Stygina n.sp.

Fig. 214

Material. – Two cranidia, 1 librigena and 5 pygidia.

List of material. – □ Cranidia K 1165 (c), K 1208 (c) [MGUH 22.926]. □ Librigena K 1023 (t) [MGUH 22.925]. □ Pygidia K 1065 (c) [MGUH 22.924], K 1172 (t) [MGUH 22.927], K 1198 (c) [MGUH 22.922], K 1215 (im) [MGUH 22.923], K 1345 (pim).

Occurrence. – The specimens are from bed interval 0–9 of Killeröd site b, i.e. the *A. raniceps* Zone. This is the earliest known occurrence of *Stygina*. Within Baltoscandia and elsewhere the genus has been reported only from considerably younger faunas so far (cf. Přibyl & Vaněk 1971).

Description. – The material is rather fragmentary. Largest cranidium 5.5 mm long, largest pygidium ca. 7.7 mm long. The description of the cranidium is based on specimen K 1208 (Fig. 214E). Anterior margin gently convex (dorsal view); cranidium moderately convex sagittally, broad, PW:L ratio 1.16; width across palpebral lobes presumably smaller. Glabella gently to moderately vaulted and raised above genae except for outer palpebral areas incl. lobes. Glabella subparallel sided posteriorly, but expands in front of eyes (axial furrows diverge at an angle of about 30° to sagittal line); glabellar front rounded and without mesial impression. Posterior glabellar width is half of the anterior maximum glabellar width, which in turn accounts for half of the maximum preocular cranial width; glabella stretches for slightly more than 0.7 of the cranial length. A pair of nebulous lateral glabellar furrows is indicated close to occipital furrow. Glabella delimited all the way by rather shallow axial and preglabellar furrows. A pair of indistinct fossulae occurs in the axial furrows ca. 0.35 of the glabellar length from front, equal to 0.4 of the cranial length from anterior margin; a second pair of depressions occurs in the axial furrows close to occipital furrow. Occipital furrow narrow (sag.), rather shal-

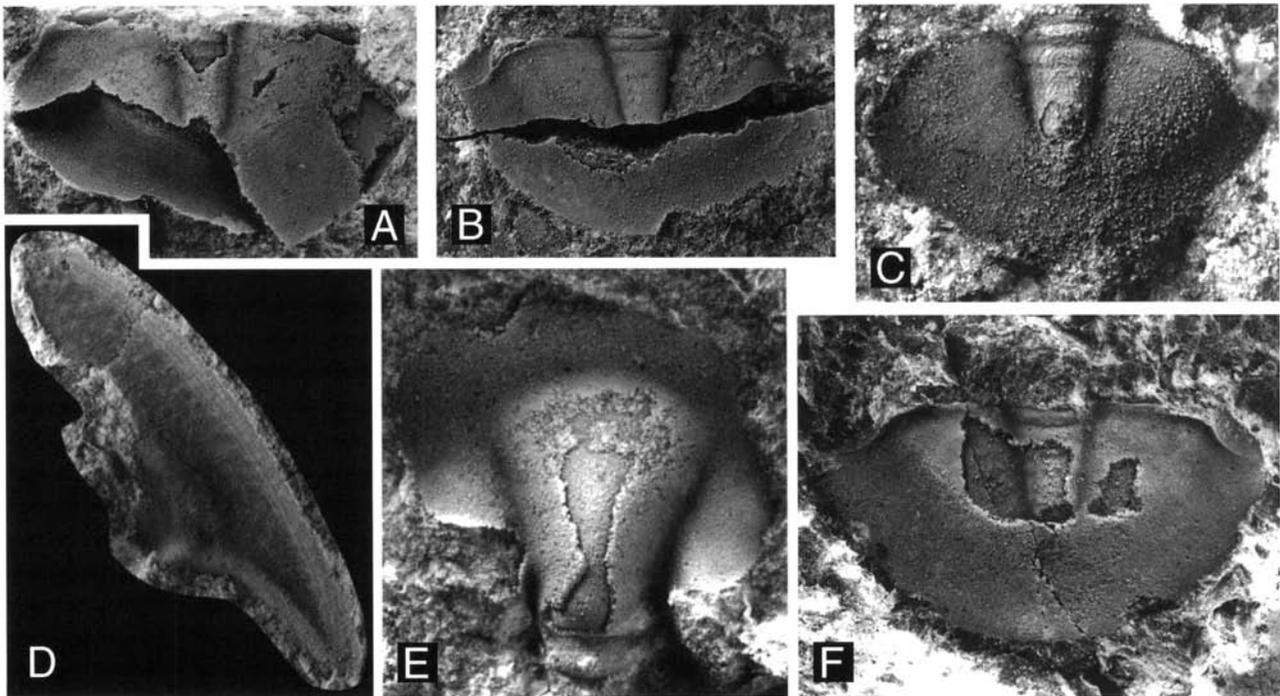


Fig. 214. *Stygina* sp. □A. Partly exfoliated pygidium showing part of doublure, $\times 4$. MGUH 22.922 (K 1198), bed 8, Killeröd site b. □B. Pygidium, $\times 5$. MGUH 22.923 (K 1215), bed 9, Killeröd site b. □C. Slightly corroded small pygidium, $\times 15$. MGUH 22.924 (K 1065), bed 0, Killeröd site b. □D. Internal mould of librigena, $\times 6$. MGUH 22.925 (K 1023), bed 0, Killeröd site b. □E. Fragmentary, partly exfoliated cranidium, $\times 9$. MGUH 22.926 (K 1208), bed 9, Killeröd site b. □F. Partly exfoliated pygidium, $\times 6$. MGUH 22.927 (K 1172), bed 8, Killeröd site b.

low, deepest mesially. Occipital ring elevated slightly above rear part of glabella and expanded mesially, carrying a fairly prominent tubercle. Anterior area of fixigena strongly inclined in anterior direction; paradoublural line not indicated. Anterior border wide, flat, defined by a marked change of slope; frontal area accounts for about 0.15 of the cranial length mesially. Palpebral area of fixigenae gently convex and slants strongly in adaxial direction. Palpebral lobes not preserved; lobe length (exsag.) estimated to ca. 0.15 of the cranial length, distance to posterior margin is equivalent to less than the lobe length. Eye ridges not visible. Posterior fixigenae not preserved. Anterior branches of facial suture diverge at an angle of about $20\text{--}25^\circ$ to sagittal line in front of eyes, then turn inwards approximately level with front of glabella to run either extremely close to cephalic margin or in a marginal position. Both cranidia at hand are too corroded to show surface sculpture.

Available librigena fragmentary (Fig. 214D). It is steeply rising to the eye; a wide, rather shallow posterior border furrow is indicated behind eye level. Main outer part flattened and constitutes a broad lateral border, which tapers very gently backwards, but enters genal spine. Genal angle continues into a broad-based prominent spine. Posterior margin and inner margin of spine raised.

Pygidium subsemicircular in outline, L:W ratio 0.54–0.58 (mean 0.57; $N = 4$). Adult pygidia of low relief; a juvenile pygidium, 2.2 mm long, is more vaulted. Anterolateral corners rounded. Axis short, stretching for 0.49–0.52 of the pygidial length in adults ($N = 3$), and for 0.55 in the juvenile specimen at hand; axial width at anterior margin corresponds to 0.18–0.20 of the maximum pygidial width in adults ($N = 3$) and 0.24 in the juvenile. Axis elevated above pleural fields, most strongly so in the juvenile, and tapers gently rearwards, posterior width (tr.) is about 0.6 of the anterior axial width. Articulating half-ring short (sag.), delimited by a shallow furrow; rear axial segmentation effaced, even on internal moulds, where only the anterior one or two rings occasionally are faintly defined. No postaxial ridge. Axial furrows very shallow, wide, indistinct, but axis is well set off by a distinct change of slope. Pleural fields gently convex, descending smoothly to border; no indication of ribs or furrows, and paradoublural line is not outlined. Border wide, gently concave, steeper in the juvenile specimen; it is defined only by a change of slope. Border accounts for 0.26–0.27 ($N = 4$) of the pygidial length postaxially, but is nearly of uniform width throughout. Articulating facets small, the inner posterior part raises in a sharp crest above the pleural fields. Terrace lines are possibly present on the axis, but

otherwise the dorsal pygidial surface appears smooth (preservation poor). Doublure fairly strongly concave and very wide, being present below half of the pygidium (sag.); it is approximately of uniform width throughout. Inner margin shows small axial embayment. Doublure covered with faintly impressed terrace lines; it is suspected that the lines are disturbed in the axial area. There are about 25 lines across the doublure posterolaterally.

Remarks. – The shape of the glabella, the presence of a wide anterior cephalic border, the posteriorly situated eyes, the moderately prominent, short genal spine, the comparatively short pygidial axis and the wide pygidial border point to an assignment to *Stygina* Salter, 1853 (compare Skjeseth 1955). The material cannot belong to *Raymondaspis*, as representatives of that genus have a more strongly arched, less forward expanding glabella, a much narrower frontal area and anterior border, typically better indicated lateral glabellar furrows and an overall higher convexity of cranidia and pygidia (an exception may be the poorly known *R. marginata* (see Raymond 1925, pp. 70–71; Whittington 1965, pp. 405–406), but the inadequate knowledge on this species is an impediment to a close comparison). Set against *Protostygina* Prantl & Přibyl, 1948 (see Prantl & Přibyl 1948; Přibyl & Vaněk 1971) the present material seems to have a better defined, higher vaulted and more strongly forward expanding glabella, the eyes are situated further rearwards, the genal spine is not so broad-based and markedly shorter, and the pygidia are more elongate, showing a wider border and a broader doublure.

The new material does not match any of the established species of *Stygina*. *S. latifrons* (Portlock) (see Whittington 1950; Skjeseth 1955) seems to have a comparatively longer cranidium with a narrower anterior border and a longer glabella with a more rounded front; the pygidium has a postaxial ridge, better defined axial segments and a sigmoidal doublure with a narrow, flattened inner strip. Most of these differences also apply to *S. minor* Skjeseth (cf. Skjeseth, 1955). *S. angustifrons* Warburg has a wide anterior cranial border (see Warburg 1925, Pl. 3:1), but the glabella is narrow, elongate, the pygidium shows a distinct postaxial ridge and a narrow concave border, and the species is overall rather different from the Komstad Limestone material at hand. *S. nitens* (Wiman) (for generic assignment, see Warburg 1925) has a strongly forward expanding glabella, more strongly expanding than in the present specimens, the anterior and lateral borders of cephalon are narrower and the pygidium is without border. *S. plautini* (Schmidt), which is among the oldest known members of *Stygina*, has a quite wide frontal area and very faint lateral glabellar furrows (cf. Schmidt 1904, pp. 62–63; Pl. 8:11), but the cranidium is slightly narrower and has a slender glabella compared to the specimens at hand. Despite these differences this species seems to be the form closest to the present material. The pygidium of *S. plautini* is unknown.

Genus *Raymondaspis* Přibyl, 1948

Přibyl in Prantl & Přibyl 1948; *pro Holometopus* Angelin, 1854 (*non* Milne-Edwards, 1853) and *Warburgella* Raymond, 1937 (*non* Reed, 1931)

Type species. – (OD) *Holometopus limbatus* Angelin, 1854.

Raymondaspis material. – Seventy cranidia, 16 librigenae, and 99 pygidia, of which 8 fragmentary cranidia and 2 fragmentary pygidia are indeterminable at the species level. No hypostomes have been identified as yet.

Remarks on genus

Much confusion has prevailed concerning the status of *Raymondaspis*, see Whittington (1950), Skjeseth (1955) and V. Poulsen (1969). The differences between *Raymondaspis* and the related genera *Stygina* Salter, 1853, *Bronteopsis* Nicholson & Etheridge, 1879, *Protostygina* Prantl & Přibyl, 1948, and *Hallanta* Poulsen, 1965 are discussed by Wiman (1906a, pp. 293–294), Skjeseth (1955, pp. 10–12) and V. Poulsen (1969, p. 409). Other related genera are discussed by Přibyl & Vaněk (1971), see also Lane & Thomas (1983).

Turgicephalus Fortey, 1980, is rather similar to *Raymondaspis*, but is diagnosed by a more strongly convex cephalon (sag.), blunt genal angles and a slender pygidium with small articulating facets, as well as other minor differences (see Fortey 1980a, pp. 51–52; Whittington 1965, pp. 406–408). However, the taxon is undoubtedly closely related to the *Raymondaspis* group, and in order to signal the close relationship I prefer to separate *Raymondaspis* and *Turgicephalus* only as subgenera.

Remarks on Baltoscandian species

Angelin (1854, pp. 58, 90; Pls. 33:5–7; 41:17) assigned *H. aciculatus*, *H. ornatus*, *H. limbatus* and *H. elatifrons* to the newly established genus *Holometopus*. The latter species was allocated to *Orometopus* by Brögger (1896, p. 68). ‘*H. aciculatus* and ‘*H. ornatus* must be treated as *nomina dubia*; judging from Angelin (1854, Pl. 33:5, 6) these pygidia probably do not belong to *Raymondaspis*, but are more *Bronteopsis*-like (see also Olin 1906, p. 73; Pl. 4:20–21).

The label *Holometopus* [*Raymondaspis*] *limbatus* was earlier used as a collective term for the majority of raymondaspids occurring in the Lower Ordovician of Scandinavia, and references prior to Tjernvik (1956) are not reliable. The type material of ‘*H. limbatus*’ was redescribed by V. Poulsen (1969).

Apart from ‘*H. limbatus*’ few other Baltoscandian species have been defined. Pompecki (1890, pp. 86–87; Pls. 4:16; 5:8, 9) established the species *Holometopus? gracilis*, *H.? laevis* and *H.? radiatus*, based on a few pygidia deriving from erratic

boulders of northern Poland. ‘H.’? *gracilis* and ‘H.’? *laevis* seem to belong to *Raymondaspis*, whereas ‘H.’? *radiatus* presumably represents a different genus (cf. Pompecki 1890, Pl. 4:16). Unfortunately neither the description nor the figures permit a confident identification, and until the type material has been retrieved (it is most likely not preserved) and reinvestigated these names must be regarded as *nomina dubia*.

Holometopus Törnquisti Moberg & Segerberg 1906, based on an isolated pygidium from the *Ceratopyge* Limestone of southern Öland, was tentatively allocated to *Bronteopsis* by Skjeseth (1955) and Tjernvik (1956).

For remarks on non-Scandinavian species, see Ross (1967) and Fortey (1980a).

Raymondaspis (*Raymondaspis*) Příbyl, 1948

Příbyl in Prantl & Příbyl 1948

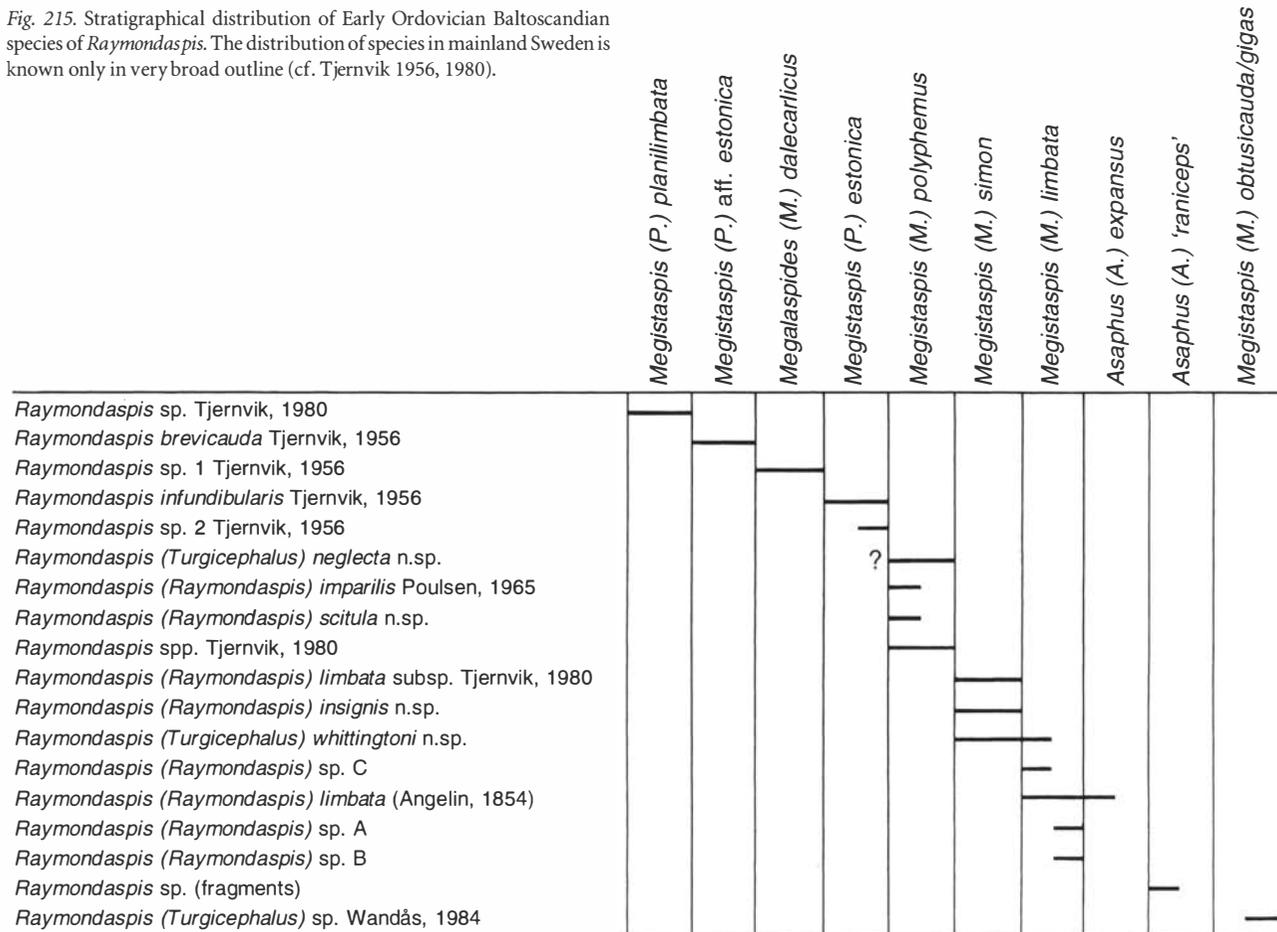
Type species. – (OD) *Holometopus limbatus* Angelin, 1854.

Raymondaspis (*Raymondaspis*) *limbata* (Angelin, 1854)

Synonymy. – □v 1854 *Holometopus limbatus* n.sp. – Angelin, p. 58; Pl. 33:7–7a (brief diagnosis, illustrations of cephalon and pygidium). □v non 1906a *Holometopus limbatus* A – Wiman, pp. 293–294; Pl. 29:21, 22. [= *R. (R.) ?cf. insignis* n.sp.]. □non 1950 *Raymondaspis limbatus* (Angelin, 1854) – Whittington, pp. 549–550; Pl. 72:11–14. [= *R. (T.) whittingtoni* n.sp.]. □v non 1952 *Raymondaspis limbatus* (Angelin, 1854) – Skjeseth, pp. 171–172; Pl. 4:16, 17, 19–21. [= *R. (T.) cf. neglecta* n.sp.]. □v non 1955 *Raymondaspis limbatus* (Angelin, 1854) – Skjeseth, p. 21; Pls. 4:2, 4, 4–9; 5:6, 8. [Various species]. □v non 1965 *Raymondaspis limbata* (Angelin, 1854) – V. Poulsen, p. 85–88; Pl. 6:1–4. [= *R. (T.) neglecta* n.sp.]. □v 1969 *Raymondaspis limbata* (Angelin, 1854) – Poulsen, pp. 407–415, Textfigs. 1–2 (redescription of the type material, discussion of the genus, occurrence, illustrations of cephalon, pygidium).

Lectotype. – Cephalon Ar 5139b, probably the original of Angelin (1854, Pl. 33:7), designated and refigured by V.

Fig. 215. Stratigraphical distribution of Early Ordovician Baltoscandian species of *Raymondaspis*. The distribution of species in mainland Sweden is known only in very broad outline (cf. Tjernvik 1956, 1980).



Poulsen (1969, Fig. 1). The specimen is from the Komstad Limestone of Fågelsång; it almost certainly originates from the basal part of the *A. expansus* Zone.

Remarks. – *R. limbata* has been interpreted rather disparately by previous authors, partly reflecting the circumstance that Angelin's type material for long was considered lost (cf. Whittington 1950; Skjeseth 1952, 1955; Poulsen 1965, 1969), and references to *Holometopus* [*Raymondaspis*] *limbatus* prior to Tjernvik (1956) are not reliable. Wiman (1906a, pp. 293–294; Pl. 29:21, 22) figured a couple of pygidia identified with *Holometopus limbatus*; the specimens were allegedly from the *Planilimbata* limestone of Öland. The material has been examined, and the associated trilobites point to a more likely provenance from the upper part of the *M. polyphemus* Zone. Tjernvik (1956) assigned these pygidia to *Raymondaspis* n.sp. no. 2; possibly they belong to *R. scitula* n.sp.. Whittington (1950, pp. 549–550) described two pygidia from Fågelsång, assumed to represent *R. limbata*. These topotype pygidia, which here are attributed to *R. whittingtoni* n.sp., lack a border, which led Whittington (1950) to exclude pygidia with a well-defined concave border from *R. limbata*. Skjeseth (1952, pp. 171–172; Pl. 4:16–17, 19–21) described sparse material, identified with *R. limbata*, from the Heramb Member, Oslo region (representing either the upper part of the *M. estonica* Zone or the *M. polyphemus* Zone). *R. limbatus sensu* Skjeseth 1952 is closely related to *R. neglecta* n.sp.. Skjeseth (1955, p. 21; Pls. 4:2, 4–9; 5:6, 8) figured additional material assigned to *R. limbatus*, but most of it, if not all, does not belong to *R. limbata* (*s.str.*), although alternative identifications, based only on the published figures, are not attempted. The specimens are from different parts of Scandinavia, and most often the exact stratigraphic level is unknown. V. Poulsen (1965, pp. 85–89; Pl. 6:1–6) described *R. limbata* from the 'Skelbro Limestone' of Bornholm, basal *M. polyphemus* Zone; that material is here distributed among *R. (R.) scitula* n.sp. and *R. (T.) neglecta* n.sp. I have found no specimens confidently assignable to *R. (R.) limbata* (*s.str.*) in the Komstad Limestone or the Huk Formation (compare, however, *Raymondaspis* sp. B). Tjernvik (1980) listed the species from the *M. limbata* Zone of Sweden.

The characterization of *R. limbata* is hampered by the fragmentary state of the lectotype, which at present is the only known cephalon of *R. limbata*; it is described at length by V. Poulsen (1969). The specimen has been reexamined, and for comparative purposes the following features are emphasized: Rear part of glabella unusually narrow, the posterior minimum width corresponds to 0.55 of maximum glabellar width, which in turn accounts for ca. 0.60 of greatest preocular cranidial width. Anterior fixigena extraordinarily wide (tr.). Sagittal cranidial convexity moderate for the genus; anterior concave border fairly wide; anterior margin very gently convex, almost truncate (dorsal view), faintly swollen; glabellar muscle areas moderately impressed; paradoublural furrow (border furrow *sensu* Poulsen 1969) distinct in comparison to other species. Judging from the pre-

served inner part of palpebral area, the palpebral lobes are comparatively little elevated, and presumably about level with sagittal part of glabella. Paradoublural furrow of librigena well-marked, inner area presumably only moderately ascending to eye. Distinct crest on genal spine.

Raymondaspis (*Raymondaspis*) *scitula* n.sp.

Figs. 216–218

Synonymy. – □ v cf. 1906a *Holometopus limbatus* A – Wiman, pp. 293–294; Pl. 29:21, 22 (illustrations of pygidia). □ v 1936 *Holometopus* n.sp. – C. Poulsen, p. 49 (listed). □ v cf. 1955 *Raymondaspis limbatus* (Angelin, 1854) [*partim*] – Skjeseth, p. 21; Pl. 4:4, 7 (figures of librigena and pygidium). □ v 1965 *Raymondaspis limbata* (Angelin, 1854) [*partim*] – V. Poulsen, pp. 85–88; non Pl. 6:1–4 [= *R. (T.) neglecta* n.sp.] (description, illustrations of cranidium, discussion of the genus, occurrence). □? 1980 *Raymondaspis limbata* (Angelin) subsp. – Tjernvik & Johansson, p. 191 (listed).

Derivation of name. – Latin *scitulus* = pretty, elegant.

Holotype. – Cranidium MGUH 22.928 (S 239) (Fig. 217A–B) from 3 cm above base of bed –20 at Skelbro, basal part of *M. polyphemus* Zone.

Paratype. – Pygidium MGUH 22.935 (S 123a) (Fig. 217K) from 4.5 cm below top of bed –21 at Skelbro, basal part of *M. polyphemus* Zone.

Additional material. – Seventeen cranidia, 5 librigenae and 12 pygidia.

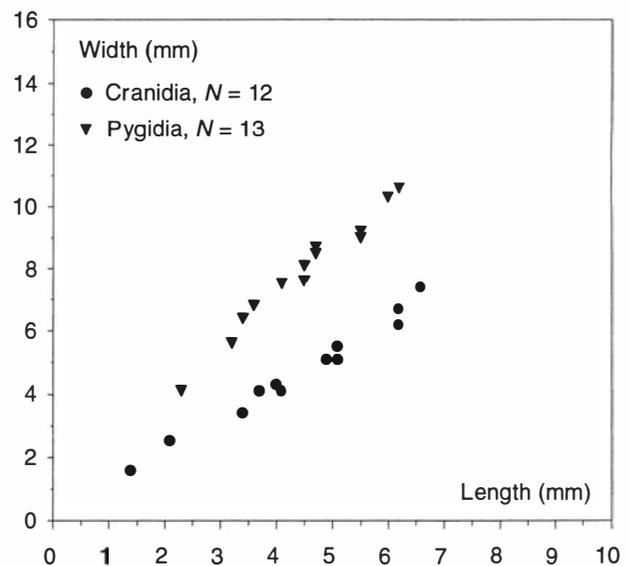


Fig. 216. Cranidia and pygidia of *Raymondaspis scitula* n.sp. Maximum width plotted against sagittal length.

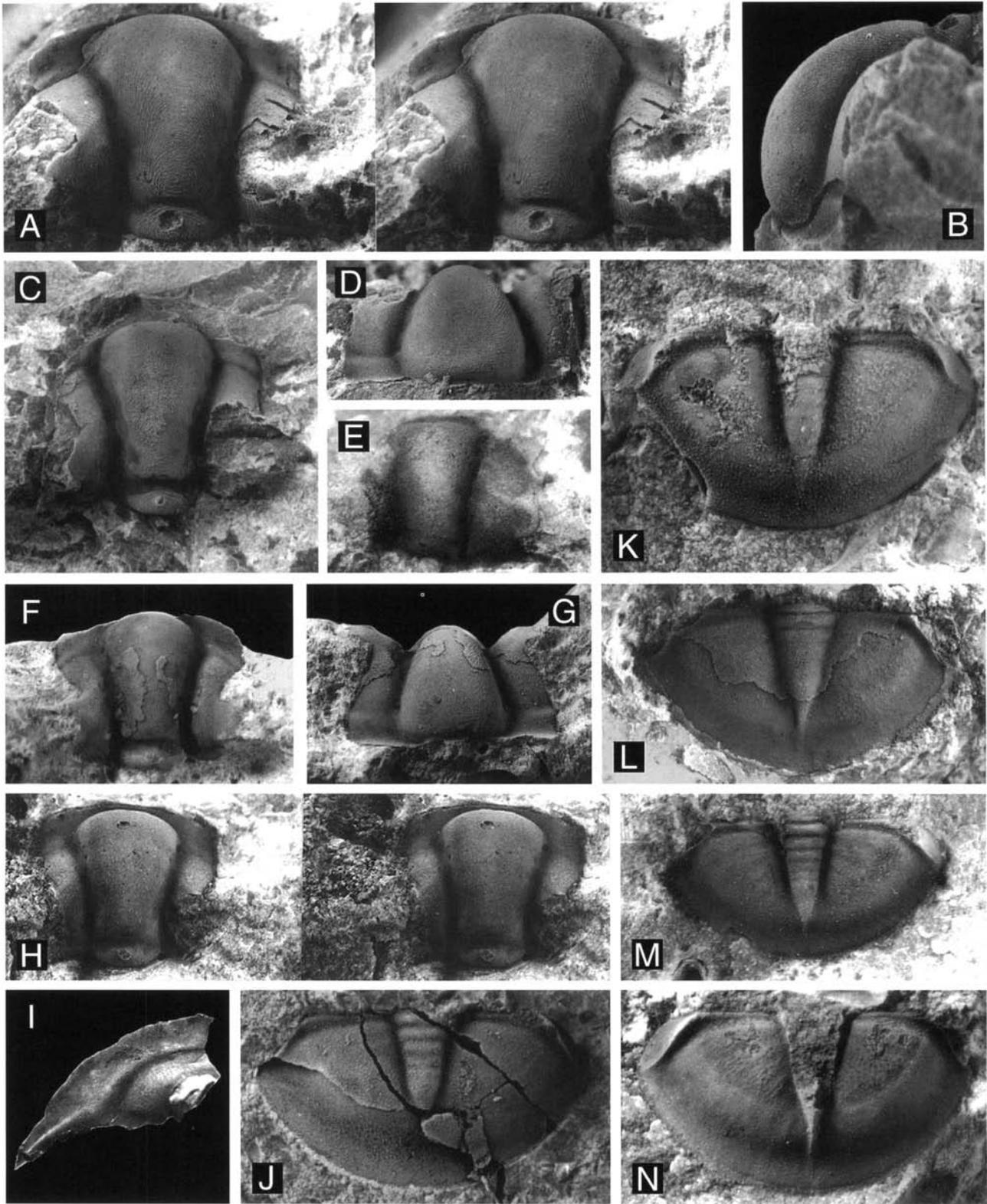


Fig. 217. *Raymondaspis (R.) scitula* n.sp. □A–B. Holotype. Cranidium, dorsal (stereo-pair) and side views, ×10. MGUH 22.928 (S 239), bed –20, Skelbro. □C–D. Cranidium, dorsal and frontal views, ×6. MGUH 22.929 (S 250), bed –20, Skelbro. □E. Fragmentary juvenile cranidium, ×20. MGUH 22.930 (GM 1987.18a), Skelbro. □F–G. Largely exfoliated cranidium, dorsal and frontal views, ×9. MGUH 22.931 (S 260a), bed –20, Skelbro. □H. Small cranidium, stereo-pair, ×9. MGUH 22.932 (S 1), bed –21, Skelbro. □I. Exfoliated librigena, ×6. MGUH 22.933 (S 298-1b), bed –20, Skelbro. □J. Internal mould of pygidium showing doublure, ×8. MGUH 22.934 (S 207), bed –21, Skelbro. □K. Paratype. Slightly corroded pygidium, ×7. MGUH 22.935 (S 123a), bed –21, Skelbro. □L. Small pygidium, ×10. MGUH 22.936 (S 297), bed –20, Skelbro. □M. Small pygidium, ×12. MGUH 22.937 (S 123b), bed –21, Skelbro. □N. Exfoliated pygidium, ×10. MGUH 22.938 (GM 1987.20), Skelbro beds, Skelbro.

List of additional material. — □Crania S 1 (im) [MGUH 22.932], S 168 (im), S 169a (pim), S 184 (pim), S 216a (im), S 250 (t) [MGUH 22.929], S 260-1 (im) [MGUH 22.931], S 260-4 (im), S 294 (pim), S 372 (im), S 373b? (im), GM 1987.12 (im), GM 1987.15 (im), GM 1987.16 (im), GM 1987.18a (im) [MGUH 22.930], GM 1987.18b (em), GM 1987.18c (em). □Librigenae S 12a (im), S 12b (is), S 169b (pim), S 251b (im), S 298b (im) [MGUH 22.933]. □Pygidia S 41 (im), S 70 (im), S 119 (im), S 123b (im) [MGUH 22.937], S 126 (im), S 139-1 (pim), S 207 (d) [MGUH 22.934], S 251 (im), S 297 (pim) [MGUH 22.936], GM 1987.19 (im), GM 1987.20 (im) [MGUH 22.938], DGU 7-1 (pim).

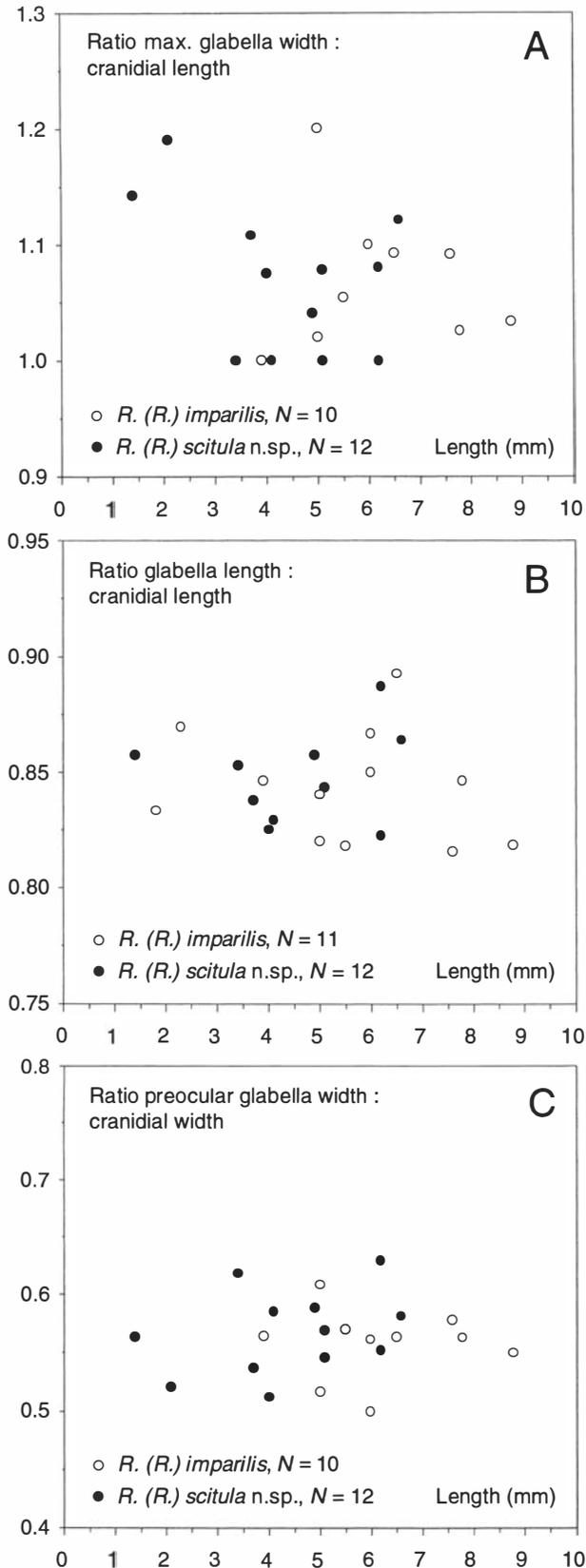
Occurrence. — *R. (R.) scitula* n.sp. has been found solely in beds –21 and –20 at Skelbro, i.e. lowermost part of the *M. polyphemus* Zone. The museum material examined undoubtedly originates from the same interval.

R. (R.) scitula n.sp. is currently known with certainty only from the Komstad Limestone, but it may correspond to *Raymondaspis limbata* subsp. *sensu* Tjernvik (1980 p. 191), reported from the *M. polyphemus* Zone of Sweden. A couple of the specimens figured by Skjeseth (1955, Pl. 4:4, 7) are very like *R. scitula* n.sp.; the lithology of the samples and the associated fossils suggest a provenance from the *M. polyphemus* Zone. Two pygidia, illustrated by Wiman (1906a), are likewise similar to *R. scitula* n.sp.; note that the drawings are inaccurate and the apparent differences in axial outline are not real (cf. Wiman 1906a, Pl. 29:21 vs Pl. 29:22). These pygidia also seems to be derived from the *M. polyphemus* Zone (see introductory remarks above).

Diagnosis. — Small form. Glabella expands only moderately forwards; frontal area extremely narrow, but anterior border present; occipital ring level with rear part of glabella; occipital tubercle comparatively prominent. Librigena with well-marked paradoublural furrow, long, slender genal spine, and a low crest running from posterior bend of paradoublural furrow and onto spine. Pygidium of low relief with long, slender, evenly tapering axis; doublure narrow.

Description. — Small to medium-sized species; largest cranidium 6.6 mm long, largest pygidium 6.2 mm long. Cranidium strongly convex (sag.), with a gently convex (dorsal view) anterior margin. Greatest width of cranidium is across posterior fixigenae, FW:L ratio 1.34–1.43 (mean 1.39; $N=3$). PW:L ratio 1.00–1.19, highest in small cranidia; two juveniles, 1.4 and 2.1 mm long, show a ratio of 1.14–1.19, whereas specimens more than 3.4 mm long show values between 1.00 and 1.12 (mean 1.05; $N=10$). Width across palpebral lobes equal to greatest preocular width. Glabella prominent, strongly inflated; posterior part nearly parallel-sided, gently expanding forwards, more strongly so in front of palpebral area (axial furrows diverge at an angle of about 20° to sagittal line), and glabella assumes a club-shaped outline; front truncately rounded. Posterior glabella width 0.57–0.67 of anterior (maximum) glabella width (mean 0.61; $N=11$); maximum glabella width in turn accounts for 0.51–0.63 of the greatest preocular cranidial width (mean 0.57; $N=12$). Glabella on the average stretches for 0.85 ($N=11$) of the cranidial length. Four pairs of lateral glabellar furrows of

which F3 and F4 are impressed only on internal moulds, and barely indicated by a slight change of terrace-line pattern on testaceous material; the furrows are faintly dark-coloured in some specimens with intact test. F4 short and shallow, situated approximately 0.35 times the length of glabella from its front. F3 situated approximately at mid-length of glabella; these furrows are slightly longer (tr.) than F4, but do not unite across glabella. F1 and F2 more deeply impressed, situated level with palpebral lobes, converging to form a triangular depression on each side of glabella with apex touching axial furrow. These posterior depressions are also visible when the test is intact. Glabellar front has a shallow, but comparatively distinct median depression situated immediately above preglabellar furrow. The depression is most obvious on internal moulds, but is also defined on testaceous specimens. Glabella delimited by well-impressed axial and preglabellar furrows; a pair of fossulae occurs in the axial furrows 0.25 of the glabella length from front, and a second pair of depressions occurs in axial furrows level with the eyes. Occipital furrow fairly wide, rather deeply impressed; a pair of shallow lateral depressions, best defined on internal moulds, is situated in the occipital furrow immediately above junction with axial furrows. Occipital ring well-defined, slightly expanded mesially, carrying a comparatively prominent tubercle; the prominence of the tubercle may depend upon the small size of this species. Occipital ring approximately level with rear part of glabella. Anterior area of fixigena very strongly inclined in anterior to anterolateral direction; paradoublural furrow shallow, running subparallel to anterior margin from fossula in axial furrow to edge of fixigena; concave anterior border defined by a pronounced change in steepness of fixigenae. Border rather narrow, extremely narrow in front of glabella. The test is thickened in the flexure, hence it is mesially twice as wide on internal moulds. Palpebral area of fixigena convex, gently down-sloping in anterior and posterior direction, strongly so in adaxial direction; width of palpebral area, exclusive of palpebral lobe, approaches that of the adjacent half of glabella. Palpebral lobes slightly elevated above glabella; they are situated posteriorly, hind corners positioned approximately 0.15 of the cranidial length from posterior margin; lobes small, length (exsag.) equivalent to 0.22–0.25 of the cranidial length (mean 0.24; $N=3$). Palpebral lobes continue anteriorly into oblique and almost straight eye ridges, best defined on internal moulds (vestigial on the outside of test), joining axial furrows slightly anterior to mid-length of cranidium. Very well-preserved cranidia exhibit double eye ridges, consisting of two raised lines, of which the anterior one is less distinct, but this composite structure is generally indistinguishable. Posterior area of fixigena narrow (exsag.), long (tr.), pointed; adaxial half, immediately behind palpebral area, slants in posterior direction, whereas abaxial slender half is less inclined; distal tip bends slightly backwards. Internal moulds show faint border furrow on middle part of fixigena; it shallows up in both directions, and is almost



effaced on testaceous material. Anterior branches of facial suture diverge in front of eyes at an angle of about 30–35° to sagittal line, then, after intersection with paradoublural furrow, turn inwards, intersect margin and run marginally to merge smoothly in front of glabella. Posterior branches of facial suture run straight outwards, gently backwards from palpebral lobes, to curve slightly back distally before intersecting posterior margin. Terrace lines, arranged in a Bertillon pattern, are dense on glabella and genal region; 15–20 lines/mm were counted on glabella in a cranidium about 5 mm long. Terrace lines are less distinct and more dispersed in furrows, and the lateral glabellar furrows are outlined by the lack of lines. The terrace lines are concentric around the eyes on genae, roughly parallel to sagittal line on the palpebral lobes, essentially concentric around a point situated immediately in front of occipital furrow on the posterior part of glabella, whereas the lines on the anterior main part of glabella follow the glabellar contour. The terrace lines on the occipital region are semicircular around the median posterior point.

Librigena sickle-shaped, about twice as wide as long (maximum measures); outer margin evenly curved, not thickened. Paradoublural furrow continues from fixigena onto librigena, becoming better impressed, and the comparatively distinct furrow separates a steeply rising inner part of librigena from a flatter outer part. Eye not preserved. Outer part of librigena concave, forming a continuation of anterior border, tapering slightly backwards, but enters genal spine. Genal spine fairly prominent, despite that the base is comparatively narrow; it projects obliquely backwards at an angle of about 140° to sagittal line. A characteristic low ridge stretches from the posterior bend of paradoublural furrow and onto spine, here becoming sharper, and the outer border becomes correspondingly somewhat steeper. External test ornamentation unknown; the steep inner part has a caecate mould surface. Doublure appears to be strongly concave, almost forming a half cylinder anteriorly, widening backwards (poorly exposed in the available material).

Hypostome and thorax unknown.

Pygidium subsemicircular in outline; L:W ratio 0.53–0.61 (mean 0.57; N = 13), but changes during growth, and smaller pygidia tend to be relatively wide. Anterolateral corners obliquely truncate. Axis long, stretching for about 0.55–0.65 of the pygidial length (mean 0.59; N = 11), but the axial

Fig. 218. Cranidia of *Raymondaspis scitula* n.sp. and *R. imparilis*. □A. Ratio between maximum glabellar width and sagittal cranial length plotted against cranial length. □B. Ratio between glabella length and sagittal cranial length plotted against cranial length. □C. Ratio between preocular cranial width and sagittal cranial length plotted against cranial length.

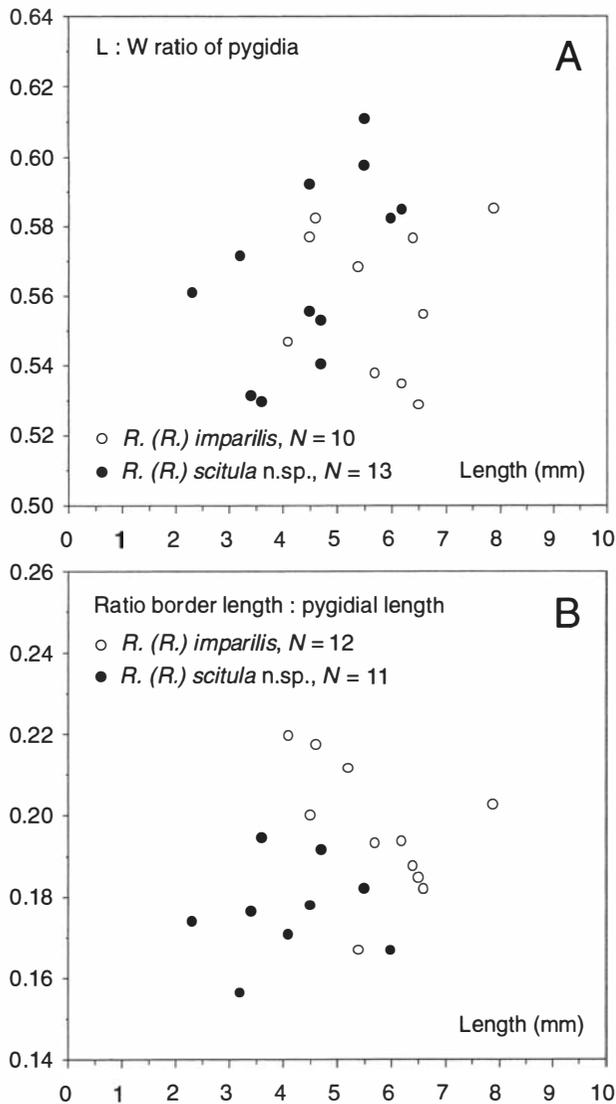


Fig. 219. Pygidia of *Raymondaspis scitula* n.sp. and *R. (R.) imparilis*. □ A. Pygidial L:W ratio plotted against pygidial length. □ B. Ratio between border length (sag.) and length of pygidium plotted against pygidial length.

termination is difficult to define exactly as axis continues smoothly into a tapering postaxial ridge, running almost to the posterior margin; ridge very faint on the concave border. Axis occupies about 0.20–0.23 of maximum pygidial width at anterior margin (mean 0.21; $N = 10$); it is slightly elevated above pleural fields, tapers gently, posterior width about half of anterior width. Articulating half-ring prominent, followed by 7 axial rings, including the acuminate terminal piece, separated by moderately and uniformly impressed ring furrows, which become progressively fainter in posterior direction, and the segmentation is vestigial behind the third ring. Axial furrows fairly deep and wide, but shallows up at intersection with paradoublural line. Pleural fields

show half rib delimited by a shallow and wide furrow, followed by 4 or 5 faint pleural ribs, separated by nearly effaced pleural furrows, best seen on internal moulds; the ribs terminate at inner margin of doublure. Border strongly concave, and of nearly uniform width throughout; it is defined only by a change of slope. Postaxially the border accounts for 0.16–0.19 of the pygidial length (mean 0.18; $N = 11$). Articulating facets comparatively large, rather steeply downsloping anterolaterally, oblique, situated at an angle of about 130–135° to sagittal line, and delimited rearwards by a distinct crest. Dorsal surface sculpture known only from a couple of fragmentary pygidia. One specimen shows fairly dense, gently anastomosing terrace lines on the pleural fields, running obliquely inwards-backwards, while the anterolateral border is smooth; axis and posterior border exfoliated. Another specimen with intact test on the right pleural field seems to have a smooth test without terrace lines; the two specimens are approximately of the same size. Internal moulds show a fine punctation, particularly on the pleural fields. Doublure of pygidium pronouncedly concave, broad, but only moderately so for a *Raymondaspis*. The width corresponds to the pygidial length minus the axial length, and it approximately maintains the same width all the way; paradoublural line indicated by termination of the faint pleural furrows and ribs. Sagittal depression in doublure very faint. Doublure covered with weakly impressed, barely visible continuous terrace lines. A single specimen suggests the presence of ca. 18 lines across the doublure.

Affinities. – *Raymondaspis (R.) scitula* n.sp. is primarily distinguished from the associated *R. (R.) imparilis* Poulsen by the more strongly forwards expanding glabella and by the longer pygidial axis. Besides, *R. scitula* n.sp. is smaller, has a more pronounced sagittal convexity of the cranium, a slightly more convex anterior cranial margin (dorsal view), a narrower anterior border, comparatively less impressed lateral glabellar furrows, a lower occipital ring, longer posterior fixigenae, a different course of the anterior branches of the facial suture, a gracile genal spine with well-defined crest, and a narrower pygidial doublure and border.

R. (R.) scitula n.sp. is very like *R. (R.) limbata* (Angelin, 1854), and these species are probably closely related. *R. scitula* n.sp. is distinguished by having a slightly broader glabella, or, more precisely, the posterior part is comparatively broader, so the forward expansion is less pronounced, hence glabella is club-shaped, while the *R. limbata* glabella is somewhat pestle-shaped; the glabellar muscle areas are slightly less impressed, the convexity of cranium (sag.) is higher, the anterior fixigenae are narrower (tr.) and the palpebral lobes are more elevated. The librigena of *R. scitula* n.sp. has a more steeply ascending inner area, and the border concavity is slightly stronger. The pygidial doublure of *R. scitula* n.sp. is wider than in *R. limbata*, so the axis is longer and not funnel-shaped.

Raymondaspis (Raymondaspis) imparilis Poulsen, 1965

Figs. 219–222

Synonymy. – □v 1936 *Holometopus* n.sp. – C. Poulsen, p. 49 (listed). □v 1965 *Raymondaspis limbata* (Angelin, 1854) [*partim*] – Poulsen, pp. 85–88 (one cranidium of *R. imparilis* included in the material, see discussion below). □v 1965 *Raymondaspis imparilis* n.sp. – Poulsen, pp. 88–89; Pl. 6:5–6 (description and illustrations of two pygidia).

Holotype. – Pygidium MGUH 9451 from the Skelbro beds, Skelbro, figured by V. Poulsen (1965, Pl. 6:6); herein refigured on Fig. 221K.

Material. – Fourteen cranidia, 4 librigena, and 13 pygidia. Pygidia MGUH 9450 and 9451 were figured by V. Poulsen (1965, Pl. 6:5–6).

List of material. – □Cranidia S 63a (im) [MGUH 22.942], S 171 (pim), S 216b (im), S 227 (pim) [MGUH 22.940], S 287 (im), S 319 (im), S 326 (im), S 349a (im), S 355 (pim), S 363 (im) [MGUH 22.941], S 373a (pim), GM 1987.11 (im), GM 1987.13 (im) [MGUH 22.939], GM 1987.14 (im). □Librigenae S 63b (im), S 228 (im) [MGUH 22.944], S 299 (im) [MGUH 22.943], S 319 (im). □Pygidia S 92 (t) [MGUH 22.946], S 230 (t), S 277 (im) [MGUH 22.948], S 295a (pim), S 295b (im), S 298 (im) [MGUH 22.945], S 312 (im), S 316 (pim) [MGUH 22.947], S 346 (im), S 349b? (im), S 364 (pim), MGUH 9450 (im), MGUH 9451 (im) [holotype].

Occurrence. – *R. (R.) imparilis* has been found only in beds –21 and –20 at Skelbro, i.e. lowermost part of the *M. polyphemus* Zone. The museum material investigated undoubtedly originates from the same beds. The species is currently not known from outside Bornholm.

Diagnosis. – Medium-sized species. Sagittal convexity of cranidium moderate; glabella narrow (tr.), with F1 and F2 well-impressed; anterior margin of cranidium truncate; wide anterolateral cephalic border; palpebral lobes approximately level with crest of glabella (adult state); occipital ring slightly elevated above rear part of glabella; occipital tubercle small. Genal spine broad-based and carries poorly defined ridge. Pygidium of low relief, with broad concave border, short and funnel-shaped axis and broad doublure. [Emended from V. Poulsen 1965.]

Description. – Medium-sized for a *Raymondaspis*, largest cranidium 8.8 mm long, largest pygidium 7.9 mm long. Basic outline of cranidium like *R. (R.) scitula* n.sp., but *R. imparilis* differs, e.g., by having a less strongly forward expanding glabella (differences enumerated on p. 303). The axial furrows diverge at an angle of about 16–17° to sagittal line in front of palpebral area, and posterior (minimum) glabella width is 0.61–0.73 times the anterior (maximum) glabellar width (mean 0.66; $N = 11$). Maximum glabellar width corresponds to 0.50–0.61 of the greatest preocular cranial width (mean 0.56; $N = 10$), a ratio which is equal to that of *R. scitula* n.sp., and, accordingly, it is the rear part of glabella that is relatively wide in *R. imparilis*. The moderate expansion of

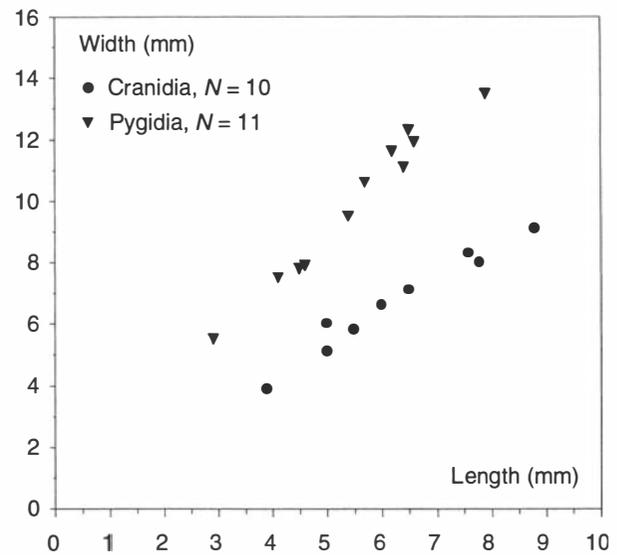


Fig. 220. *Raymondaspis imparilis*. Maximum width plotted against sagittal length of cranidia and pygidia.

glabella amplifies its arched appearance. Glabella front truncately rounded; glabella accounts for 0.82–0.89 of the cranial length (mean 0.84; $N = 12$). PW:L ratio 1.00–1.20 (mean 1.07; $N = 10$; all specimens >3.9 mm long); FW:L ratio 1.22–1.29 (mean 1.25; $N = 3$), i.e. the posterior fixigenae are comparatively short (tr.). Compared to *R. scitula* n.sp., the anterior margin of cranidium is slightly less convex and appears truncate (dorsal view). Lateral glabellar furrows as in *R. scitula* n.sp., but better impressed, and all furrows are visible even on testaceous specimens; furthermore, terrace lines are weakly developed or absent in the furrows. Occipital furrow comparatively wide, but well-impressed. Occipital ring slightly elevated above rear part of glabella, and somewhat expanded mesially, carrying a small tubercle. Paradoablural furrow shallow, but better defined than in *R. scitula* n.sp. Anterior border comparatively wide laterally, very narrow in front of glabella. Palpebral lobes in a posterior position, distance between hind corner to posterior margin of cranidium equivalent to approximately 0.15 of cranial length; lobe length (exsag.) equivalent to 0.21 of cranial length in one specimen (the palpebral lobes are damaged in all but the one cranidium). Lobes are positioned at a level just above crest of glabella. Anterior eye ridges as in *R. scitula* n.sp., but they appear marginally better defined. Posterior fixigena narrow (exsag.), pointed, short (tr.) (cf. low FW:L ratio), distal part turned somewhat backwards, more distinctly so than in *R. scitula* n.sp.. There is a shallow, but comparatively well-defined posterior border furrow in the middle part of the fixigena. Anterior branches of facial suture diverge in front of palpebral lobes at an angle of about 25–30° to sagittal line. Terrace lines prominent, arranged in a pattern essentially like the one described for *R. scitula* n.sp.; the

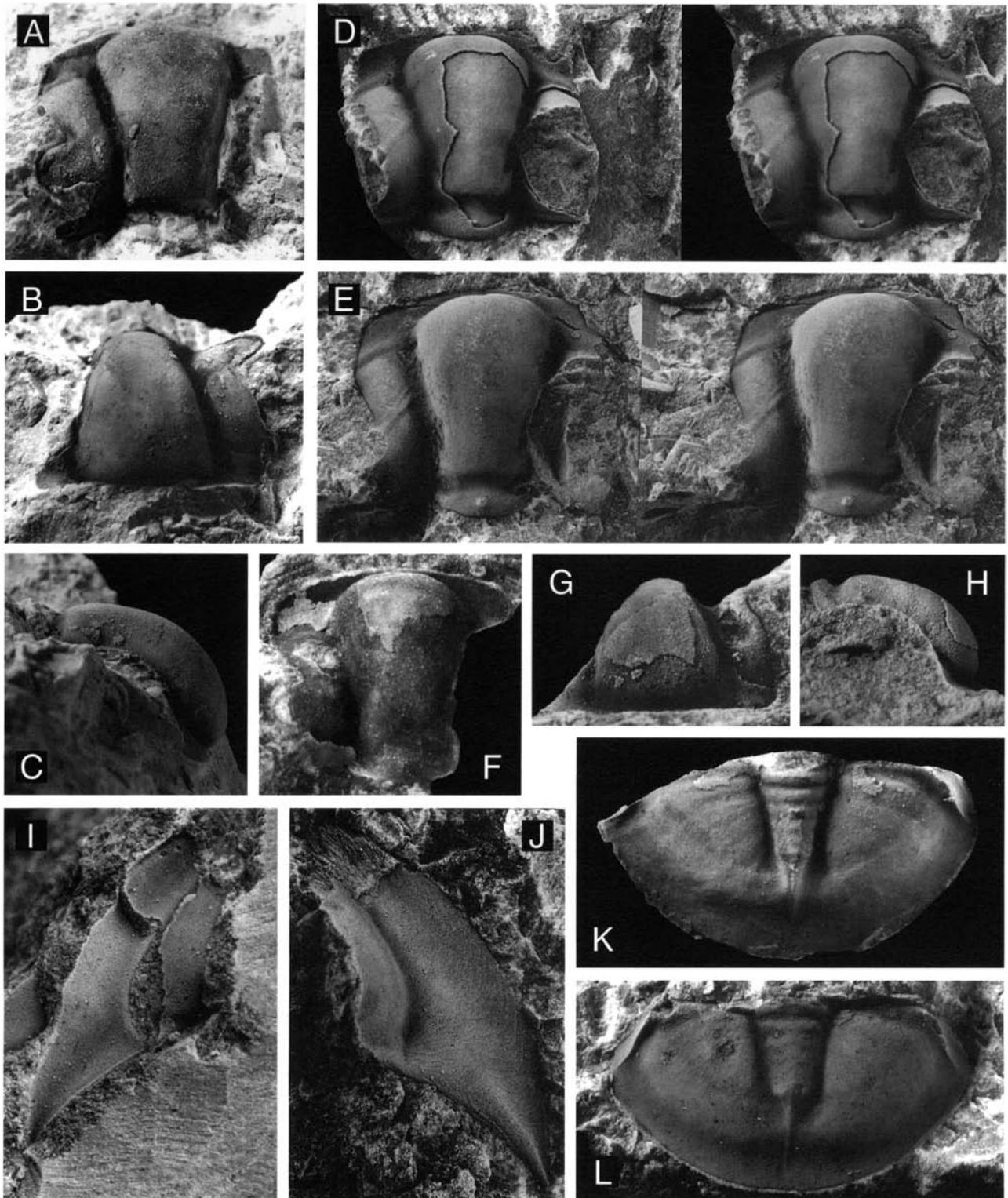


Fig. 221. *Raymondaspis (R.) imparilis* Poulsen, 1965. □A–C. Exfoliated cranidium, dorsal, frontal and side views, $\times 6$. MGUH 22.939 (GM 1987.13), Skelbro. □D. Partly exfoliated cranidium, stereo-pair, $\times 5$. MGUH 22.940 (S 227), bed –20, Skelbro. □E. Exfoliated cranidium, stereo-pair, $\times 5$. MGUH 22.941 (S 363), bed –20, Skelbro. □F–H. Largely exfoliated small cranidium, dorsal, frontal and side views, $\times 9$. MGUH 22.942 (S 63a), bed –21, Skelbro. □I. Internal mould of librigena showing doubleure, $\times 10$. MGUH 22.943 (S 299), bed –20, Skelbro. □J. Librigena showing surface sculpture, $\times 10$. MGUH 22.944 (S 228), bed –20, Skelbro. □K. Holotype. Exfoliated pygidium, $\times 12$. Previously figured by V. Poulsen (1965, Pl. 6:6). MGUH 9451, Skelbro beds, Skelbro. □L. Exfoliated pygidium showing axis, $\times 7$. MGUH 22.945 (S 298), bed –20, Skelbro.

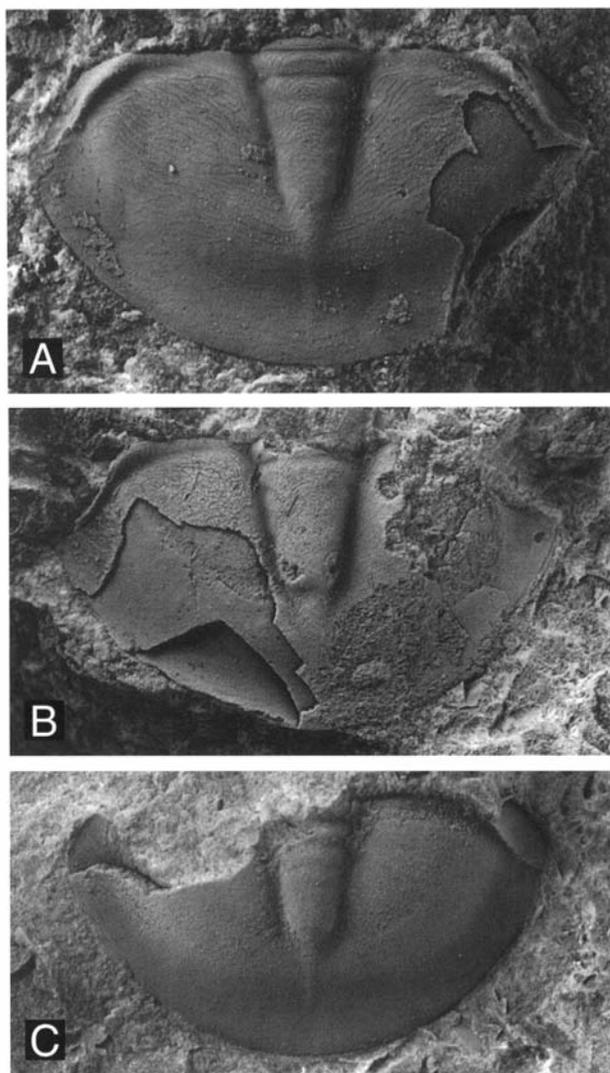


Fig. 222. *Raymondaspis (R.) imparilis* Poulsen, 1965. □A. Pygidium showing terrace-line sculpture, $\times 10$. MGUH 22.946 (S 92), bed -21, Skelbro. □B. Partly exfoliated pygidium, $\times 6$. MGUH 22.947 (S 316), bed -20, Skelbro. □C. Exfoliated pygidium, $\times 6$. MGUH 22.948 (S 277), bed -20, Skelbro.

lateral glabellar furrows are, though, more clearly set off by indistinctness or absence of ornament. About 20 lines/mm were counted on glabella in a cranidium ca. 8 mm long.

Librigena readily separated from *R. scitula* n.sp. Paradoublural furrow comparatively less impressed and terminates posterolaterally in a slight depression. Inner part, inside paradoublural furrow, apparently ascends less strongly to the eye, compared to *R. scitula* n.sp.; eye and eye socle not preserved. Outer part relatively broader, lateral border widens backwards to about middle of gena, thence tapers gently rearwards, but enters spine. Genal spine with stout base, and only a weakly defined low crest, present merely on the spine, proper. The spine is directed obliquely backwards at an angle of about $115\text{--}120^\circ$ to sagittal line (estimate). All librigenae at

hand are exfoliated; a latex cast (Fig. 221J) shows general outline of dorsal surface sculpture. Inside paradoublural furrow fine lines are approximately concentric around the eye (not visible on reproduced photo). The lines are twice as closely spaced inside paradoublural furrow, as on the outer part. Doublure concave, slightly less so than in *R. scitula* n.sp., widening backwards (Fig. 221I). It is covered with weakly impressed, continuous terrace lines; the number cannot be verified.

Hypostome and thorax unknown.

Pygidium subsemicircular in outline, L:W ratio 0.53–0.59 (mean 0.56; $N = 11$). Anterolateral corners obliquely truncate. Axis short, stretching for 0.47–0.54 of the pygidial length (mean 0.51; $N = 11$); the width at anterior margin is equivalent to 0.17–0.24 of the maximum pygidial width (mean 0.20; $N = 12$). Axis elevated above pleural fields the whole way; it tapers rather evenly backwards with a slight decrease from the third axial ring; posterior width is about 0.55 of the anterior axial width. Half-ring fairly prominent, presumably followed by 7 axial rings, including terminal piece, separated by moderately and uniformly impressed ring furrows, which becomes progressively fainter in posterior direction, so the segmentation is indistinct behind the third ring. Terminal piece less pointed than in *R. scitula* n.sp., which, combined with the shortness of the axis, engenders a funnel-shaped axial appearance. Axis continues into an inconspicuous, slender, narrowing postaxial ridge, which is barely indicated on testaceous material. The transition axis/ridge is comparatively well-defined. The postaxial ridge typically disappears close to the border and is followed by a shallow, wide impression in the concave border, but in rare cases it continues almost to the posterior margin (cf. V. Poulsen 1965, Pl. 6:5–6). Axial furrows wide, but deep and are more distinct than in *R. scitula* n.sp.; they shallow up at intersection with paradoublural line. Pleural fields show half rib, delimited by a shallow, wide furrow, slightly more distinctive than in *R. scitula* n.sp.; segmentation of pleural fields vestigial on internal moulds and effaced on testaceous specimens. There are presumably 4, maybe 5, pairs of pleural ribs, terminating at paradoublural line. Border wide, of uniform width throughout, postaxially occupying 0.20–0.22 of the pygidial length (mean 0.21; $N = 9$). Articulating facets large, sloping steeply in anterolateral direction, and strike at an angle of $130\text{--}135^\circ$ to sagittal line. Dorsal terrace lines most closely spaced on the surface of axis and the pleural fields (Fig. 222A), and more sparse on the border. About 10 lines/mm were counted on the pleural fields and less than 5 lines/mm were counted on the border in a couple of pygidia, 4.4 and 6.6 mm long. Internal moulds show no impressions of terrace lines, and the punctation displayed by *R. scitula* n.sp. has not been seen. Doublure basically as in *R. scitula* n.sp., but is wider, approximately twice as wide as the border, and more gently concave; again the width of doublure is equal to the pygidial length minus the axial length. The doublure is covered with faintly impressed terrace lines; the total num-

ber can not be verified. Paradoublural line indicated by a faintly inflated crest, but is often signalled also by colour changes of test (probably reflecting test thickness).

Affinities. – *R. (R.) imparilis* has many points of resemblance to *R. infundibularis* Tjernvik, 1956, but is distinguished by the comparatively longer pygidium, with an axis less rapidly backward-tapering in the anterior part, and by the better defined, although still faint, postaxial ridge. The cranidium of *R. infundibularis* is unknown, and the subgeneric assignment is uncertain.

For differences between *R. (R.) imparilis* and *R. (R.) scitula* n.sp., *R. (T.) whittingtoni* n.sp. and *R. (T.) neglecta* n.sp., see the respective species.

R. (R.) imparilis differs from *R. (R.) limbata* (Angelin, 1854) by having a broader glabella (tr.), especially posteriorly, the posterior glabellar muscle areas are better impressed, glabella typically has a slight median impression at front, just above preglabellar furrow, and the sagittal cranial convexity is stronger. The librigena is quite different from *R. limbata*, while it at present is impossible to point to diagnostic differences between the pygidia.

Remarks. – V. Poulsen (1965, pp. 88–89) recognized only the pygidium of *R. imparilis*, but cranidium GM 1987.16, by him attributed to *R. limbata*, actually belongs to *R. (R.) imparilis*.

One of the pygidia from the 'Planilimbata Limestone', figured by Wiman (1906a, Pl. 29:21), is drawn like *R. imparilis*, but is inaccurately portrayed. In reality, the axis is longer and not funnel-shaped.

Raymondaspis (Raymondaspis) insignis n.sp.

Figs. 223–224

Derivation of name. – Latin *insignis* = naturally remarkable, referring to the stout librigena of the new species.

Holotype. – Cranidium LO 7086 (Fig. 223A) from Tommarp, collected by Funkquist from 'Undra Kalken' (= 'Lower Limestone'). The sample (LU 27) also contains *Megistaspis limbata* type 9 and *Rhombampyx frater* n.sp., and undoubtedly originates from the *M. simon* Zone.

Additional material. – One poor cranidium, 3 librigenae, and 10 pygidia.

List of additional material. – □Cranidium S 841a? (em). □Librigenae K 688 (t) [MGUH 22.949], K 714 (pim) [MGUH 22.950], LU 36 (is). □Pygidia S 841b? (c), S 865 (c) [MGUH 22.951], K 584 (c), LU 15a (em), LU 15b (t), LU 18 (pim), LU 27b (t), LU 51 (im) [LO 7093], LU 84 (t) [LO 7106], A 714? (c).

Occurrence. – *Raymondaspis (R.) insignis* n.sp. has been found in beds –10 and –6 at Skelbro, and in beds 5, 8 and 9 at Gårdlösa-4a, all of which belong to the *M. simon* Zone.

As far as can be established, the museum material also originates from the *M. simon* Zone. Samples LU 15 and LU

18 are from Andrarum, LU 51 is from Komstad and LU 84 is from Smedstorp. Sample LU 51 contains a characteristic fauna (*Cyclopyge*, narrow pygidium of *M. limbata* type 9), and is most likely from a level corresponding to bed –5 at Killeröd (= beds 6 and 7 at Gårdlösa-4a). Samples LU 15 and LU 18 contain *Nileus orbiculatooides* and *Niobe (Niobella) imparilimbata*.

Pygidium A 714 from bed M-5 at Slemmestad may belong to *R. insignis* n.sp., but cannot be confidently identified (poorly preserved). Bed M-5 is within the upper part of the *M. simon* Zone.

R. insignis n.sp. is currently not known from the central Baltoscandian Confacies Belt, but see remarks below.

Diagnosis. – Width across anterior and posterior fixigenae small; lateral glabellar furrows almost effaced; palpebral lobes large; anterior cranial border short (both ways, and in fact absent in front of glabella); anterior branches of facial suture converge in front of paradoublural line. Librigena strongly vaulted, unusually broad (tr.), with wide lateral border and short, gracile genal spine. Pygidium of *R. limbata* type, but relatively longer, and the dorsal terrace-line pattern is denser and more extensive.

Description. – Small to medium-sized for a *Raymondaspis*, largest cranidium (holotype) 4.5 mm long, largest pygidium 7.4 mm long. The description of the cranidium is based on the holotype specimen (Fig. 223A–C). Anterior margin of cranidium truncate, sagittal convexity very strong; FW:L ratio 1.24, which is a comparatively low value; PW:L ratio 0.98, which is also a low value. Glabella essentially as described for *R. (R.) scitula* n.sp. Posterior glabella width equivalent to 0.62 of the anterior (maximum) glabella width, which in turn accounts for 0.59 of the greatest preocular cranial width; glabellar occupies 0.82 of the cranial length. Lateral glabellar furrows (see *R. scitula* n.sp.) barely indicated by the terrace-line pattern; only the posterior composite pair (F1+F2) is very slightly impressed. Glabellar front shows shallow median impression (internal mould) immediately above preglabellar furrow; the external expression, if any, is unknown. Glabella delimited by well-impressed axial and preglabellar furrows; a pair of fossulae is situated in the axial furrows approximately one third of the glabella length from its front. Axial furrows diverge in front of eyes at an angle of about 15° to sagittal line. Occipital furrow moderately narrow, well-impressed throughout. Occipital ring as described for *R. scitula* n.sp. Anterior area of fixigena strongly inclined forwards; very faint paradoublural furrow runs from the fossula in the axial furrow and across fixigena to the cranial edge. Anterior border present on each side of glabella, it is short both ways because of the course of the facial suture; no border in front of glabella. Anterior margin gently swollen. Palpebral area of fixigena narrow (tr.), convex, sloping rather strongly adaxially; width of palpebral area, exclusive of palpebral lobe, equivalent to slightly more than 0.4 of the adjacent glabellar width. Palpebral lobes large,

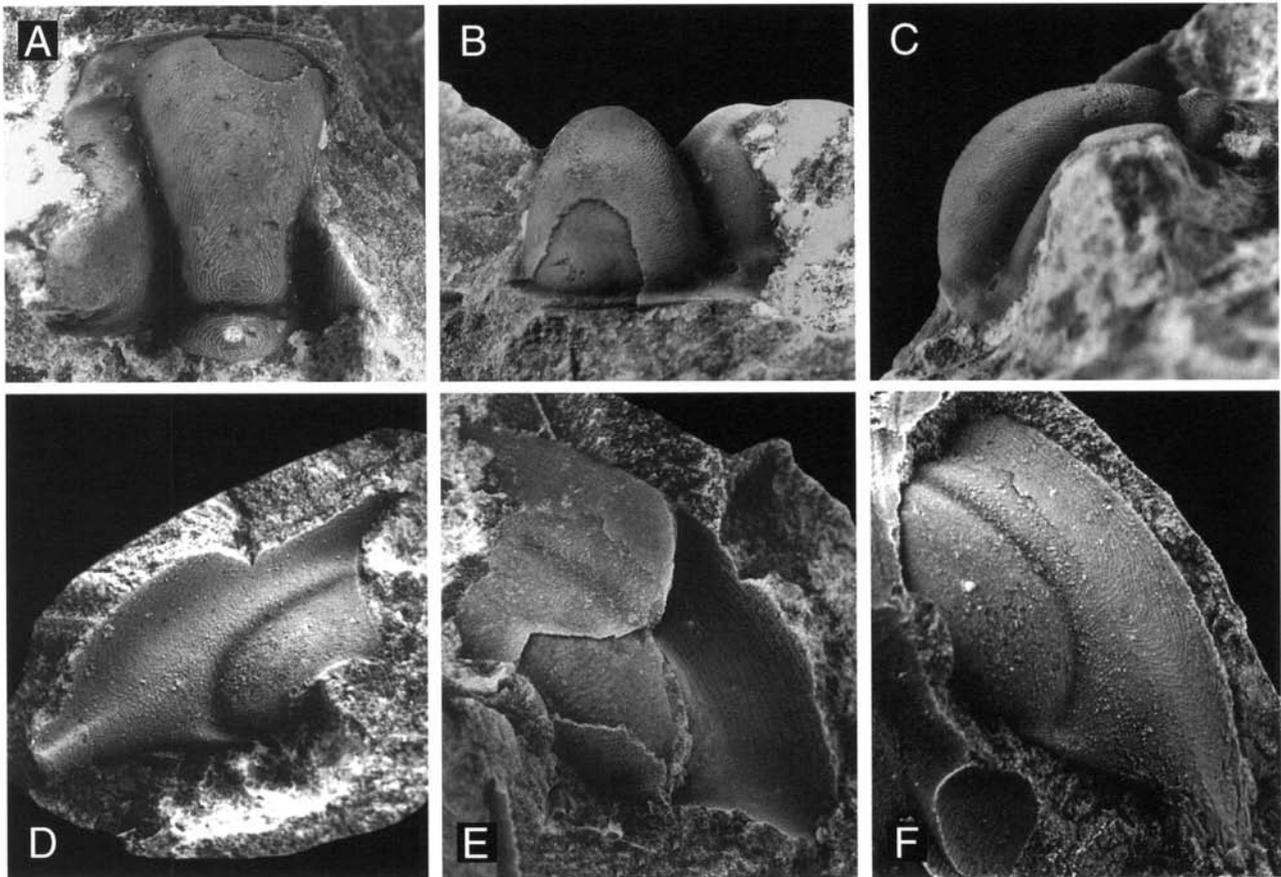


Fig. 223. *Raymondaspis (R.) insignis* n.sp. □A–C. Holotype. Cranium, slightly damaged, dorsal, frontal and side views, $\times 10$. LO 7086 (LU 27a), Tommarp. □D. Librigena (edge broken), $\times 10$. MGUH 22.949 (K 688), bed 8, Gårdlösa-4a. □E. Partly exfoliated librigena showing part of doublure, $\times 10$. MGUH 22.950 (K 714), bed 9, Gårdlösa-4a. □F. Same as E, latex cast of external mould showing external terrace-line sculpture, $\times 10$.

the length (exsag.) corresponds to 0.26 times the cranial length, distance to posterior margin of cranium from hind corner of lobe equals 0.12 times the cranial length, corresponding to 0.44 of the lobe length. Lobes slightly elevated above glabella; cranial width across lobes (tr.) corresponds to 1.13 of the cranial length. Eye ridges, as described for *R. scitula* n.sp., very faintly indicated, but they are probably better defined on exfoliated material. Posterior area of fixigena as described for *R. scitula* n.sp., but the gena is markedly shorter (tr.). Anterior branches of facial suture exhibit a most unusual course, as they diverge in front of the eyes, running straight forwards-outwards at an angle of slightly less than 25° to sagittal line, then turn inwards in front of the indistinct paradoublural furrow, converging straight forwards-inwards at an angle of about 155° to sagittal line. Suture must be marginal along main cranial front, as the swollen margin certainly represents the cephalic margin. Posterior branches of facial suture sigmoidal, running concavely backwards-outwards, then straighten to turn convexly backwards and intersect margin. Terrace-line pattern basically as described for *R. scitula* n.sp., except that the lines

on posterior part of glabella are concentric around a point, situated at some distance in front of occipital furrow, and the lines on occipital ring are concentric around a point situated immediately behind the tubercle. The swollen anterior rim is covered with continuous, fairly coarse lines. Fifteen to twenty terrace lines per millimetre were counted on the glabella of the holotype cranium, 4.5 mm long.

Librigena, excl. of the spine, almost twice as broad (tr.) as long (exsag.), somewhat sickle-shaped in outline and with a strong relief. Paradoublural furrow deepest posterolaterally, but present the whole way. Inner part, inside paradoublural furrow, comparatively narrow, convex, strongly ascending to eye, which is not preserved; eye socle low. Portion outside paradoublural furrow wide and concave, with an outer flattened part forming a fairly wide lateral border. The border is of almost uniform width all the way to genal spine, thence tapers backwards. Genal spine rather short, narrow, directed obliquely backwards at an angle of about 140° to sagittal line. Fine terrace lines, arranged roughly concentric around the eye, are present on inner part of librigena; the inner lines on the middle part of the border curve inwards (Fig. 223F),

whereas the lines on the outer part of the border run sub-parallel to margin. It appears that the area inside paradoublure furrow has a caecate mould surface. Doublure comparatively wide, concave, but only moderately strongly so. It is provided with about 20 faintly impressed terrace lines; below genal spine the lines curve inwards to follow the posterior margin. Lines most densely spaced close to outer margin.

Hypostome and thorax unknown.

Pygidium quite similar to *Raymondaspis limbata*, but is more elongate with L:W ratios varying between 0.56 and 0.63 (mean 0.60; $N = 6$). Axis also appears significantly longer judging by the eye, but because of the elongation of the pygidium the relative axial length is in fact equivalent to only 0.50–0.56 of the pygidial length (mean 0.53; $N = 6$). Axial width at anterior margin corresponds to 0.16–0.21 of the maximum pygidial width (mean 0.23; $N = 6$). Pygidium gently to moderately vaulted and almost semicircular in outline, which also relates to the elongation; concave border accounts sagittally for 0.16–0.21 of the length of pygidium (mean 0.19; $N = 6$), with a tendency of being relatively widest in the smaller pygidia. Compared to *Raymondaspis limbata* the dorsal terrace lines appear to be generally more prolific in *R. insignis* n.sp. and also present on the border; the lines on axis are more sharply bent backwards, V-shaped, not U-shaped as in *R. limbata*, and the lines on anterior part of pleural fields are shorter, irregular, but more abundant. Doublure of pygidium fairly strongly concave, wide, of uniform width throughout, the sagittal width corresponds to the pygidial length minus the length of axis. There is a very faint sagittal depression on the doublure, but virtually no axial embayment. Doublure provided with 17–18 faintly impressed, continuous terrace lines, most distinct close to inner margin. Lines slightly irregular in the sagittal area close to inner margin.

Affinities.—The pygidium of *R. (R.) insignis* n.sp. is rather like that of *R. (R.) limbata*, but the resemblance most likely reflects a shared wide doublure, which cannot be taken as a synapomorphy (several species with rather dissimilar cephalon show a wide pygidial doublure).

The cephalon of *R. insignis* n.sp. is characterized by a number of unique features, such as the size of the eyes, the anterior course of the facial suture, the terrace-line pattern, the stout and unusually broad librigena, and the species does not show obvious similarities to any described raymondaspid species, including non-Scandinavian taxa. One of the most similar species seems to be the slightly younger *R. (R.)*

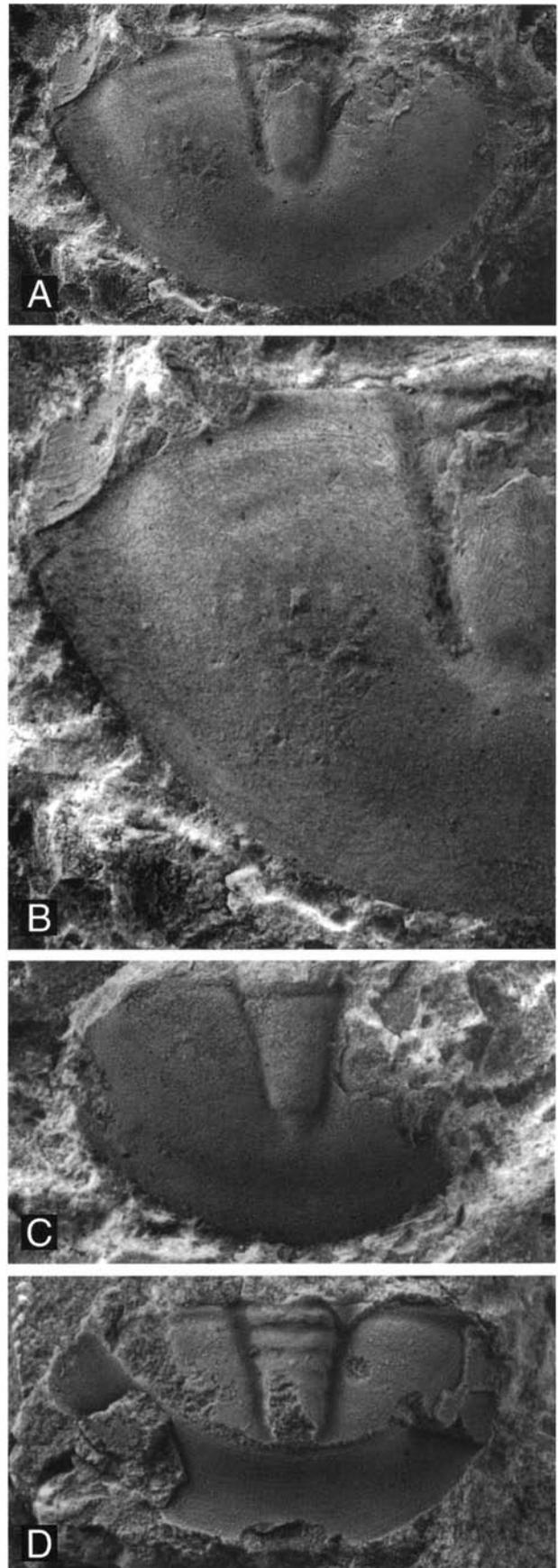


Fig. 224. *Raymondaspis (R.) insignis* n.sp. □A–B. Pygidium showing terrace-line sculpture, $\times 6$, close-up $\times 12$. LO 7106 (LU 84), Smedstorp, SE Scania. □C. Pygidium showing terrace-line sculpture, $\times 8$. MGUH 22.951 (S 865), bed –6, Skelbro. □D. Internal mould of pygidium showing doublure, $\times 8$. LO 7093 (LU 51), Komstad.

vespertina Ross, 1967, but that form has a facialsuture almost encircling the palpebral lobe, there is no anterior convergence of the facial suture, and the librigena is different.

Remarks. – *R. (R.) insignis* n.sp. appears to be characteristic of shallow-water facies within the *M. simon* Zone of the Komstad Limestone, and is expected to occur in the mainland of Sweden as well. It is possibly identical to *Raymondaspis limbata* subsp., listed from the *M. simon* Zone of Sweden by Tjernvik (1980, pp. 191, 192), but this is uncertain. The cranidium from 48.11 m in the Finngrundet core, called *Raymondaspis limbata* subsp. by Tjernvik (1980, p. 178), has a very slender glabella and does not represent *R. insignis* n.sp.; it looks more like *R. limbata*.

Raymondaspis (Raymondaspis?) sp. A

Fig. 225A–C

Material. – Fragmentary cranidium K 998 (pim) [MGUH 22.952].

Occurrence. – The specimen is from bed +18 at Killeröd, upper part of the *M. limbata* Zone.

Description. – Specimen fragmentary, about 7 mm long. PW:L ratio 1.05; sagittal convexity low, and glabella is comparatively little inflated for a *Raymondaspis*. Forward glabellar expansion small; posterior glabellar width almost 2/3 of the anterior (maximum) glabellar width, which in turn accounts for slightly less than half of the greatest preocular width of cranidium. Lateral glabellar furrows very faintly impressed on the internal mould and apparently indicated only by the terrace-line ornamentation on outside of test. The most remarkable feature of the cranidium, apart from the low glabella, is the broad anterior border, which sagittally accounts for about 0.1 of the cranidial length. Facial suture damaged, but anterior branches appear to be rather straight, diverging at an angle of ca. 20° to sagittal line in front of eyes. Anterior margin of cranidium not swollen, and it is unknown whether the suture is marginal or runs close to cephalic margin.

Remarks. – The cranidium presumably represents a new species. It may be compared to the North American *R. angelini* (Billings, 1862), which also has an exceptionally wide frontal area, and a moderately forwards expanding glabella with low relief (cf. Whittington 1965, p. 405; Pl. 56:11–13), but the Scanian specimen differs, e.g., by having a less pestle-shaped glabella.

Raymondaspis (Raymondaspis?) sp. B (cf. *limbata*)

Fig. 225D–F

Material. – Five cranidia, 1 librigena, and 3 pygidia.

List of material. – □Cranidia S 1761? (t), K 971 (t) [MGUH 22.954], GM 1987.24 (t), A 364 (em), A 388 (t) [MGUH 22.953]. □Librigena S 1617b? (t). □Pygidia S 1490? (t), S 1617? (t), K 929 (t) [MGUH 22.955].

Occurrence. – The material is from the lower part of bed +13 at Skelbro (top of the *M. limbata* Zone), from beds +15 and +16 at Killeröd (upper subzone of the *M. limbata* Zone), and from beds A-23 and A-26½ at Slemmestad (upper part of the *M. limbata* Zone). Specimen S 1761 is from a loose slab, Skelbro, presumably representing bed +10 (upper subzone of the *M. limbata* Zone). Cranidium GM 1987.24 is from Vasegård, and originates from the uppermost part of bed +13 (base of the *A. expansus* Zone).

Description. – Largest cranidium 9.3 mm long, largest pygidium 4.5 mm long. Anterior margin of cranidium evenly convex (dorsal view), moderately strongly so for a *Raymondaspis*; sagittal convexity very strong. FW:L ratio 1.44–1.46 ($N = 2$), PW:L ratio 1.06–1.08 ($N = 3$). Width across palpebral lobes large, corresponding to 1.17–1.22 of maximum preocular width (mean 1.20; $N = 3$). Glabella distinctly inflated, slightly overhanging anterior cranial margin, front rounded; basal circumference pyriform. Posterior glabellar width equivalent to 0.64–0.68 ($N = 3$) of anterior (maximum) glabellar width; maximum glabellar width accounts for 0.57–0.62 of the greatest preocular cranidial width (mean 0.60; $N = 4$); glabella occupies 0.82–0.85 ($N = 3$) of the cranidial length. Lateral glabellar furrow configuration as in *R. (R.) scitula* n.sp., outlined by absence of terrace lines, only the posterior double pair (F1+F2) is gently impressed. No mesial impression in glabellar front (test intact). A pair of well-defined fossulae situated in axial furrows 0.25 of glabella length from its front; a second pair of more indistinct depressions occurs in the axial furrows between level of posterior glabellar furrows and occipital furrow. Axial furrows converge very gently forwards from occipital furrow, then diverge from the posterior pair of lateral glabellar furrows, more strongly so in front of the eyes, there diverging at an angle of about 15–20° to sagittal line; axial furrows are shallow in front of the anterior pair of fossulae. Occipital furrow variably developed. The Norwegian specimen A 388 (Fig. 225D) has a pronouncedly curved occipital furrow, bending rearwards abaxially and provided with a pair of lateral shallow impressions; the furrow is narrowest and shallowest mesially. The occipital furrow is, on the contrary, deepest mesially and shallow up laterally in the cranidia from the Komstad Limestone. All specimens have a prominent, long (sag.) occipital ring, slightly raised above the rear part of glabella and carrying a small mesial tubercle. No paradoubtural furrow indicated on outside of test. Anterior border very narrow or absent; anterior margin gently swollen. Palpebral lobes situated posteriorly, distance from hind corner of lobe to posterior margin corresponds to 0.55 of the lobe length (exsag.), which is equal to about 0.13 of the cranidial length. Lobes moderately small, length (exsag.) equivalent to 0.19–0.23 of the cranidial length (mean 0.21; $N = 3$). Lobes

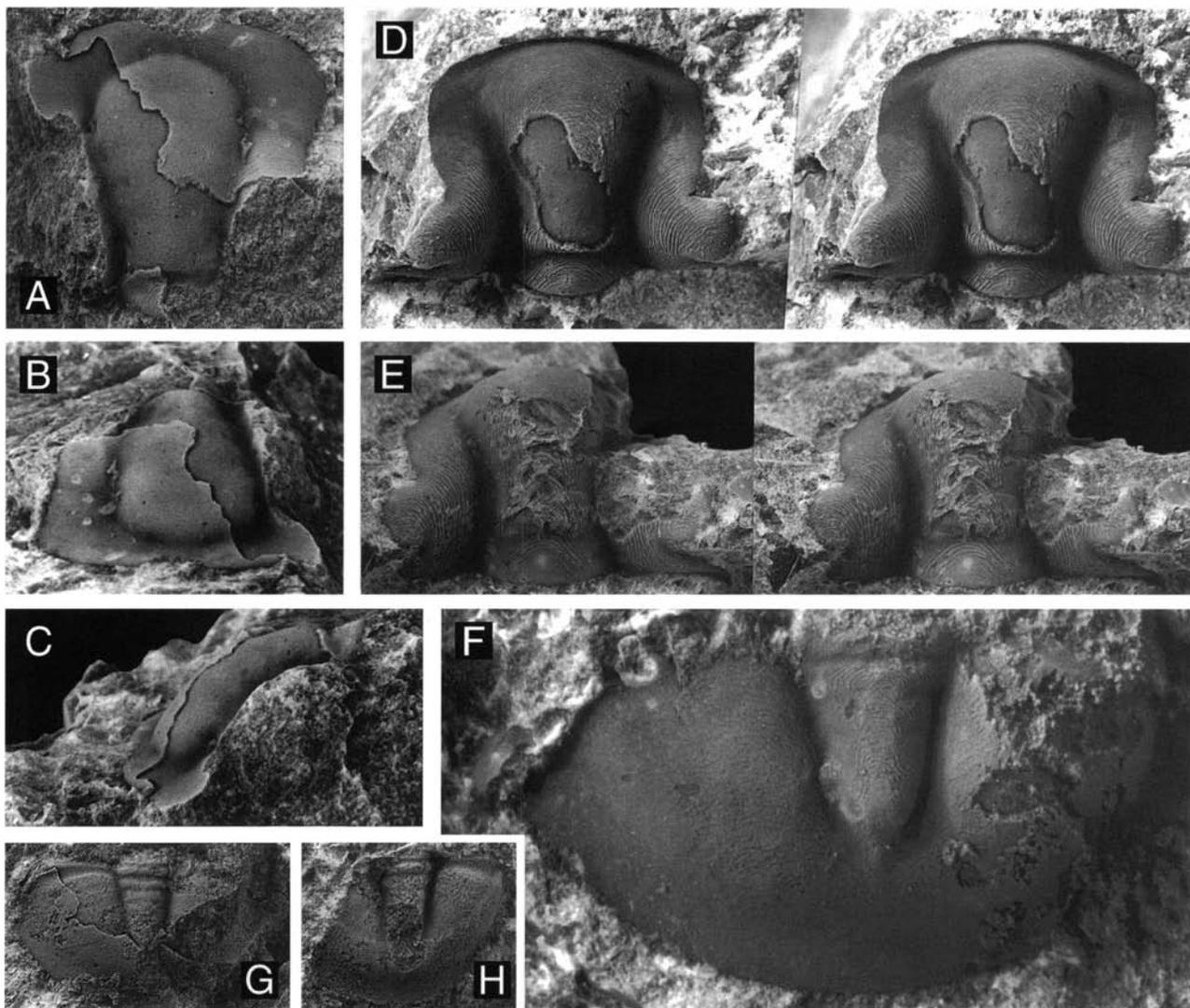


Fig. 225. □A–C. *Raymondaspis* sp. A, fragmentary, partly exfoliated cranidium, dorsal, frontal and side views, $\times 6$. MGUH 22.952 (K 998), bed +18, Killeröd. □D–F. *Raymondaspis* sp. B. □D. Cranidium, stereo-pair, $\times 6$. MGUH 22.953 (A 388), bed A-26½, Slemmestad. □E. Damaged cranidium, stereo-pair, $\times 6$. MGUH 22.954 (K 971), bed +16, Killeröd. □F. Slightly corroded pygidium, $\times 10$. MGUH 22.955 (K 929), bed +15, Killeröd. □G–H. *Raymondaspis* sp. C. □G. Fragmentary, partially exfoliated pygidium, $\times 5$. MGUH 22.956 (A 815a), bed M-7, Slemmestad. □H. Exfoliated, fragmentary pygidium, $\times 5$. MGUH 22.957 (A 815b), bed M-7, Slemmestad.

distinctly raised above the surface of glabella in the Norwegian specimens, less so in the cranidia from the Komstad Limestone. Posterior area of fixigena narrow (exsag.), long (tr.), pointed, and slopes rather strongly backwards for the whole of its length, distal tip turned rearwards. No external border furrow observed, but the material at hand contains no internal moulds. Anterior branches of facial suture diverge in front of eyes, but bend gently and evenly inwards all the way, so it is difficult to measure an angle of divergence; the strongest divergence, just in front of eyes, is in the size order of 15° to sagittal line. Immediately before anterior margin the facial sutures turn inwards and intersect the margin, thence run marginally. Posterior branch of facial

suture sigmoidal, descending concavely from palpebral lobe, then runs outwards, slightly obliquely backwards, being gently convex to turn more sharply backwards distally and intersects posterior margin. Surface sculpture apparent from illustrated specimens (Fig. 225D–E). Terrace lines are absent on the anterolateral part of fixigenae, in axial and preglabellar furrows, and on the lateral glabellar 'furrows'. Thirteen lines per millimetre were counted on anterior part of glabella, and 10 lines/mm were counted on the steep part of anterior fixigena in a 6.4 mm long cranidium.

A fragmentary small librigena, presumably matching the described cranidia, is sickle-shaped and shows a concave lateral border, gently tapering rearwards, but enters genal

spine. Genal angle drawn out into a long, moderately slender spine carrying a low ridge; the spine is directed obliquely backwards, probably at an angle of about 130° ($\pm 10^\circ$) to sagittal line. Inner part of gena not preserved.

Hypostome and thorax unknown.

The pygidia at hand are in general poorly preserved and fragmentary; for remarks on identification, see below. The description is based on specimen K 929 (Fig. 225F) unless otherwise stated. Pygidium subsemicircular in outline, rather strongly vaulted; L:W ratio 0.54. Axis somewhat funnel-shaped, stretching for 0.56 of the pygidial length; axial width at anterior margin equivalent to 0.23 of the maximum pygidial width. Axis distinctly arched, slightly raised above the pleural fields, most so posteriorly. The deep, wide axial furrows amplifies the arched appearance. Smaller pygidia from Skelbro show an even more distinctly inflated axis and shallower axial furrows. Anterior half-ring set off by a narrow furrow, the remaining axial segmentation is effaced (specimen testaceous). Axis continues into an indistinct, short postaxial ridge, which tapers out before the concave border. No segmentation of pleural fields; paradoublural line not indicated. Border gently concave, moderately wide, post-axially occupying 0.14 of the pygidial length. Articulating facets and dorsal surface sculpture as described for *R. (R.) imparilis*. Specimens S 1490 and S 1617 almost lack terrace lines, even on the pleural fields, but this may depend upon the small size of the specimens (ca. 2.5 and 3.5 mm long). About 15 lines/mm were counted on the pleural fields of pygidium K 929, 4.5 mm long, but the exact density is difficult to state as the lines are short and irregular. Doublure seems to be moderately broad.

Affinities. – *Raymondaspis* sp. B is distinguished from the other species of *Raymondaspis* described here by the comparatively strongly inflated glabella with rounded front (so the basal circumference is pyriform), by the very strong cranial convexity (sag.), by the absence of anterior border and paradoublural furrow, by the great width across palpebral lobes and posterior fixigenae, by the wide (sag.) occipital ring, and by the lack of a cephalic posterior border furrow. The pygidium is distinguished by the fairly high convexity, the funnel-shaped axis, the short, indistinct postaxial ridge, the terrace-line pattern and the concave border. The pygidium of *R. (R.) imparilis* is somewhat similar, but has a lower relief, the border is wider, the postaxial ridge is more distinct, and the doublure seems to be slightly wider.

Remarks. – The association of the described cranidia, librigena, and pygidia is uncertain. The cranidia from the Komstad Limestone, which originate from basically the same level as the librigena, exhibit a few minor differences from the Norwegian material. The latter cranidia have a slightly less convex anterior margin (dorsal view), the sagittal convexity is slightly less strong, the outline of the occipital furrow differs a little (see description), and the palpebral lobes are raised significantly higher above the surface of glabella (Fig.

225D–E). It is, accordingly, possible that the material is mixed.

The preserved parts of the described librigena closely resemble the librigena of *R. limbata* (cf. V. Poulsen 1969, Fig. 1B), except for the smooth test (the specimens are of equal size). The resemblance suggests that sp. B belongs to *R. (Raymondaspis)*, which is in accordance with the outline of the pygidia. The best preserved specimen (Fig. 225F) is very like *R. limbata* (compare V. Poulsen 1969, Fig. 2B), and differs mainly by having a slightly narrower concave border. The variation of this character is, however, unknown, but it is not likely to be an important feature for taxonomy. Hence it is possible that K 929 in fact belongs to *R. limbata*. However, the described cranidia clearly differ from *R. limbata*, e.g., by showing a much more anteriorly inflated glabella, a stronger sagittal convexity, higher raised palpebral lobes and no anterior border.

Raymondaspis (Raymondaspis?) sp. C

Fig. 225G–H

Material. – Two cranidia and 4 pygidia, all poorly preserved.

List of material. – □Cranidia A 800 (pc), A 812 (im). □Pygidia A 813? (c), A 815a (pim) [MGUH 22.956], A 815b (im) [MGUH 22.957], A 840 (c).

Occurrence. – The specimens are from bed M-7 at Slemmestad, base of the *M. limbata* Zone.

Remarks. – The very poorly preserved material does not match any established Scandinavian species. Tjernvik (1980, p. 192) listed *Raymondaspis limbata* ‘with a short pygidial axis’ from the *M. limbata* Zone of Sweden, but the pygidia at hand have a long axis and a relatively narrow border. By comparison to the lectotype of *R. limbata* the cranidia have a slightly stronger sagittal convexity and the glabella is more evenly expanding forwards, being club-shaped, less pestle-shaped.

Subgenus *Raymondaspis (Turgicephalus)* Fortey, 1980

Type species. – (OD) *Turgicephalus falcatus* Fortey, 1980.

Raymondaspis (Turgicephalus) *whittingtoni* n.sp.

Figs. 226–228

Synonymy. – □v 1919 *Ceratopyge* sp. – Funkquist, pp. 21, 39 (listed). □1950 *Raymondaspis limbatus* (Angelin, 1854) – Whittington, pp. 549–550; Pl. 72:11–14 (pygidia from Fågel-sång described, discussed and figured).

Derivation of name. – In honour of Dr. H.B. Whittington, who originally described the pygidium of this species.

Holotype. – Cranidium MGUH 22.958 (K 482) (Fig. 226A) from 2 cm below top of bed 1, Gårdlösa-4a (upper part of the *M. simon* Zone).

Paratype. – Pygidium MGUH 22.963 (S 1088) (Fig. 228A–B) from 2 cm above base of bed +1, Skelbro (lower part of the *M. limbata* Zone).

Additional material. – Nine cranidia, 2 librigenae and 32 pygidia.

List of additional material. – □Cranidia S 1130 (im) [MGUH 22.959], S 1163 (pc) [MGUH 22.961], S 1291 (em), S 1298 (c), K 228 (t), K 486 (t), K 599 (c), K 650 (c) [MGUH 22.960], LU 123 (c). □Librigenae K 776 (pim) [MGUH 22.962], IK P38b (t). □Pygidia S 778 (t) [MGUH 22.968], S 779 (t) [MGUH 22.964], S 809a (c), S 809b (c), S 826 (c), S 914 (t), S 923 (t), S 925 (t), S 932 (t), S 961 (t), S 965 (t) [MGUH 22.969], S 1054 (t), S 1090 (t), S 1093 (c), S 1095 (em), S 1114 (t), S 1143 (c), S 1166 (im) [MGUH 22.965], S 1300 (im), S 1648 (t) [MGUH 22.966], S 1659 (c), S 1683 (c), K 46 (t), K 99 (t), K 167 (im/c), K 222 (c), K 485 (t) [MGUH 22.967], K 503 (t), K 541 (t), K 646 (c), K 740 (c), K 759 (c).

Occurrence. – *R. (T.) whittingtoni* n.sp. ranges through the entire *M. simon* Zone and the lower half of the *M. limbata* Zone of the Komstad Limestone. It has been found in bed interval –12 to +7 at Skelbro, in bed interval 1 to 12 at Gårdlösa-4a, and in bed interval –8 to +7 at Killeröd. Pygidium S 1683 from Skelbro is not sampled *in situ*, but most likely comes from bed +9 or the lower part of bed +10, so *R. whittingtoni* n.sp. may range higher up than verified (i.e. into the basal part of the upper subzone of the *M. limbata* Zone). The new species was not encountered at Fågelsång; the sparse material described from this locality by Whittington (1950) presumably originates from the upper subzone of the *M. limbata* Zone. Cranidium LU 123 is from Komstad, most likely from an interval corresponding to beds –8 to –1 at Killeröd, i.e. the upper part of the *M. simon* Zone.

R. (T.) whittingtoni n.sp. is the dominant *Raymondaspis* species in the Komstad Limestone above the *M. polyphemus* Zone. So far, it has not been recorded outside the Komstad Limestone area.

Diagnosis. – Large species. Glabella of low relief, pestle-shaped; usually no anterior cranial border; anterior margin of cranidium rounded (dorsal view); genal angle rounded; cephalic terrace lines sparse. Pygidium quite convex, short; no concave border. Axis long, slender, inconsiderably raised above pleural fields, evenly tapering backwards. Surface sculpture of pygidium consists of a few vaguely impressed terrace lines on anterior portion of pleural fields close to axis. Doublure narrow (cephalon and pygidium).

Description. – Large for a *Raymondaspis*, largest cranidium 11.5 mm long, largest pygidium 14.8 mm long. Anterior margin of cranidium gently rounded (dorsal view), but comparatively strongly so for a *Raymondaspis*; margin slightly arched in frontal view. Cranidium markedly convex

sagittally; greatest width is across posterior fixigenae, measured to 1.29 times the cranial length in one specimen. PW:L ratio 1.09–1.28 (mean 1.19; $N = 7$) (all adult specimens); it is suspected that this range is enlarged by compaction. Width across palpebral lobes on the average equivalent to 1.04 ($N = 4$) times the maximum preocular width. Glabella well-defined, but comparatively little inflated, and a large portion of the palpebral area, including palpebral lobes, is elevated above glabella. Glabella almost reaches anterior margin of cranidium; ‘frontal area’ consists only of the furrow between glabella and the swollen margin. Glabella stretches for 0.84–0.90 of the cranial length (mean 0.87; $N = 7$); anterior (maximum) glabellar width accounts for 0.52–0.58 of the greatest preocular cranial width (mean 0.55; $N = 8$); posterior (minimum) glabellar width corresponds to 0.55–0.66 of the anterior glabellar width (mean 0.59; $N = 8$) (the variation is possibly enlarged by compaction). Glabella pronouncedly pestle-shaped as the anterior part expands strongly in front of palpebral area (axial furrows diverge at an angle of about 25–30° to sagittal line) and the front is truncate. A shallow, wide, median depression is present in glabella front. Four indistinct pairs of lateral glabellar furrows are arranged in a configuration identical to the one described for *R. scitula* n.sp.. The furrows are, however, barely impressed and may be difficult to discern even on internal moulds. Occipital furrow fairly wide and comparatively shallow, but impressed throughout, joining the axial furrows. Occipital ring comparatively long, mesially slightly expanded, carrying a tubercle; it is approximately of the same height as the rear part of glabella. A pair of distinct fossulae occurs in the axial furrows approximately 0.2 times the glabella length from its front; the axial furrows are shallower and less well-defined in front of the fossulae. A second pair of depressions are situated in the axial furrows level with palpebral lobes. Anterior area of fixigena strongly inclined forwards; no paradoublure furrow. Typically no anterior border, or the foremost part of fixigenae shows an insignificant change in steepness; two cranidia have a very narrow flattened border on each side of glabella. Anterior margin of cranidium swollen. Width of palpebral area exclusive of the palpebral lobe equivalent to about 0.6–0.7 of the adjacent glabellar width. Palpebral lobes situated posteriorly, distance (exsag.) from posterior corners to posterior margin of cranidium approximately equivalent to 0.15 of the cranial length; lobe length (exsag.) varies between 0.18 and 0.23 of the cranial length (mean 0.21; $N = 4$). The lobes are comparatively highly elevated above the surface of glabella. Eye ridges faint on internal moulds and may even be vestigial; they are effaced on testaceous material. Posterior fixigenae intact in only one specimen; they are long (tr.), narrow, distal tip bent backwards; inner part quite strongly convex, sloping backwards-inwards. A faint posterior border furrow is indicated on the middle part; it shallows up in both directions. It is suspected that larger cranidia lack the border furrow. Anterior branches of facial suture diverge in front of palpe-

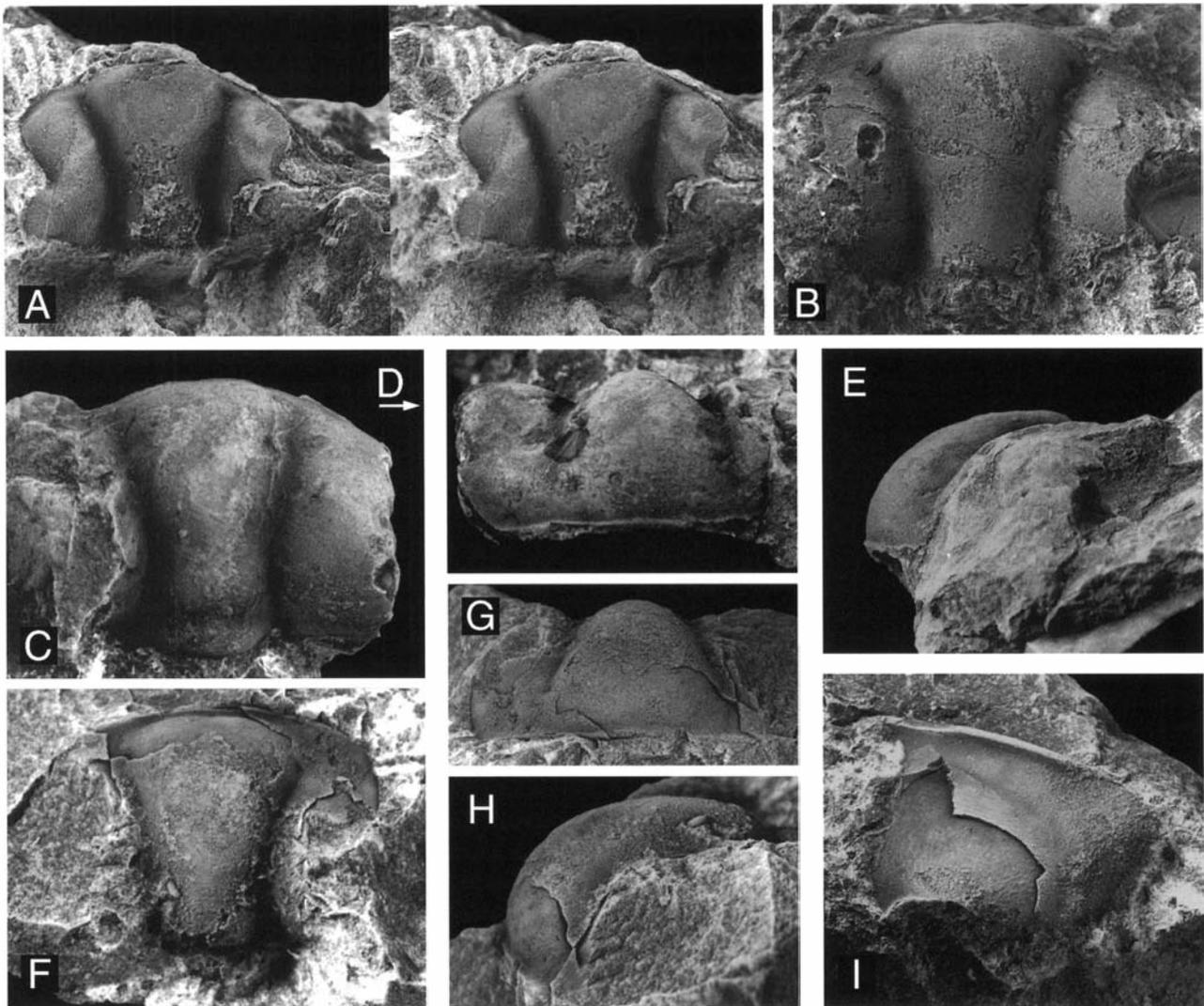


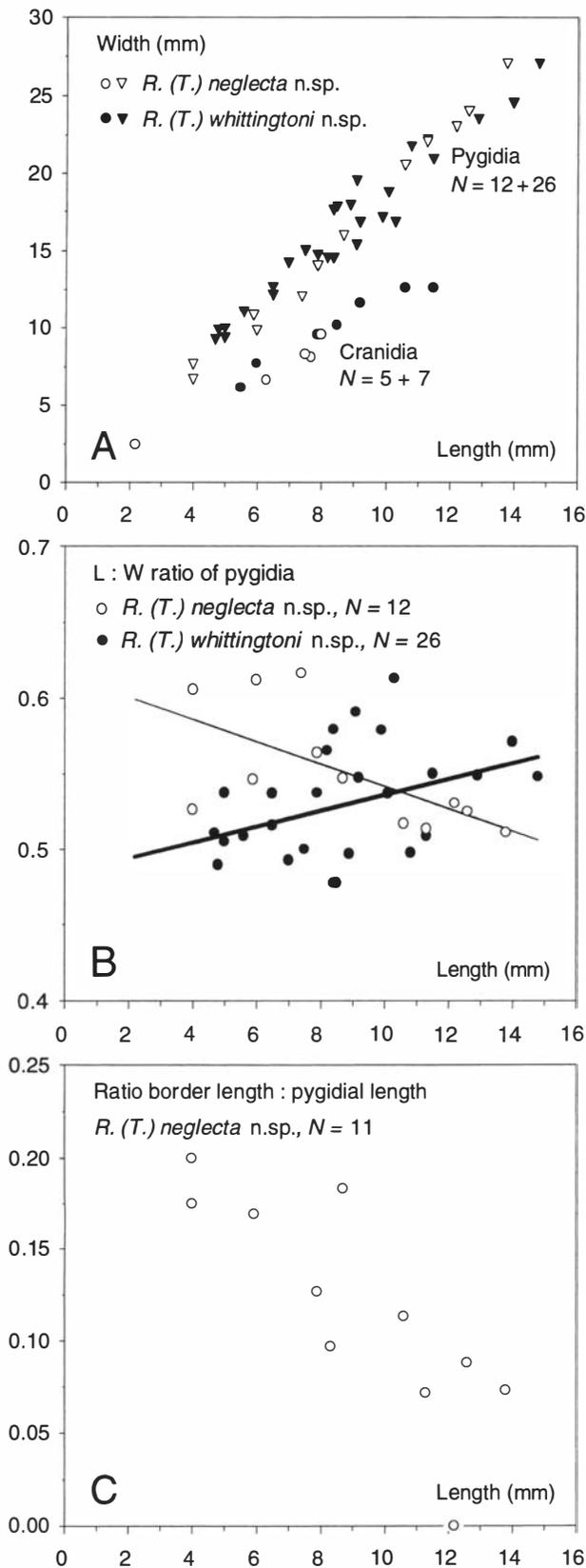
Fig. 226. *Raymondaspis (T.) whittingtoni* n.sp. □A. Holotype. Slightly corroded cranium, stereo-pair, $\times 5$. MGUH 22.958 (K 482), bed 1, Gårdlösa-4a. □B. Exfoliated, slightly damaged cranium, $\times 5$. MGUH 22.959 (S 1130), bed +3, Skelbro. □C-E. Exfoliated, slightly damaged cranium, dorsal, frontal and side views, $\times 5$. MGUH 22.960 (K 650), bed 7, Gårdlösa-4a. □F-H. Corroded cranium, dorsal, frontal and side views, $\times 5$. MGUH 22.961 (S 1163), bed +3, Skelbro. □I. Partly exfoliated librigena, $\times 6$. MGUH 22.962 (K 776), bed 12, Gårdlösa-4a.

bral area at an angle of about 25° to sagittal line, then, after intersection with paradoublural line, curve gently inwards. The suture is most likely marginal in front of glabella, as the swollen anterior rim must be the margin of cephalon. Fine terrace lines are present on the cranium, arranged in a pattern similar to the one described for *R. scitula* n.sp., but the lines are less densely spaced. Twelve to fourteen lines per millimetre were counted on glabella in a cranium approximately 5.7 mm long, and 8–9 lines/mm were counted on glabella in a cranium 11.6 mm long; the lines are less dense on the anterior fixigenae. The swollen anterior rim carries coarse, continuous terrace lines.

Librigena slightly broader (tr.) than long (exsag.), semi-parabolic in outline (Fig. 226I). No paradoublural furrow

anteriorly, but a furrow, or rather terrace is indicated rearwards. Inner part of gena raises to the eye, most steeply so anteriorly; eye socle very low, visual surface strongly arcuate, with about 8 lenses per dorso-ventral file. Outer part of librigena widens backward; a narrow lateral border is defined anteriorly, it tapers backwards and does not reach genal angle; outer margin distinctly swollen. Genal angle rounded. Widely spaced terrace lines are arranged roughly concentric around the eye on the inner part. Continuous lines also occur on the marginal rim, while the remaining test surface is smooth. A faint caecate pattern is indicated on the mould surface of the inner part. Doublure not exposed, but must be comparatively narrow.

Hypostome and thorax unknown.



Pygidium reniform in outline, distinctly convex (sag.), about twice as wide as long, L:W ratio 0.48–0.61 (mean 0.53; $N = 26$; see Fig. 227B). Anterolateral corners truncately rounded. Axis occupies about 0.59–0.67 of the pygidial length (mean 0.62; $N = 26$); the length is difficult to determine as the axis tapers gently and continues into a postaxial ridge. This narrow ridge is of very low relief, tapers, but continues to the posterior margin; it is normally defined only on internal moulds, but large specimens may show an external ridge. Anterior axial width corresponds to 0.16–0.23 of the maximum pygidial width (mean 0.19; $N = 25$). Axis inconsiderably elevated above pleural fields, posterior part is actually below the level of the adjacent pleural fields in a few specimens. Axis comprises articulating half-ring and at least 7, presumably 8, axial segments, including the acuminate terminal piece, but only the first 2 rings plus the articulating half-ring are clearly defined, the remaining are nebulous on internal moulds and virtually effaced on testaceous material, except in exceptionally preserved specimens. Axial furrows deep and wide, but shallows up at intersection with paradoublural line. Pleural fields show anterior halfrib, delimited by wide, fairly well-impressed furrow; no segmentation is otherwise apparent on testaceous material, but 4 or 5 pleural segments are indicated on a few internal moulds (Fig. 228E), primarily by a faint reticulate pattern, the relief is negligible. The pattern terminates at paradoublural line. Pygidium fully convex, except for a single pygidium from Scania, which shows a narrow, steep posterior border. Articulating facets comparatively small, triangular, the posterior parts are rising somewhat above the pleural fields. The facets are rather steeply downsloping anterolaterally, oblique, situated at an angle of about 140–145° to sagittal line. Dorsal terrace lines sparse. Isolated, vaguely impressed terrace lines, running subparallel to margin, typically occur on the adaxial anterior part of the pleural fields, turning backwards close to the axis, following the axis for some length (Fig. 228I). Rearwards opening U-shaped terrace lines occur on the anterior part of axis; posteriorly the lines become effaced mesially (Fig. 228B). A few specimens show scattered lines behind the axis, running subparallel to margin on the convex 'border'. The bulk of the pygidial surface, including the main part of the pleural fields, is smooth in all but one specimen (Fig. 228C–D). This pygidium, found in the basal part of the *M. simon* Zone, has a more extensive terrace-line pattern, with widely

Fig. 227. *Raymondaspis whittingtoni* n.sp. (closed symbols) and *R. neglecta* n.sp. (open symbols). □A. Maximum width plotted against sagittal length of crania and pygidia. □B. Ratio between sagittal pygidial length and maximum pygidial width plotted against pygidial length. □C. Ratio between pygidial border length (sag.) and sagittal pygidial length plotted against pygidial length. (*R. neglecta* only).

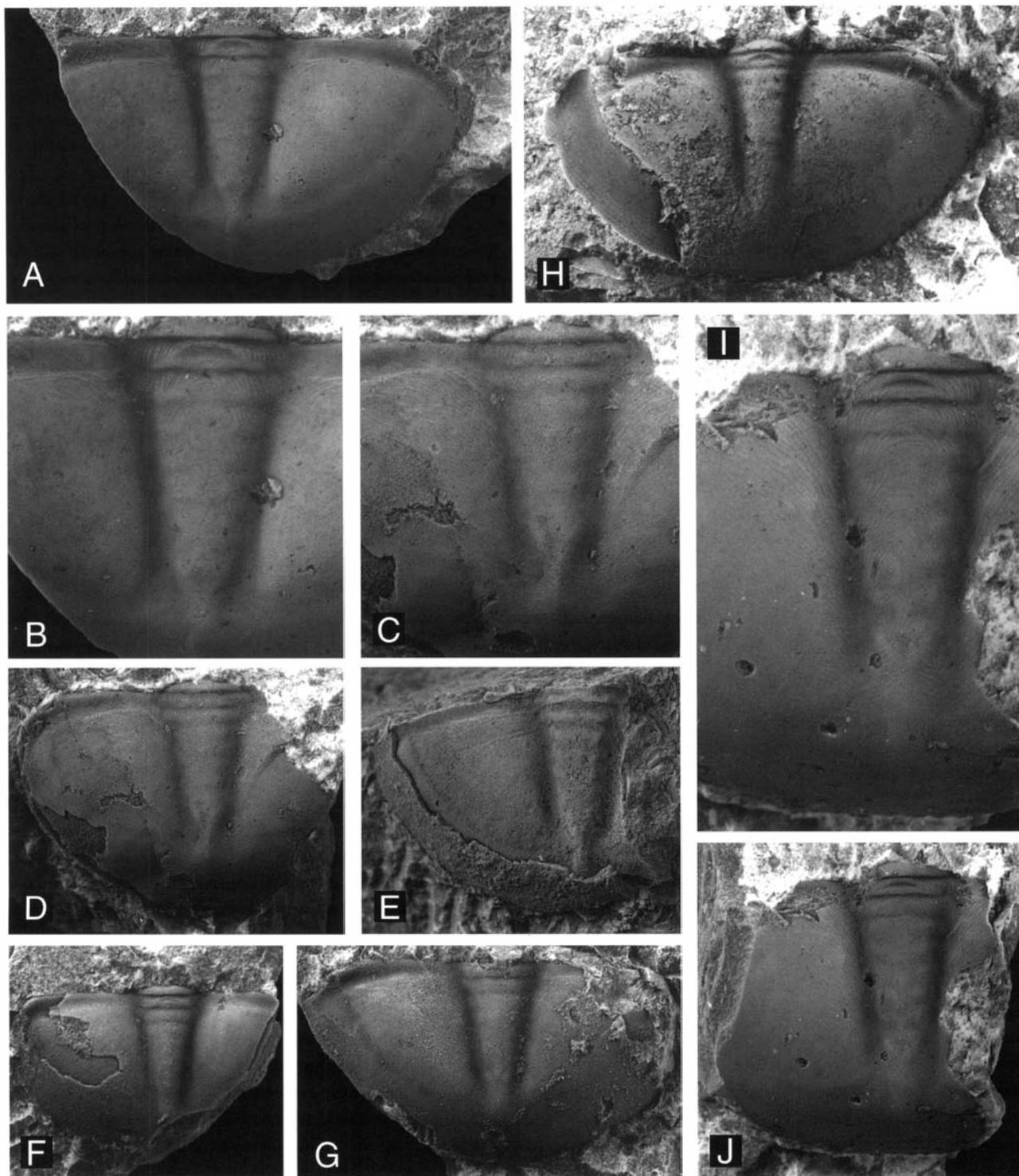


Fig. 228. *Raymondaspis (T.) whittingtoni* n.sp. □A–B. Paratype pygidium, $\times 5$; close up shows the sparse external terrace lines, $\times 8$. MGUH 22.963 (S 1088), bed +1, Skelbro. □C–D. Atypical pygidium almost covered with terrace lines, $\times 5$; close up $\times 8$. MGUH 22.964 (S 779), bed –12, Skelbro. □E. Exfoliated pygidium showing reticulate pattern on pleural fields, $\times 3$. MGUH 22.965 (S 1166), bed +3, Skelbro. □F. Small, fragmentary pygidium, $\times 6$. MGUH 22.966 (S 1648), bed 0, Skelbro. □G. Pygidium, $\times 5$. MGUH 22.967 (K 485), bed 1, Gårdlösa-4a. □H. Internal mould of pygidium showing part of doublure, $\times 5$. MGUH 22.968 (S 778), bed –12, Skelbro. □I–J. Fragmentary pygidium with well-preserved cuticle showing moderately abundant external terrace lines, $\times 5$; close up $\times 8$. MGUH 22.969 (S 965), bed –4, Skelbro.

spaced fine terrace lines covering the entire pygidial surface. The lines run obliquely inwards-backwards on the pleural fields, are U-shaped on the axis, and run subparallel to outer margin on the convex 'border'. In the other end of variation range a few small specimens appear to lack terrace lines altogether. Doublure gently concave, rather steeply sloping, comparatively narrow, and approximately of equal width all the way. It is provided with 20–21 fine, semi-continuous terrace lines (counted posterolaterally). Doublure width corresponds to the pygidial length minus the axial length; inner limit of doublure is indicated on dorsal surface by a very shallow paradoublural furrow.

Affinities. – The strong cephalic convexity (sag.), the glabellar shape, the absence of a cephalic border, the rounded genal angle and the slender pygidium with small articulating facets indicate that the new species should be attributed to *R. (Turgicephalus)*.

Compared to *Raymondaspis (T.) neglecta* n.sp., *R. (T.) whittingtoni* n.sp. has a more convex (dorsal view), pronouncedly swollen anterior cranial margin, the sagittal cephalic relief is stronger, the anterior lobe of glabella is less inflated, but more strongly forwards expanding, pestle-shaped, not club-shaped, the genal angle is more rounded, the pygidium is without border, so the L:W ratio is typically also lower, and the axis is comparatively longer. Despite these differences, the two forms are rather similar and *R. neglecta* n.sp. is a plausible ancestor of *R. whittingtoni* n.sp..

Among non-Scandinavian representatives of *Turgicephalus*, viz. *R. (T.) turgida* Whittington, *R. (T.) falcatus* (Fortey) and *R. (T.) hinloppensis* (Fortey), the new species most closely resembles *R. (T.) turgida*, e.g., with respect to border morphology and outline of the librigena. *R. (T.) whittingtoni* n.sp. is distinguished by the different cephalic terrace-line pattern, the less distinctly indicated anterior fossulae, the less impressed composite posterior pair of lateral glabellar furrows, the longer and narrower pygidial axis and the much more restricted pygidial terrace-line pattern.

Raymondaspis arcuata Dean, 1971, presumably also belongs to *R. (Turgicephalus)*, but the poor preservational state of the type material is an impediment to a detailed evaluation.

Compared to *R. (R.) imparilis* and *R. (R.) scitula* n.sp., *R. (T.) whittingtoni* n.sp. is appreciably larger, the glabella is more strongly forward-expanding and less vaulted, an anterior cranial border is absent, the anterior cranial margin is more rounded (dorsal view), the palpebral area of fixigena is broader, the genal angle is blunt, and the pygidium is more slender, lacks a concave border, and the axis nearly level with the pleural fields. Besides, there are differences in the terrace-line pattern of the pygidium, at least by comparison to *R. (R.) imparilis*. The majority of these differences also apply to *R. (R.) limbata* vs. *R. (T.) whittingtoni*; besides, the doublure (cephalon, pygidium) of the latter is narrower.

Remarks. – Funkquist's (1919) surprising report of *Ceratopyge* in the Komstad Limestone was based on a tiny (<4 mm long), rather poorly preserved cranidium of *R. (T.) whittingtoni* n.sp. (here numbered LU 123) from Komstad.

Raymondaspis (Turgicephalus) neglecta n.sp.

Figs. 227, 229

Synonymy. – □v aff. 1952 *Raymondaspis limbatus* (Angelin, 1854) – Skjeseth, pp. 171–172; Pl. 4:16, 17, 19–21 (description and illustrations of cranidia and pygidia, discussion of occurrence). □v aff. 1955 *Raymondaspis limbatus* (Angelin, 1854) [*partim*] – Skjeseth, p. 21; Pl. 5:6, 8 (description, illustrations of cranidium and pygidium, discussion of occurrence and phylogeny). □? 1956 *Raymondaspis* sp. no. 2 – Tjernvik, p. 263 (brief characteristic of pygidium, occurrence). □v 1965 *Raymondaspis limbata* (Angelin, 1854) [*partim*] – V. Poulsen, p. 87; Pl. 6:1–4 (description and illustrations of cranidium and pygidium). □ 1971 *Raymondaspis* sp. – Neben & Krueger, Pl. 13:13 (illustrations of pygidium).

Derivation of name. – Latin *neglectus* = neglected, overlooked.

Holotype. – Cranidium MGUH 22.971 (S 234) (Fig. 229B) from 3.5 cm below top of bed –20, Skelbro (base of the *M. polyphemus* Zone).

Paratype. – Pygidium MGUH 9449 (Fig. 229I) from the Skelbro Beds, most likely bed –21, Skelbro (base of the *M. polyphemus* Zone). Previously figured by V. Poulsen (1965, Pl. 6:4).

Additional material. – Nine cranidia, 1 librigena, and 17 pygidia.

List of additional material. – □Cranidia S 394 (t) [MGUH 22.970], S 448 (im), S 588a (im), S 588b? (t), S 595-5? (c), S 629? (t), S 717? (t), S 757 (t) [MGUH 22.972], GM 1936.87 (im). □Librigena IK P25d (t) [MGUH 22.973]. □Pygidia S 383 (im) [MGUH 22.977], S 387 (c), S 390 (im) [MGUH 22.975], S 417a (im) [MGUH 22.976], S 417b (im), S 472 (im), S 576 (c), S 595-4 (t), S 670 (im) [MGUH 22.974], S 699 (im), S 708 (c), GM 1948.5 (im), GM 1988.15 (c), IK P25a (im), IK P25b (c), IK P25c (im), IK P29 (im).

Occurrence. – *R. (Turgicephalus) neglecta* n.sp. is typical of the upper part of the *M. polyphemus* Zone at Skelbro, bed interval –19 to –14, but ranges from the base of the zone (bed –21). The bulk of the museum material studied originates from bed interval –19 to –14 of Skelbro, but cannot be assigned precisely to specific beds.

R. (T.) neglecta is currently not known from outside Bornholm, but a close form occurs in the Herram Member of Ringsaker (*M. estonica* or *M. polyphemus* Zone), southern Norway (see discussion below).

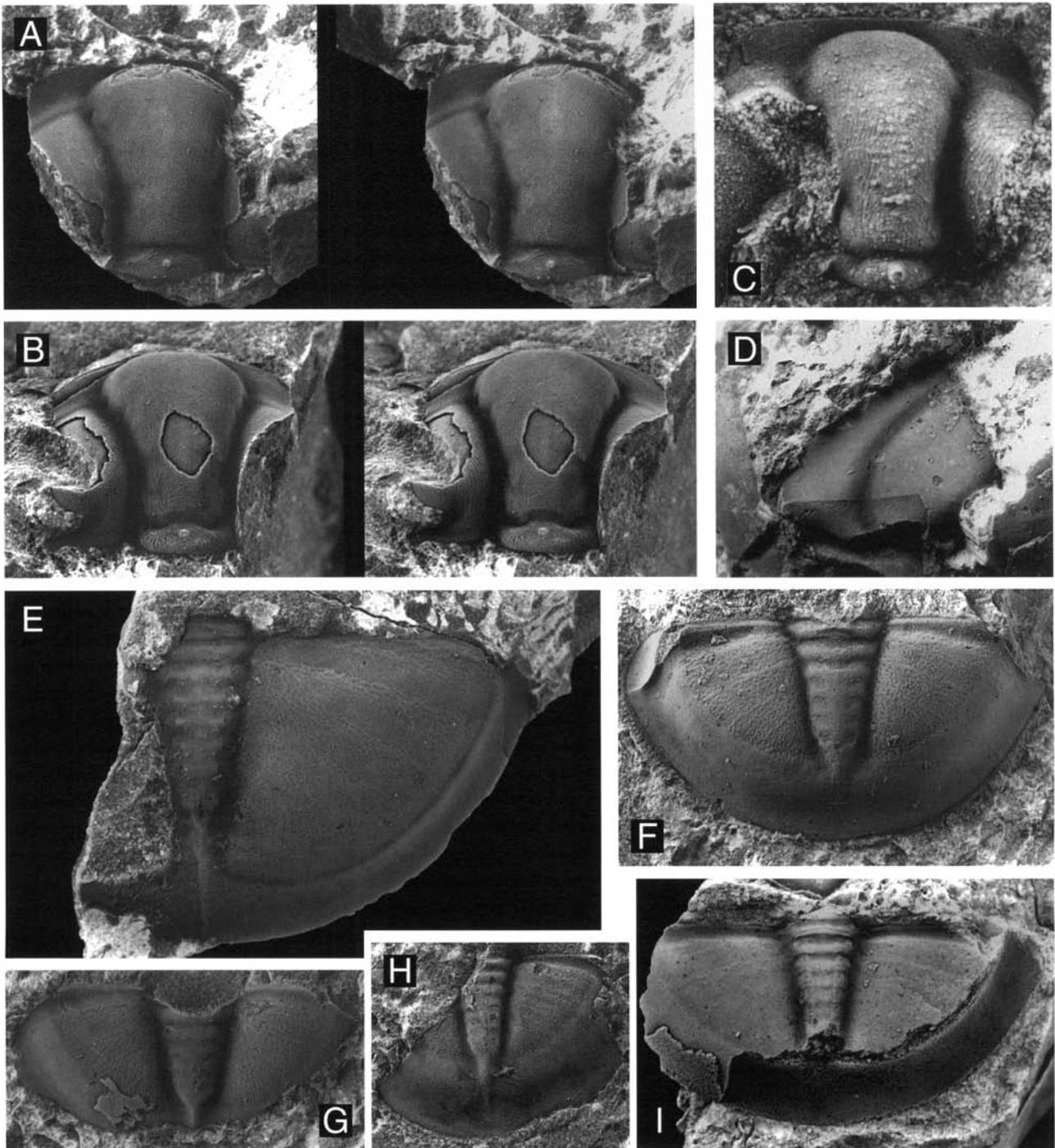


Fig. 229. *Raymondaspis (T.) neglecta* n.sp. □A. Cranidium, stereo-pair, $\times 5$. MGUH 22.970 (S 394), bed -20, Skelbro. □B. Holotype. Cranidium, stereo-pair, $\times 5$. MGUH 22.971 (S 234), bed -20, Skelbro. □C. Juvenile cranidium, $\times 10$. MGUH 22.972 (S 757), bed -14, Skelbro. □D. Exfoliated librigena, $\times 5$. MGUH 22.973 (IK P-25d), Skelbro. □E. Exfoliated large pygidium, almost lacking a concave border, and showing reticulate pattern on pleural fields, $\times 5$. MGUH 22.974 (S 670), bed -16, Skelbro. □F. Exfoliated medium-sized pygidium showing fairly wide concave border, $\times 5$. MGUH 22.975 (S 390), bed -19, Skelbro. □G. Fragmentary, exfoliated pygidium showing reticulate pattern on pleural fields, $\times 5$. MGUH 22.976 (S 417a), bed -16, Skelbro. □H. Exfoliated small pygidium showing wide concave border, $\times 5$. MGUH 22.977 (S 383), bed -19, Skelbro. □I. Paratype. Internal mould of pygidium showing doublure, $\times 5$. Previously figured by V. Poulsen (1965, Pl. 6:4). MGUH 9449, Skelbro beds, Skelbro.

Diagnosis. – Like *R. (T.) whittingtoni* n.sp., but glabella is less forward-expanding and stronger inflated; anterior cranial border defined; cephalic terrace-line pattern denser; pygidia show a concave border, which, though, diminishes in distinctness during growth, and the largest pygidia are fully convex; pygidia tend to be more elongate than those of *R. (T.) whittingtoni* n.sp.

Description. – Medium-sized to large for a *Raymondaspis*, largest cranidium 8 mm long, largest pygidium 13.8 mm long. *R. (T.) neglecta* n.sp. is rather similar to *R. (T.) whittingtoni* n.sp., and the description focuses primarily on the differences between these species. Comparing the cranidia, *R. neglecta* n.sp. has a less forward expanding, slightly more inflated glabella, the cranial convexity (sag.) is less pronounced, the anterior margin is less or not swollen, and less convex in dorsal view and may even be rather truncate, there is an anterior border of variable width, and the paradoublural furrow is visible also on testaceous specimens; the palpebral area excl. of palpebral lobes is narrower (tr.), the occipital furrow shows lateral depressions, and the external terrace-line ornamentation is denser and slightly better impressed. Thirteen to sixteen lines per millimetre were counted on glabella in a couple of cranidia, 8 mm long. FW:L ratio 1.21 in one specimen; PW:L ratio 1.05–1.20 (mean 1.11; $N = 4$), the variation is not size related. Width across palpebral lobes about 1.05–1.06 ($N = 2$) of the maximum preocular cranial width; frontal lobe of glabella occupies 0.52–0.60 of the cranial preocular width (mean 0.55; $N = 4$), and glabella stretches for 0.83–0.91 of the cranial length (mean 0.86; $N = 4$). Minimum posterior glabellar width equivalent to 0.60–0.62 ($N = 4$) of the maximum glabellar width. Length of palpebral lobe not revealed by the material. A couple of minute cranidia, 1.4 and 2.2 mm long, closely resemble the adults and differ only by having more strongly inflated glabellas, stronger cranial convexities (sag.) and a more truncate margin (Fig. 229C).

Available librigena (Fig. 229D) slightly impaired, but appears similar to that of *R. (T.) whittingtoni* n.sp., except for a marginally better defined paradoublural furrow anteriorly. Main part of specimen exfoliated; the mould surface is smooth.

The most distinct difference between the pygidia of *R. (T.) whittingtoni* n.sp. and *R. (T.) neglecta* n.sp. is the presence of a concave border in the latter. However, the border becomes increasingly steeper and relatively narrower with increasing size (Fig. 227C), and the largest pygidia lack a border and are exceedingly like pygidia of *R. (T.) whittingtoni* n.sp. Because of the presence of a border, the pygidia of *R. (T.) neglecta* n.sp. tend to be relatively longer than those of *R. (T.) whittingtoni* n.sp., L:W ratios varies between 0.51 and 0.62 (mean 0.55; $N = 12$), and axis is therefore generally relatively

shorter, stretching for 0.52–0.63 of the pygidial length (mean 0.58; $N = 13$). Axis occupies at anterior margin 0.17–0.24 of the pygidial maximum width (mean 0.20; $N = 13$); the variation does not reflect preservational distortion. All testaceous pygidia are poorly preserved, but external terrace-line ornamentation appears very limited and is presumably identical to that of *R. (T.) whittingtoni* n.sp.

Affinities. – *R. (T.) neglecta* n.sp. is a likely ancestor of the succeeding *R. (T.) whittingtoni*. Both species are large, glabella is of comparatively low relief, anterior border of cranidium is narrow or not defined, the cranial terrace-line ornamentation is rather dispersed, the librigenae are very similar, and the pygidia exhibit a sparse terrace-line ornamentation. Large pygidia of the two species are similar for all practical purposes. Differences are highlighted in the description above.

Librigena and pygidium of *R. neglecta* n.sp. is of typical *Turgicephalus* outline, whereas the cranidium is rather *Raymondaspis*-like. The species is possibly an early member of *Turgicephalus*, close to the split from *Raymondaspis*.

Compared to the associated *R. (R.) scitula* n.sp. and *R. (R.) imparilis*, *R. (T.) neglecta* n.sp. is larger, the glabella is less distinctly vaulted, the anterior border is narrower, the cranial terrace-line ornamentation is less dense, the genal angle is blunt, and the pygidial border is narrower or even absent. Besides, it appears that the pygidial terrace-line ornamentation is very sparse in *R. neglecta* n.sp. Most of these differences also apply to *Raymondaspis (T.) neglecta* n.sp. versus *R. (R.) limbata*.

Remarks. – The paratype pygidium of *R. neglecta* n.sp. was described and figured by V. Poulsen (1965, p. 87; Pl. 6:4), who assigned it to *R. limbata*. The associated cranidium, figured by V. Poulsen (Pl. 6:1–3), is probably from bed –20.

The material from Herramb, identified with *R. limbata* by Skjeseth (1952, 1955), is clearly related to *R. (T.) neglecta* n.sp., but the pygidia are unusually short and have numerous terrace lines on the pleural fields. The cranidium is poorly preserved (Skjeseth 1952, Pl. 4:19–20), but has a wide (tr.) palpebral area, in this respect resembling *R. (T.) whittingtoni* n.sp. *R. limbatus sensu* Skjeseth was considered identical to the so-called *Raymondaspis* sp. no 2 by Tjernvik (1956, p. 263), hence this old form may also be related to *R. (T.) neglecta* n.sp.

Genus *Hallanta* Poulsen, 1965

Type species. – (OD) *Hallanta modesta* Poulsen, 1965.

Remarks. – See V. Poulsen (1965, p. 83) and Příbyl & Vaněk (1971) for a discussion of genus.

Hallanta cf. *modesta* Poulsen, 1965

Fig. 230.

Synonymy. – □ v cf. 1965 *Hallanta modesta* n.sp. – V. Poulsen, pp. 84–85; Pl. 5:8–12 (description, occurrence, illustrations of cranidia).

Holotype. – Cranidium MGUH 9446, figured by V. Poulsen (1965, Pl. 5:8–10).

Material. – Two cranidia (internal moulds; specimens S 980 and S 1758 [MGUH 22.978]). The material originally described by Poulsen (1965) has also been examined.

Occurrence. – Both specimens are from Skelbro, S 980 is from bed –4 (*M. simon* Zone), and S 1758 is from a loose slab. The latter in all probability originates from bed –20 (lower part of the *M. polyphemus* Zone), judging from the lithology and associated trilobites, notably *Nileusexarmatus*. *Hallanta modesta* has previously been described from beds –21 and –20 by V. Poulsen (1965).

During the present study no specimens referable to *Hallanta* were found in Scania. Funkquist (1919, Pl. 2:8) figured a ‘head of trilobite’ from Komstad, which may represent *Hallanta*. According to V. Poulsen (1965, p. 85), who examined the specimen, the preservation is insufficient for detailed study, but it may represent a new species, characterized by a slightly less truncate glabella.

Remarks. – For description, see V. Poulsen (1965, pp. 84–85), although both specimens are slightly different from his material, and they may belong to a new species, or, alternatively and more likely, *H. modesta* is more variable than hitherto recognized. The differences regard the glabella, which expands just slightly more in anterior direction, the glabellar front is less truncate and exhibits a shallower median impression. The anterior part of the cranidia is difficult to prepare (the matrix adheres to the test), which renders observation difficult, but it appears that the anterior cranial margin is slightly more convex in dorsal view, with only a faint median introflexion, and the lateral anterior border is even narrower than in *H. modesta*.

There are also differences between the two specimens described by V. Poulsen (1965). Specimen MGUH 9447 (Poulsen 1965, Pl. 5:11–12) shows by comparison to the holotype (Poulsen 1965, Pl. 5:8–10) a slightly less forward expanding glabella (not obvious on the plates!), a more distinct median impression in the glabellar front, a stronger inflated glabella, better impressed occipital and axial furrows, and the posterior pair of lateral glabellar furrows are deeper, so the rear part of glabella is hump-shaped. The new cranidia, one of which is from a somewhat higher level than the specimens described by Poulsen (1965), most closely resemble the holotype, but until more material is available it is preferred to treat them as *Hallanta* cf. *modesta* Poulsen, 1965. The new specimens appear identical, albeit the comparison is hampered by the circumstance that cranidium S 980 is flattened and the test is dissolved.

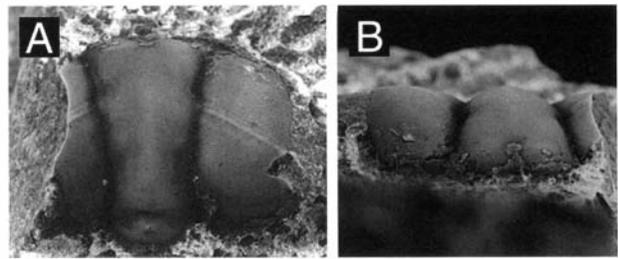


Fig. 230. *Hallanta* cf. *modesta* Poulsen, 1965. Exfoliated cranidium, dorsal and frontal views, $\times 3$. MGUH 22.978 (S 1758), Skelbro.

Subfamily *Bumastinae* Raymond, 1916Genus *Dysplanus* Burmeister, 1843

Type species. – *Asaphus* (*Illaeus*) *centrotus* Dalman, 1827 (SD Hawle & Corda 1847).

Material of DYSPLANUS. – Four complete specimens, 3 cephalae, 34 cranidia and 11 pygidia.

Remarks. – *Dysplanus* is assigned to the Styginidae, following Lane & Thomas (1983). Only two Scandinavian species have been described so far, viz. *Dysplanus acutigenia* Jaanusson, 1957, and *Dysplanus centrotus* (Dalman, 1827). The eastern Baltic *Dysplanus muticus* Volborth, 1863, which Holm (1886) regarded synonymous with ‘*Illaeus*’ *centrotus*, is inadequately known, but Volborth’s (1863, p. 31) description leaves no doubt that it is of ‘*acutigenia* type’. The lack of genal spines suggests that *D. muticus* probably is not identical to *D. acutigenia acutigenia*. For the time being *D. muticus* must be regarded a *nomen dubium*. *Illaeus bisulcatus* Pompecki is also clearly of ‘*acutigenia* type’ (cf. Pompecki 1890, p. 67; Pl. 3:18). The peculiar longitudinal furrows on the glabella indicate that it is not identical to *D. acutigenia* (*s.str.*), but may be regarded as a related species or subspecies. Tjernvik (1956) mentioned two cranidia, tentatively assigned to *Dysplanus*, from the *M. planilimbata* and *M. dalecarlicus* Zones of Sweden, and Lamansky (1905) listed *Dysplanus* from all zones of BII. Hence additional species and/or subspecies of *Dysplanus* may remain to be recognized. In the present context a new subspecies, *D. acutigenia vetustus* n.subsp., is described from the *M. polyphemus* Zone.

Dysplanus centrotus (Dalman, 1827)

Figs. 231–232

Synonymy. – (Key papers only, see Jaanusson (1957) for further references) □ 1882 *Dysplanus centrotus* Dalm. [*partim.*] – Brögger, p. 96; Pl. 6:5; non Pl. 2:4, 4a–b [= *Dysplanus acutigenia* Jaanusson, 1954] (occurrence, illustration of complete specimen). □ 1957 *Dysplanus centrotus* (Dalman, 1827) – Jaanusson, pp. 95–99; Pl. 1:1–9; Textfigs. 10–11 (description, occurrence, illustrations of cephalae, pygidia

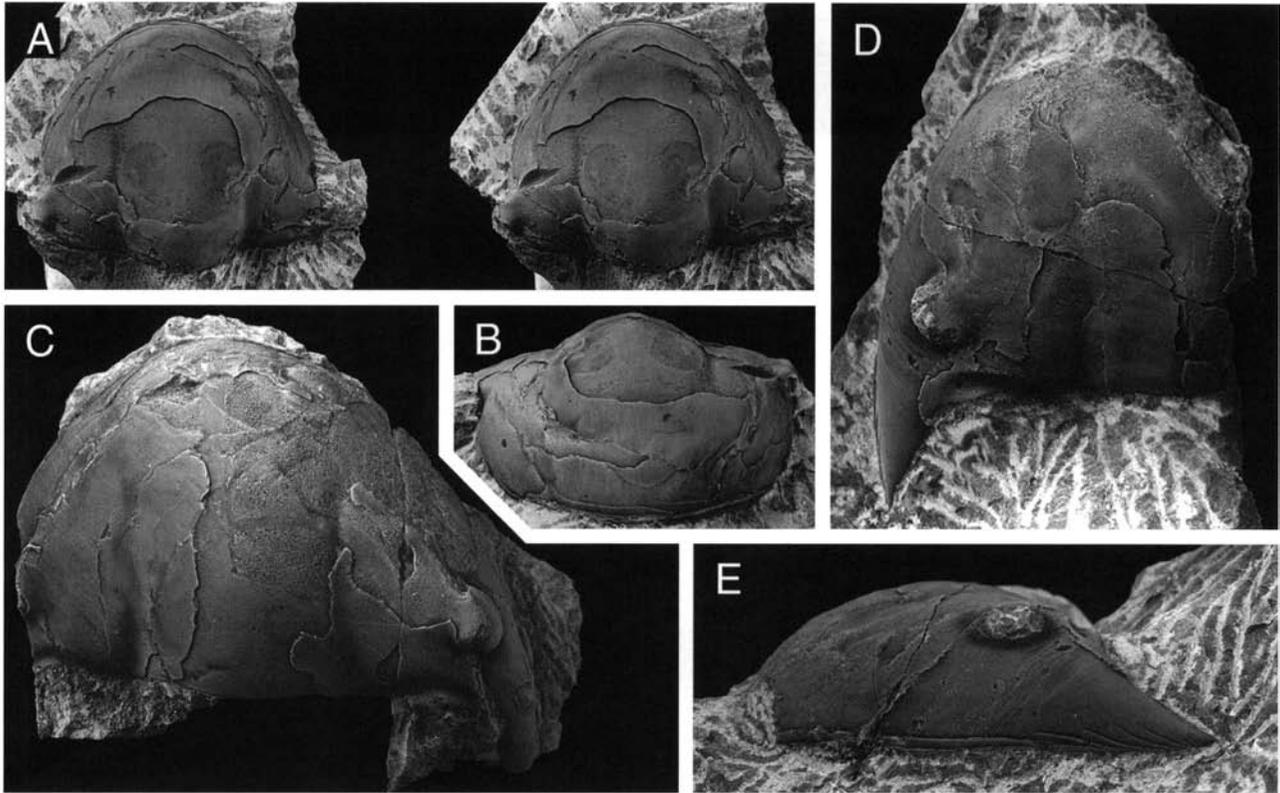


Fig. 231. *Dysplanus centrotus* (Dalman, 1827). □A–B. Partly exfoliated cranidium showing paired muscle impressions on glabella, stereo-pair and frontal view, $\times 1.5$. MGUH 22.979 (A 447), bed A-34, Slemmestad. □C. Largely exfoliated cephalon, $\times 2$. MGUH 22.980 (GM 1969.171), Lysaker Member, Slemmestad. □D–E. Fragmentary cephalon, dorsal and side views $\times 2$. MGUH 22.981 (A 435), bed A-31, Slemmestad.

and complete specimens). □1980 *Dysplanus centrotus* (Dalman) – Reymont, Fig. 2d [sic]; Fig. 4a (non Fig. 4b!) (illustrations of lectotype; see notes below).

Lectotype. – Enrolled specimen, assumed original of Dalman (1827, Pl. 5:1a–c), figured by Reymont (1980, Fig. 4).

Material. – Four complete specimens, 3 cephalon, 9 cranidia, and 4 pygidia.

List of material. – □Complete specimens A 441 (im), A 444 (im), A 460 (poor; im), A 471 (im). □Cephalon K 905 (c; with thoracic segments), A 435 (t) [MGUH 22.980], GM 1969.171 (pim) [MGUH 22.980]. □Cranidia A 430a? (t), A 430b (pim), A 442 (im), A 447 (pim) [MGUH 22.979], A 461 (im), A 477 (pim), A 484 (pim), A 1111 (im), A 1153 (pim). □Pygidia K 352 (c), K 1342 (c), A 419 (im), A 458 (im) [MGUH 22.982].

Occurrence. – The bulk of the material is from the *A. expansus* Zone of Slemmestad. The species has been found in bed interval A-29–A-51 of the Lysaker Member, but is most frequent in beds nos. A-31–A-36. Cephalon MGUH 22.980 is from the Lysaker Member at Slemmestad, exact level unknown. A few specimens are from bed +22 (upper part) to +24 at Killeröd; this interval corresponds to the lowermost part of the *A. expansus* Zone. *D. centrotus* is characteristic of the *A. expansus* Zone of Sweden (Jaanusson 1957).

Remarks. – For description, see Jaanusson (1957). The material has not been studied in greater detail, but appears in all

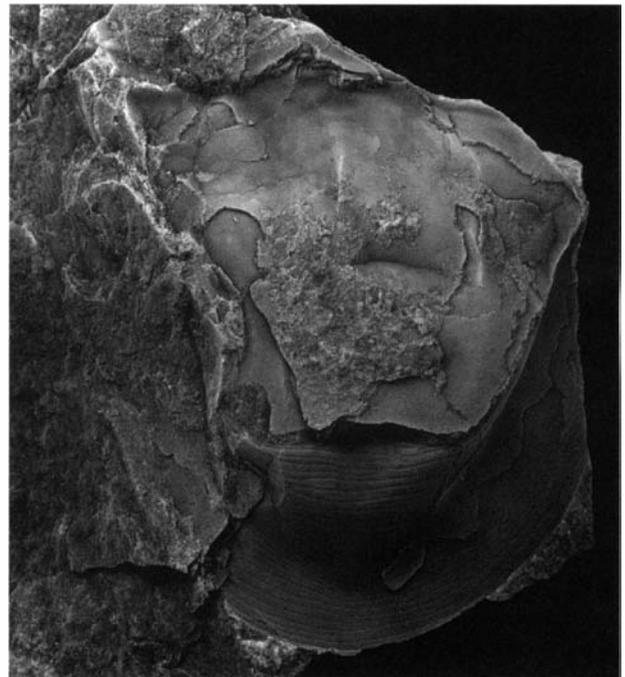


Fig. 232. *Dysplanus centrotus* (Dalman, 1827). Internal mould of pygidium showing doublure, $\times 2.5$. MGUH 22.982 (A 458), bed A-36, Slemmestad.

aspects to comply with this description; the stratigraphic range seems to be as stated by Brögger (1882) and Jaanusson (1957).

Reyment (1980) figured the presumed original of *D. centrotus*, but the figures were erroneously mixed with *Calymene polytoma*, and, thus, the explanation called Fig. 2d ('*C. polytoma*') refers to Fig. 4a, whereas the text labelled Fig. 4b ('*D. centrotus*') corresponds to Figs. 2a–c.

Dysplanus acutigenia acutigenia Jaanusson, 1957

Figs. 233–234

Synonymy. – (See also Jaanusson 1957) □1882 *Dysplanus centrotus* Dalm. [*partim*] – Brögger, p. 96; Pl. 2:4, 4a–b (short description, occurrence, illustrations of cephalon). □cf. 1890 *Illaeus* sp. – Pompecki, p. 72; Pl. 3:20 (illustrations of

cranidium). □v 1936 *Illaeus* sp. – Poulsen, p. 48 (listed). □1957 *Dysplanus acutigenia* n.sp. – Jaanusson, pp. 99–104; Pls. 1:10–13; 2:1–8; Textfig. 12 (description, occurrence, illustrations of complete specimen, cephala, cranidium, pygidia). □1960 *Dysplanus acutigenia* Jaan. – Jaanusson, p. 345 (occurrence). □1980 *Dysplanus acutigenia* Jaanusson – Tjernvik & Johansson, p. 192 (listed).

Holotype. – (OD) Enrolled specimen Ar 17471, figured by Jaanusson (1957, Pl. 2:6–8).

Material. – Twenty-two cranidia and 7 pygidia

List of material. – □Cranidia S 795 (t) [MGUH 22.986], K 83 (t), K 390 (pim) [MGUH 22.983], LU 36 (pim) [LO 7091], A 765 (pim), A 806 (im), A 813 (pim), A 817 (im), A 868 (pim), A 911 (im), A 913 (t), A 916 (pim) [MGUH 22.985], A 927 (im), A 935 (im), A 944? (im), A 978 (im), A 985 (im), A 1005 (im), A 1010 (im), A 1013a (im), A 1013b (im), A 380 (im) [MGUH 22.984]. □Pygidia GM 1835.44 (im) [MGUH 22.987], K 689 (im), A 819? (im), A 933 (im), A 988 (im), A 993 (im), A 995 (im).

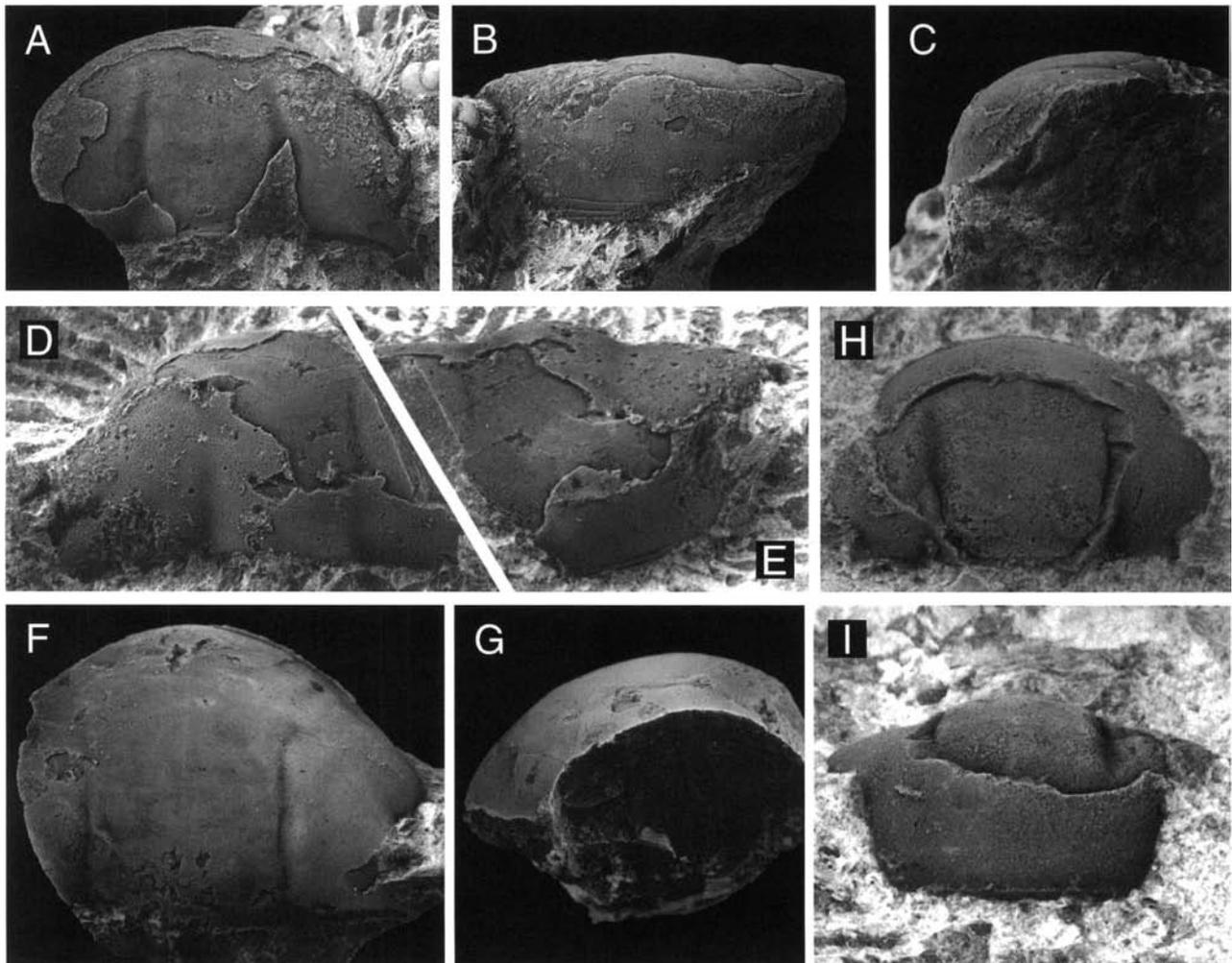


Fig. 233. *Dysplanus acutigenia acutigenia* Jaanusson, 1957. □A–C. Partly exfoliated cranidium, dorsal, frontal and side views, $\times 3$. LO 7091 (LU 36), Andrarum. □D–E. Partly exfoliated fragmentary cranidium, dorsal and frontal views, $\times 4$. MGUH 22.983 (K 390), bed –7, Killeröd. □F–G. Exfoliated late cranidium, looking intermediary towards *D. centrotus*, dorsal and side views, $\times 4$. MGUH 22.984 (A 380), bed A-26, Slemmestad. □H–I. Small, partly exfoliated cranidium, $\times 6$. MGUH 22.985 (A 916), bed M-9, Slemmestad.

Occurrence. – *D. acutigenia acutigenia* is rare in the Komstad Limestone, and has been found in SE Scania only in the upper part of the *M. simon* Zone (beds –6 and –7 at Killeröd; bed 9 at Gårdlösa-4a [= lower part of bed –6 at Killeröd]). Cranidium LU 36 is from Andrarum (level unrecognizable). An isolated cranidium was found in bed –12, *M. simon* Zone, Skelbro, and pygidium MGUH 22.987 is from an unknown level at the same locality.

D. a. acutigenia is frequent in bed interval M-7 to M-11 at Slemmestad, i.e. the lower part of the *M. limbata* Zone; a single specimen is from the top of bed M-6, which is correlated with the *M. simon* Zone, and another isolated specimen is from bed A-26, which is close to the top of the *M. limbata* Zone. The latter cranidium (Fig. 233F–G) has a slightly lower convexity (sag.), compared to the older representatives, and is perhaps transitional to *D. centrotus*.

Dysplanus acutigenia has previously been mentioned from the Hukodden Limestone by Brögger (1882, p. 96) and Jaanusson (1960, p. 345). Jaanusson stated that specimens were collected from ‘the lowermost part of this limestone at Slemmestad’ which has caused some confusion (e.g., S. Bergström 1986, p. 65), as *D. acutigenia* has been taken as indicative of the *M. limbata* Zone. No specimens have been found in the lowermost part of the limestone at Slemmestad during the present study, the first specimen was collected 2 cm below top of bed M-6, i.e. ca. 0.9 m above the Tøyen Shale,

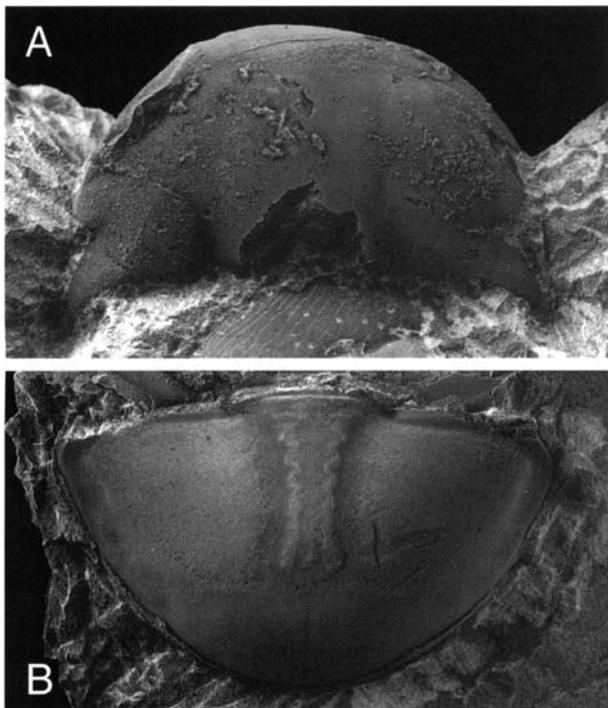


Fig. 234. *Dysplanus acutigenia acutigenia* Jaanusson, 1957. □A. Stratigraphically important cranidium from bed –12, Skelbro. $\times 3$, MGUH 22.986 (S 795). □B. Exfoliated pygidium showing axis and reticulate pattern on pleural fields, $\times 2.5$. MGUH 22.987 (GM 1835.44), Skelbro.

and the last typical specimen was found in bed M-11, ca. 1.3 m above base of Hukodden Limestone.

D. acutigenia acutigenia has hitherto been regarded characteristic of the *M. limbata* Zone (Jaanusson 1957; Tjernvick 1980), which is also basically the case at Slemmestad, but the subspecies actually appears already in the uppermost part of the *M. simon* Zone (Slemmestad and SE Scania), and even earlier at Skelbro (which, however, still may be in the upper part of the *M. simon* Chronozone). *D. a. acutigenia* also occurs in the ‘*Lepidurus* Limestone’ of northern Öland.

Remarks. – For description, see Jaanusson (1957). Specimen MGUH 22.987 (Fig. 234B), listed by C. Poulsen (1936), was suggested to represent a new species of *Dysplanus* by Jaanusson (1957, p. 141, footnote). In my opinion the pygidium cannot be separated from *D. acutigenia acutigenia*. Unfortunately the exact stratigraphic provenance is unknown, except that the specimen is from below the *A. expansus* Zone. The internal mould is well-preserved, and shows traces of 9–10 axial rings; the pleural fields exhibit a reticulate pattern with 4–5 nebulous pairs of ribs; the paradoublural line is rather sharply indicated by a change in ornamentation of mould surface from reticulate to smooth; the entire pygidium incl. the smooth ‘border’ area and axis shows a widely spaced fine punctation; a very shallow median furrow leads from the axis and to the posterior pygidial margin.

Dysplanus acutigenia vetustus n. subsp.

Fig. 235

Synonymy. – □? 1905 *Iliaenus centrotus* Dalm. [*partim?*] – Lamansky, pp. 53, 54, 67, 169 (listed). □? 1957 *Dysplanus* cf. *acutigenia* [*partim?*] – Jaanusson, pp. 102, 103, 104 (brief discussion of the eastern Baltic ‘*I. centrotus*’ sensu Holm 1886, and Lamansky 1905).

Derivation of name. – Latin *vetustus* = ancient, old-fashioned, alluding to the early occurrence and the primitive features of this form.

Holotype. – Cranidium MGUH 22.990 (S 1660) (Fig. 235C–D) from a loose slab, Skelbro, believed to represent bed –16 (*M. polyphemus* Zone).

Paratype. – Pygidium MGUH 22.992 (S 712) (Fig. 235H–I) from 3.5 cm below top of bed –15, Skelbro (upper part of the *M. polyphemus* Zone).

Additional material. – Two cranidia and 1 pygidium.

List of additional material. – □Cranidia S 698 (im) [MGUH 22.988], S 705 (im) [MGUH 22.989]. □Pygidium S 757 (im) [MGUH 22.991].

Occurrence. – The new subspecies has been found in beds interval nos. –16 to –14 at Skelbro, representing the upper half of the *M. polyphemus* Zone. Sample S 1660 (with holotype) is a loose slab from Skelbro; the lithology indicates beyond reasonable doubt that it represents the same interval,

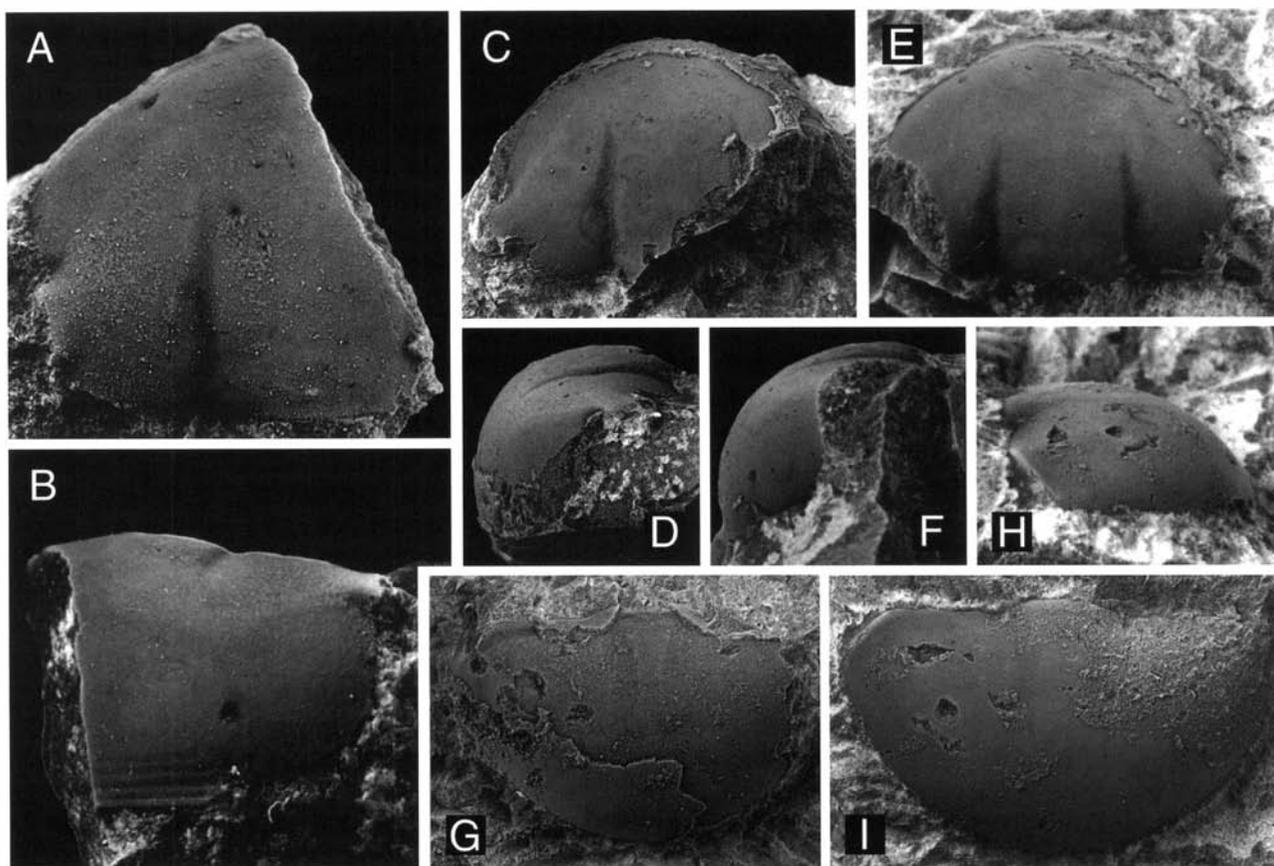


Fig. 235. *Dysplanus acutigenia vetustus* n. subsp. □A–B. Exfoliated, fragmentary small cranium, dorsal and frontal views, the latter showing anterior 'dysplanid' pit, $\times 10$. MGUH 22.988 (S 698), bed –16, Skelbro. □C–D. Exfoliated cranium, dorsal and side views, $\times 4$. MGUH 22.989 (S 705), bed –16, Skelbro. □E–F. Holotype. Exfoliated small cranium, side and dorsal views, $\times 6$. MGUH 22.990 (S 1660), Skelbro. □G. Partly exfoliated pygidium showing faint axis, $\times 4$. MGUH 22.991 (S 757), bed –14, Skelbro. □H–I. Paratype. Pygidium, dorsal and side views, $\times 4$. MGUH 22.992 (S 712), bed –12, Skelbro.

presumably bed –16. It is possible that *D. a. vetustus* n. subsp. also occurs in the eastern Baltic area, see discussion below.

Diagnosis. – Cranial angle ca. 90° or even slightly overturned; glabella narrow (tr.), insignificantly inflated, and with minute median tubercle situated near posterior margin; rudimentary eye ridges. Pygidium moderately convex; internal moulds show barely indicated, long, slender, hourglass-shaped axis, which is effaced on testaceous material. Doublure of pygidium wide with broad median inner bulge. External surface ornamentation restricted (cranium and pygidium).

Description. – Small form, largest cranium 8.4 mm long, largest pygidium 8.1 mm long (paratype). Anterior margin of cranium slightly swollen, rather convex (dorsal view), so cephalon is most likely about semicircular in outline. Posterior part of cranium almost flat, horizontal; anterior part vertically bent down; cranial angle about 90° or even less (80° , overturned, in one specimen). Greatest cranial width is across posterior fixigenae, FW:L ratio slightly greater than 1.6 in one cranium ($N = 1$); width across palpebral lobes

slightly more than 1.5 times the sagittal length ($N = 1$); PW:L ratio 1.25–1.39 (mean 1.32; $N = 3$). Glabella comparatively narrow, occupying 0.3 of the posterior cranial width ($N = 1$). Glabella defined only posteriorly, delimited by subparallel, fairly impressed axial furrows; it is very little arched (tr.), hardly rising above level of fixigenae. Axial furrows shallow up on the flexure to the steep anterior part of cranium; no preglabellar furrow. On internal moulds a vague anterior continuation of axial furrows may be present, diverging forwards from the flexure towards two rather distinctly impressed pits near anterior margin; it is unknown whether these pits are visible on testaceous material. A diminutive median tubercle is situated posteriorly on glabella near posterior margin; it may correspond to an occipital tubercle. Lateral glabellar furrows and occipital furrow effaced. Shallow lateral pits occur in the axial furrows approximately at level with anterior corner of palpebral lobe. No anterior border. Palpebral area of fixigenae rather wide, barely convex and almost flat; width of palpebral area excl. of palpebral lobe is two thirds of the adjacent glabella width, width incl. palpebral lobe is slightly less than 0.9 of the adjacent glabellar

width. Palpebral lobes situated immediately behind steep part of cranidium; distance to posterior margin is equal to the lobe length (exsag.), which in turn is equivalent to about 0.2 of the cranial length (sag.). Outline of lobes as in *D. acutigenia acutigenia*; they are slightly below the level of glabella. It appears that the palpebral lobes continue anteriorly into faint, oblique and almost straight eye ridges, terminating immediately in front of the axial furrows. These inconspicuous ridges may, alternatively, be interpreted as creases connected with the marked change of cranial slope. Posterior area of fixigenae continues posterolaterally into thorn-like, backwards curving projections. Adaxial main portion of posterior gena almost flat, sloping gently rearwards, distal tip insignificantly flexed downwards. No posterior border furrow on testaceous specimens; internal moulds show a 'furrow' or, rather, depression running next to posterior margin. Anterior branches of facial suture parallel in front of eyes, descending straight to anterior margin. Posterior branches of facial suture are gently convex, diverging obliquely backwards-outwards from palpebral lobe. Except for a few isolated terrace lines running along anterior margin of cranidium, the dorsal surface is devoid of lines. The surface of the flat posterior part of cranidium is covered with fine, openly spaced pits except on the central and posterior part of glabella and in the axial furrows. It is unknown whether or not the anterior steep part is pitted.

Librigena, hypostome and thorax unknown.

Pygidium semicircular in outline, rather strongly vaulted, L:W ratio about 0.55–0.60. Anterior margin straight; antero-lateral corners rather acute. No axial relief on outside of test, except close to anterior margin, where it is gently vaulted; width of axis at anterior margin equivalent to 0.5 of the pygidial width. The available internal mould shows a barely raised, slender axis, stretching for about 0.6 of the pygidial length (Fig. 235G); it tapers gently backwards to a constriction 0.6 of the axial length from front, and then expands, so outline is hourglass-shaped. Axial segmentation nebulous and only the anterior articulating half-ring is clearly set off by a shallow furrow. Pleural fields slope evenly towards margin, and no border is defined. Segmentation of pleural fields effaced, even on the internal mould, which shows a low anterior half rib delimited by a shallow furrow. Articulating facets small, triangular, slanting laterally at an angle of about 45° from horizontal. Facet delimited rearwards by a very low crest, which is directed obliquely backwards at an angle of about 140° to sagittal line. A few terrace lines occur on posterior part of articulating facets, otherwise the dorsal surface of pygidium is without lines. The test of pleural fields and axial area show clusters of fine pits, but it cannot be verified whether the pitting is original or caused by secondary corrosion; it is believed original. 'Border region' smooth. Doublure not exposed; paradoublure line is indicated on the internal mould by a slight textural change of the mould surface. The doublure appears slightly broader (all the way), and with a slightly broader (tr.) and therefore more smooth inner median bulge, compared to *D. acutigenia acutigenia*.

Affinities. – *D. acutigenia vetustus* n.subsp. is smaller than *D. acutigenia acutigenia* Jaanusson, and is characterized by having a more prominent glabellar tubercle, by showing faint eye ridges, the bend between posterior and anterior cranial parts is sharper, the external test ornament of the cranidium is finer, the pygidium appears to be slightly more rounded in outline (pygidia of *D. acutigenia acutigenia* display a hint of triangularity) with a more hour-glass-shaped axis, axial furrows effaced, the pygidial doublure is probably slightly broader and with a wider (tr.) more smooth inner median bulge, and the surface sculpture of the pygidium lacks the distinct punctation seen in *D. a. acutigenia*.

The relative prominence of the mesial glabellar tubercle and the possible presence of eye ridges, and perhaps also the finer surface pitting, may be regarded as primitive characters, and, supported by the stratigraphical distribution, makes *D. acutigenia vetustus* n.subsp. an obvious candidate for an ancestor of *D. acutigenia acutigenia* Jaanusson.

D. acutigenia vetustus n.subsp. is readily distinguished from *D. centrotus* (Dalman), e.g., by having a much smaller, comparatively shorter, broader cephalon and pygidium, by the much stronger cephalic convexity (sag.), by the far more distinct anterior pits near cephalic margin, by the lack of well-defined cephalic posterior border furrows, and by possessing a narrower and almost effaced pygidial axis.

The inadequate knowledge on *D. muticus* Volborth, 1863 hinders a comparison, in particular because the librigena of *D. acutigenia vetustus* n.subsp. is unknown.

Remarks. – It is uncertain whether *D. acutigenia vetustus* n.subsp. is identical to the oldest representatives of the East Baltic '*Illiaenus*' *centrotus*, reported from the BII α Zone by Lamansky (1905; see also Jaanusson 1957, pp. 102–104). The pygidium figured by Holm (1886, Pl. 10:9) should probably not be assigned to *D. a. vetustus* n.subsp., as the axis is too well-defined.

Genus *Platillaenus* Jaanusson, 1954

Type species. – (OD) *Illiaenus ladogensis* Holm, 1886.

Platillaenus aff. *ladogensis* (Holm, 1886)

Material. – One poorly preserved cranidium (A 551).

Occurrence. – The specimen is from bed A-56 of the Lysaker Member at Slemmestad (upper part of the *A. expansus* Zone).

Remarks. – *Platillaenus* is assigned to *Styginidae*, following Lane & Thomas (1983). Two species are known, *P. ladogensis* (Holm, 1886), occurring in the *A. expansus* Zone, and *P. mirus* (Wiman, 1907), occurring in the *A. 'raniceps'* Zone and perhaps also in younger strata (Jaanusson 1957). The former has also been reported from the southern Urals (Ancin 1977). The available cranidium resembles *P. lado-*

gensis, but the convexity (both ways) is slightly stronger, the anterior fixigena looks slightly narrower (tr.) immediately in front of eye (perhaps because the glabella is broader), the axial furrow does not continue anteriorly into a lateral 'border' furrow, and the palpebral lobe may be more arcuate, but the outline may be incidental, as the posterolateral margin is damaged. It cannot be excluded that distortion caused by compaction is responsible at least for some of the apparent differences. The specimen is not suited for illustration.

Family *Panderiidae* Bruton, 1968

Genus *Panderia* Volborth, 1863

pro *Rhodope* Angelin, 1854 (non Kölliker, 1847) and *Pogrebovites* Balashova, 1976

Type species. – (OD) *Panderia triquetra* Volborth, 1863.

Remarks. – The *Panderia* group is ranked as a family, following Lane & Thomas (1983). For discussion of genus, see Volborth (1863), Holm (1886), Jaanusson (1954), and in particular Bruton (1968).

Balashova (1976, p. 132) erected *Pogrebovites* to accommodate a group of species, which, however, previously had been included in *Ottenbyaspis* by Bruton (1968) (see discussion of *Ottenbyaspis* herein). Despite the fact that *Pogrebovites* was intended to cover *Ottenbyaspis*, the genus is more likely a subjective synonym of *Panderia*, as the type species from the *A. expansus* Zone, '*Niobe*' *volborthi* Schmidt, 1907, presumably belongs to that genus. This species is peculiar in having a fairly well-defined concave border (cephalon and pygidium), but is otherwise characterized by rounded genal angles, a central glabellar tubercle, eight thoracic segments, and a strongly vaulted, cylindrical pygidial axis (Balashova 1976, pp. 133–134; Pl. 40:4).

Panderia cf. *triquetra* Volborth, 1863

Fig. 236A–C, E–F

Synonymy. – (Key papers only, see Bruton 1968 for additional references.) □cf. 1863 *Panderia triquetra* n.sp. – Volborth, pp. 32–34; Pl. 3:13–17 (description, occurrence, illustrations of complete enrolled specimens). □cf. 1886 *Illaeus triquetrus* (Volborth) 1863 – Holm, pp. 159–162; Pl. 11:5–10 (description, occurrence, illustrations of complete specimens, cephalon, pygidium). □cf. 1968 *Panderia* cf. *triquetra* Volborth, 1863 – Bruton, pp. 9–10; Pl. 1:1–6 (description of cranidium, discussion of species, occurrence, illustrations of cranidia).

Type material. – Not designated.

Material. – One cranidium and 4 pygidia. All specimens are internal moulds.

List of material. – □Cranidium A 322 [MGUH 22.993]. □Pygidia A 295 [MGUH 22.994], A 298, A 314 [MGUH 22.995], A 319.

Occurrence. – The specimens are from bed A-19 of the Lysaker Member at Slemmestad (upper part of the *M. limbata* Zone). *Panderia triquetra* is characteristic mainly of the Kunda Stage elsewhere in Baltoscandia (Bruton 1968), but it perhaps occurs also in the *M. limbata* Zone, see remarks below.

Description. – Cranidium ca. 2.5 mm long (anterior margin damaged), largest pygidium 3.3 mm long. The cranidium (Fig. 236A–C) is like *P. cf. triquetra sensu* Bruton (1968, pp. 9–10; Pl. 1:1, 3–5), except that the cranial angle is over-turned (ca. 65°), and the course of the axial furrows may be described as intermediate between *P. cf. triquetra* and *P. baltica* (cf. Bruton 1968).

Pygidium subsemicircular in outline, L:W ratio varies between 0.58 and 0.64 (mean 0.61; $N = 4$); convexity moderate in comparison to other illaenimorphs. Axis distinctly arched and barely tapers backwards, i.e. is roughly cylindrical in outline, terminal piece truncately rounded; axis stretches for 0.67–0.73 of the pygidial length (mean 0.71; $N = 4$); width at anterior margin corresponds to 0.30–0.33 of the maximum pygidial width (mean 0.31; $N = 4$). Anterior half-ring delimited by a rather shallow furrow, succeeded by six very faintly outlined axial segments including the terminal piece; the segmentation is indicated by paired lateral swellings, which probably are effaced on testaceous material. Pleural fields flat; anterior half rib delimited by a moderately impressed furrow, otherwise the pleural fields are smooth, or a nebulous anterior pair of ribs may be indicated. A border region is delimited by a low paradoublure crest; border generally convex, gently down-sloping, and of equal width throughout; anterolaterally the inner half is gently concave in the two largest specimens (3 and 3.3 mm long; Fig. 236E). Dorsal surface sculpture not revealed by the exfoliated specimens. Doublure stretches inwards for about 0.3 of the sagittal length postaxially; it is of equal width throughout, and inner margin parallels the outer pygidial margin; no axial incision. The smallest pygidia, 2.2–3.0 mm long, have a concave doublure without indications of terrace lines. The largest pygidium, 3.3 mm long, has a sigmoidal doublure, the inner half is gently concave, outer half convex (Fig. 236F); six continuous fine terrace lines are present on the inner half.

Affinities. – Early representatives of *Panderia* are poorly known, and only a few cranidia have been described in some detail so far (Bruton 1968). Compared to *P. baltica*, the Norwegian cranidium has a more even and stronger sagittal curvature, and a carinate, less convex (tr.) glabella, and it is very like the larger and somewhat younger specimen described as *P. cf. triquetra* by Bruton (1968, Pl. 1:1, 3–5). The similarity is greater than to the coeval cranidium from the '*Limbata* Limestone' described by Bruton (1968, Pls. 1:7–8, 2:1–2).

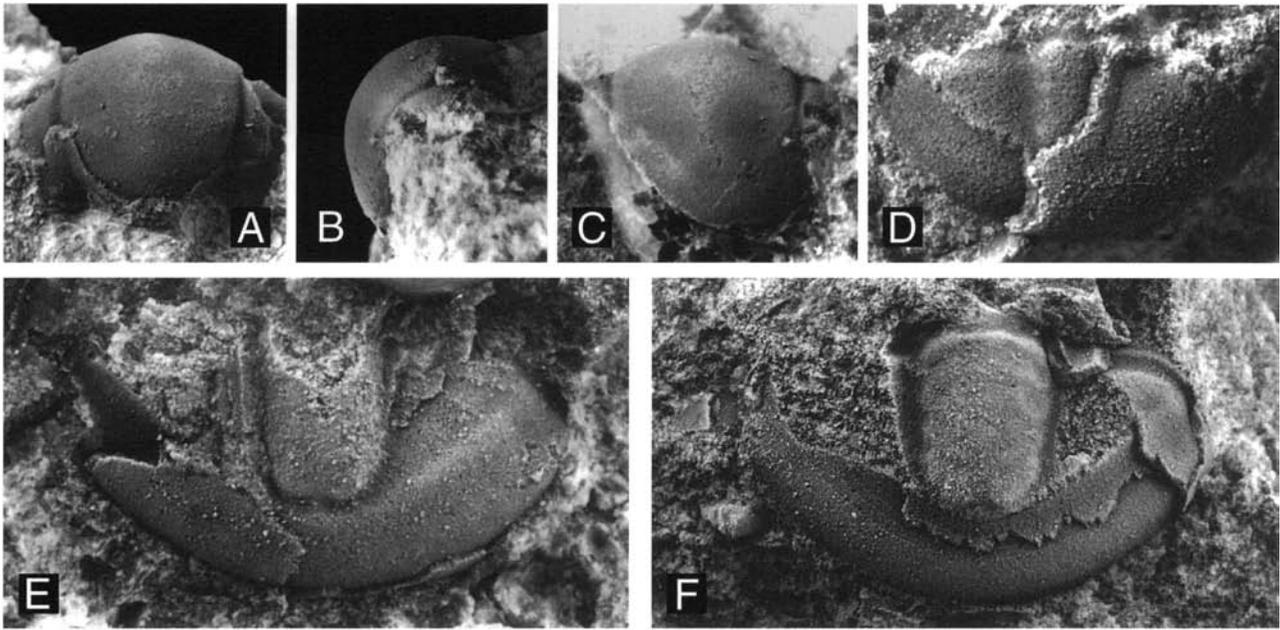


Fig. 236. □A–C, E–F. *Panderia* cf. *triquetra* Volborth, 1863. □A–C. Exfoliated small cranidium, dorsal, side and frontal views, $\times 12$. MGUH 22.993 (A 322), bed A-19, Slemmestad. □E. Largely exfoliated pygidium, $\times 18$. MGUH 22.994 (A 295), bed A-19, Slemmestad. □F. Internal mould of pygidium showing doubleure, $\times 12$. MGUH 22.995 (A 314), bed A-19, Slemmestad. □D. *Panderia* sp. A. Partly exfoliated pygidium, left side showing doubleure, $\times 16$. MGUH 22.996 (K 1213), bed 9, Killeröd site b.

The available pygidia resemble those of *P. baltica* very much, but the axis of the latter appears even more prominent, being marginally longer and broader (cf. Bruton 1968, Pl. 2:9). The differences between *P. baltica* and *P. triquetra* pygidia are, however, uncertain (Bruton 1968).

Panderia cf. *triquetra* is distinguished from most other species of *Panderia* by the pronouncedly vaulted, rather long pygidial axis.

Remarks. – The Norwegian pygidia closely resemble the material of *P. triquetra*, figured by Volborth (1863, Pl. 3:17) and Holm (1886, Pl. 11:6b), and the biometric ratios are identical for all practical purposes (compare Holm 1886, p. 161; the sagittal length used here corresponds to 'Länge nach der Krümmung gemessen'). On the other hand there may be some difference with regard to the distinctness of the axial segmentation (cf. Volborth 1863, p. 33; Pl. 3:17). Volborth (1863, p. 33) and Holm (1886, p. 160) wrote that the doubleure of the pygidium is narrow and of equal width throughout, but no further details were mentioned. As the current knowledge of the *P. triquetra* pygidium is limited, and even the identification of the cranidium is problematic (Bruton 1968, p. 10), it is preferred to refer to the new material as *P. cf. triquetra*.

Panderia triquetra Volborth is believed to occur in the lower part of the Kunda Stage (Bruton 1968), but a single very 'triquetra like' specimen originating from the 'Limbata' Limestone of Öland was mentioned by Bruton (1968, p. 10),

which at that time was the oldest known Baltoscandian representative of the genus. However, Tjernvik (1980) listed *Panderia* from the upper part of the *M. polyphemus* Zone, the *M. simon* Zone (frequent) and the *M. limbata* Zone; the assignment to species was not discussed, and these old forms remain to be studied.

Tjernvik (1980, Fig. 3) found a single pygidium of *Panderia* at 41.0 m in the Finngrundet core, i.e. at a level roughly corresponding to bed A-19 at Slemmestad. The ca. 2.5 mm long specimen is poorly preserved, but, compared to the Norwegian specimens, seems to have a significantly less arched axis, the posterior axial termination is, consequently, less well-defined, the border limit is ill-defined and the border is less steeply sloping. It is, accordingly, unlikely that the pygidium from the Finngrundet core is conspecific with the coeval Norwegian material.

Panderia sp. A (cf. *ramosa*)

Fig. 236D

Synonymy. – cf. 1968 *Panderia ramosa* n.sp. – Bruton, pp. 12–13, Pl. 12:1–3, 5, 6 (description, occurrence, illustrations of complete specimen and cephalon).

Material. – One pygidium (K 1213, pim) [MGUH 22.996].

Occurrence. – The specimen is from the lower part of bed 9 at Killeröd site b. This horizon constitutes the very top of the

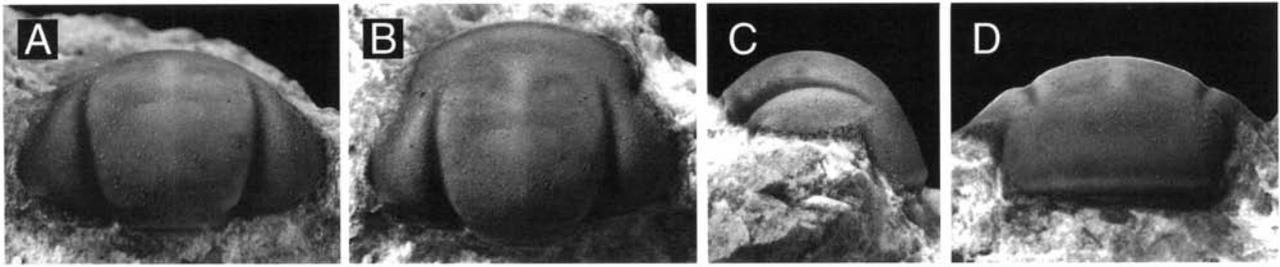


Fig. 237. *Ottenbyaspis* sp. □A–D. Exfoliated cranidium, dorsal, oblique dorsal, side and frontal views, $\times 12$. MGUH 22.997 (S 154), bed –21, Skelbro.

local *A. expansus* Biozone, which, however, is suspected to equal the basal part of the *A. 'raniceps'* Chronozone.

The range of *P. ramosa* is uncertain; it has, so far, been reported only from the *A. expansus* and/or early *A. 'raniceps'* Zone of Östergötland, Sweden (Bruton 1968).

Description. – Pygidium 1.8 mm long; outline subsemicircular, L:W ratio 0.58. Axis rather low, best defined on the exfoliated half; it stretches for two thirds of the pygidial length, width at anterior margin about 0.25 of pygidial width. The exfoliated part shows an articulating half-ring, bounded by a shallow furrow; this furrow continues onto the pleural field, delimiting a low anterior half rib. The furrow is effaced on the part with intact test. Axial furrows wide, shallow, axis defined mainly by a change of slope. Pleural fields show no trace of segmentation, and merge smoothly with the convex border region, descending to outer margin. Dorsal test surface smooth. Doublure gently convex; the width is slightly increasing rearwards to attain a maximum postaxially, there stretching for about one third of the pygidial length. Indistinct terracel lines are indicated on the doublure; the number cannot be verified.

Remarks. – The juvenile pygidium matches Bruton's (1968) description of *P. ramosa*, notably with regard to the less prominent axis in comparison to the otherwise similar *P. triquetra* and *P. baltica*, but it is impossible to confidently identify the isolated tiny specimen.

Family *Panderiidae*? Bruton, 1968

Genus *Ottenbyaspis* Bruton, 1968

Type species. – (OD) *Illaeus oriens* Moberg & Segerberg, 1906.

Remarks. – *Ottenbyaspis* is tentatively assigned to the *Panderiidae*, following Lane & Thomas (1983). The reader is referred to Bruton (1968) for a short discussion of genus and further references. For comments on *Pogrebovites* Balashova, 1976, see remarks on *Pandera* above.

Ottenbyaspis sp.

Fig. 237.

Synonymy. – □v 1965 *Symphysurina?* sp. – Poulsen, pp. 72–73; Pl. 3:3–6 (description, occurrence, discussion of generic assignment, illustrations of cranidium).

Material. – Cranidium S 154 (im) [MGUH 22.997].

Occurrence. – The specimen is from bed –21 at Skelbro, basal part of the *M. polyphemus* Zone.

Remarks. – The cranidium corresponds in all features to the specimen described as *Symphysurina?* sp. by V. Poulsen (1965, pp. 72–73), and which Bruton (1968, p. 29) allocated to *Ottenbyaspis*. The two known specimens from the base of the Komstad Limestone on Bornholm most likely represent a new and rather late species of *Ottenbyaspis*.

Family *Illaeidae* Hawle & Corda, 1847

Subfamily *Illaeinae* Hawle & Corda, 1847

Genus *Illaeus* Dalman, 1827

Type species. – *Entomostracites crassicauda* Wahlenberg, (1818) 1821 (SD Miller 1899).

Material of ILLAENUS. – Twenty complete specimens, 3 cephalae, 30 cranidia and 59 pygidia, of which 1 cranidium and 3 pygidia are too damaged to be identified at the species level.

Remarks. – *Illaeus* contains a bewildering multitude of species; the reader is referred to the excellent review and discussion by Jaanusson (1957, pp. 110–113). Other important contributions dealing with Baltoscandian illaeinids were published by Holm (1883, 1886).

Within Baltoscandia the genus generally turns up at the base of the *A. expansus* Zone and then ranges upwards, but scattered representatives of *Illaeus* occur already in the uppermost part of the *M. limbata* Zone of the Komstad Limestone and the Huk Formation. A single, damaged cra-

nidium from the much older *Megistaspis armata* Zone of Västergötland was tentatively assigned to *Illaeus* by Jaanusson (1957, pp. 113–114), but it presumably belongs to a new genus within the *Illaeinae*. However, Zhou & Fortey (1986) reported *Illaeus* from the Upper Tremadoc of northeastern China.

Jaanusson (1957) divided the plexus of illaenid species among the *Illaeus sarsi*, the *I. excellens*, the *I. sulcifrons*, and the *I. crassicauda* groups; the Middle–Late Ordovician *Parillaenus* possibly constitutes a fifth group (Jaanusson 1954, pp. 574–575; 1957, p. 113; but see Lane & Thomas 1983). These groups are primarily differentiated by the outline of the pygidial doublure (Textfig. 14 in Jaanusson 1957). All *Illaeus* species in the Komstad Limestone and the Huk Formation are members of the *I. sarsi* species group.

Illaeus fornicatus n.sp.

Figs. 238–240

Synonymy. – □v 1936 *Illaeus revaliensis* Holm – Poulsen, pp. 48, 51 (listed).

Derivation of name. – Latin *fornicatus* = vaulted, alluding to the pronouncedly vaulted, narrow glabella.

Holotype. – Cranidium MGUH 22.998 (S 1735) (Fig. 238A–C) from the uppermost part of bed +13 at Skelbro, base of the *A. expansus* Zone. The specimen is an internal mould with a patch of test preserved anteriorly.

Paratype. – Pygidium MGUH 23.004 (S 1746) (Fig. 240C), Skelbro, from the same level as the holotype.

Additional material. – Three complete specimens (compact), 4 cranidia and 18 pygidia, plus 2 complete specimens, 3 cranidia, and 2 pygidia, treated as *I. cf. fornicatus* n.sp.

List of additional material. – □Complete specimens K 328 (c) [MGUH 23.005], K 904 (c), LU 154b (c). □Cranidia S 1497 (im) [MGUH 23.000], GM 1878.1546 (im) [MGUH 22.999], GM 1878.1547 (im), K 338? (c). □Pygidia S 1456 (im), S 1542 (im), S 1575 (im) [MGUH 23.007], S 1582 (im), S 1602 (im), S 1617 (pim), S 1697 (im), S 1704 (im), S 1714 (im) [MGUH 23.009], S 1718 (im), K 363 (im) [MGUH 20.006], K 1264? (t), K 1291 (im), K 1297 (pc) [MGUH 23.003], K 1315 (pim) [MGUH 23.008], GM 1984.1804a (im), LU 70? (im), LU 152 (im).

Other material. – (*I. cf. fornicatus* n.sp.) □Complete specimens A 498 (t) [MGUH 23.002], PMO 83725 (t). □Cranidia A 370 (im), A 371 (pim) [MGUH 23.001], A 416 (im). □Pygidia A 404b? (im), A 406 (pim).

Occurrence. – *I. fornicatus* n.sp. occurs sparsely in the uppermost part of the *M. limbata* Zone on Bornholm (lower part of bed +13), but is much more frequent in the *A. expansus* Zone of the Komstad Limestone, in particular in the lower part of the zone. It has been found in the uppermost part of bed +13 at Skelbro, in the uppermost part of bed +22 and in bed +32 at Killeröd, and in beds 13–19 at Killeröd site b.

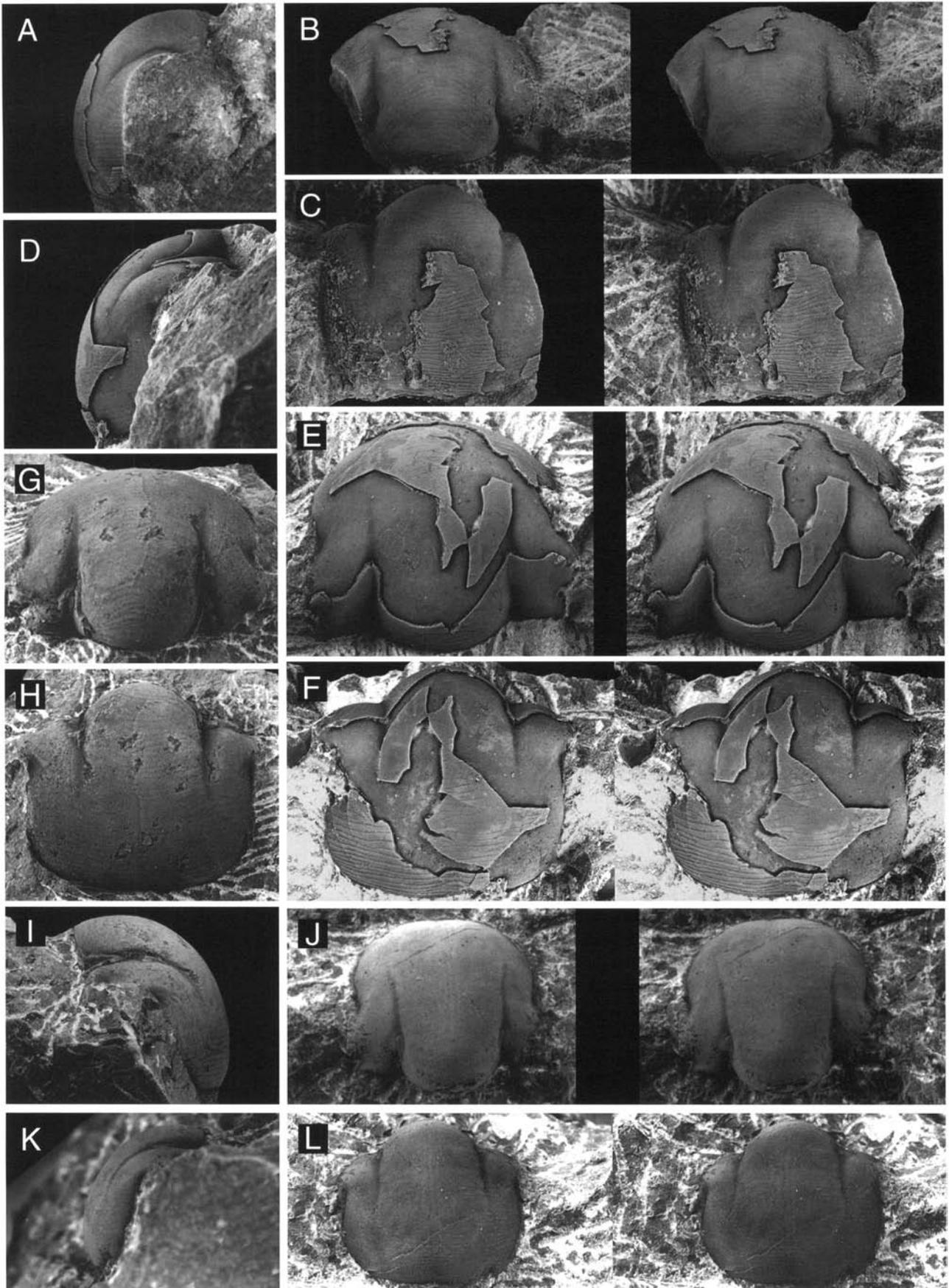
Cranidia MGUH 22.999 and GM 1878.1547 are from Duegård, Bornholm. The former appears to be from the lower part of bed +13, i.e. *M. limbata* Zone, while the latter is from the upper 6 cm of bed +13, that is, the base of the *A. expansus* Zone. Complete specimen LU 154b from Komstad is presumably from a level corresponding to the upper part of bed +22 at Killeröd; pygidium LU 152 from Andrarum in all probability originate from the *A. expansus* Zone. Pygidium LU 70 is from an unknown level at Fågelsång.

The material referred to as *I. cf. fornicatus* n.sp. is from beds A-25, A-28, A-29 and A-41 of the Lysaker Member, Slemmestad. The latter two beds belong to the *A. expansus* Zone, whereas beds A-25 and A-28 represent the uppermost part of the *M. limbata* Zone.

Illaeus fornicatus n.sp. (and *I. cf. fornicatus* n.sp.) appears to be the earliest *Illaeus* representative known at present from Baltoscandia.

Diagnosis. – Cranidium elongate with moderate sagittal convexity; glabella narrow (tr.), posteriorly distinctly arched; external terrace-line ornamentation dense. Pygidium moderately convex (sag.), axis narrow (tr.), fairly strongly vaulted; postaxial ridge well-marked on internal moulds. External ornamentation of pygidium approximately as in *I. sarsi*, but normally more extensive. Pygidial doublure of *I. sarsi* type with dense terrace lines.

Description. – Comparatively large species, largest cranidium (holotype) 26 mm long, largest pygidium 31.3 mm long. Cranidium roughly quadratic in outline, length (sag.) equal to preocular width, or the width may slightly exceed the length; anterior margin evenly convex (dorsal view), gently swollen. Width across posterior fixigenae equal to width across palpebral lobes, FW:L ratio 1.09–1.12 ($N = 3$). Cranidium strongly convex sagittally, but the curvature is moderate for an *Illaeus*. At the same time the cranidium is comparatively long, so the cranial angle is, nevertheless, about 90° or even down to 80° ('overturned'); the angle is difficult to measure exactly, because of the even curvature. Glabella moderately narrow (tr.), posterior width equivalent to 0.52–0.57 of the maximum cranial width (mean 0.54; $N = 3$); posterior part of glabella strongly vaulted and rises markedly above fixigenae. Glabella delimited by rather well-impressed axial furrows, at least on internal moulds, with distinct lateral pits situated approximately at mid-level of eyes. Anterior sections of axial furrows run almost straight forward from lateral pits; they are long, but get progressively shallower and disappear approximately one third of the cranial length from anterior margin on internal moulds; the furrows are probably notably shorter on testaceous material. Faint anterior continuations are indicated on a small internal mould (Fig. 238J–L), where they run almost parallel for a short distance, then turn inwards to die out very close to anterior margin of cranidium without uniting. Posterior sections of axial furrow short, well-impressed, diverging



backwards, but gradually less so, and they intersect posterior margin perpendicularly. Internal moulds show a diminutive median tubercle, situated immediately in front of posterior margin, and it presumably corresponds to an occipital tubercle; it is probably not visible on testaceous specimens. Lateral glabellar furrows and occipital furrow generally not defined; a single well-preserved internal mould shows faint paired muscle scars (Fig. 238J–L). This specimen and an additional internal mould have a pair of vague longitudinal furrows running adjacent to median line from a point level with anterior corners of palpebral lobes to a shallow, median impression situated immediately above anterior margin of cranidium. This anterior impression appears to be visible on outside of test as well. Palpebral area of fixigenae faintly convex, almost flat, sloping in abaxial direction; palpebral lobes show a very slight decrease of slope. Width of palpebral area, exclusive of the lobe, approaches 0.4 of the adjacent glabella width, narrower in small specimens, wider in large specimens. Palpebral lobes situated posteriorly, the distance from posterior margin to hind corner approximately equivalent to half the length of lobe. Lobe rather narrow (tr.), falcate, but comparatively long, length (exsag.) equivalent to 0.23 ($N = 3$) of the cranidial length; the relative length is small, because of the cranidial elongation. Faint double eye ridges are indicated on well-preserved internal moulds, running from anterior corner of palpebral lobe obliquely inwards to die out short off axial furrow. Posterior area of fixigena narrow (exsag.), posterolaterally continuing into an obliquely backwards directed projection, which is short, pointed triangular in outline. Internal moulds show a deeply impressed furrow parallel to posterior cranidial margin, turning backwards near distal corner; the furrow, which is effaced on testaceous specimens, reflects a thickening of the test, most likely fitting into the articulating furrow of the succeeding thoracic segment. Anterior branches of facial suture run almost straight forward from eyes to anterior margin, and then become marginal. Posterior branches of facial suture short, gently convex, running backwards-inwards from eyes, but curve gently to diverge slightly backwards.

Librigenae distorted in the available material; genal angle blunt; visual surface rather narrow; eye socle low.

External terrace lines on cephalon are prominent, widely distributed, and most often impressed also on internal

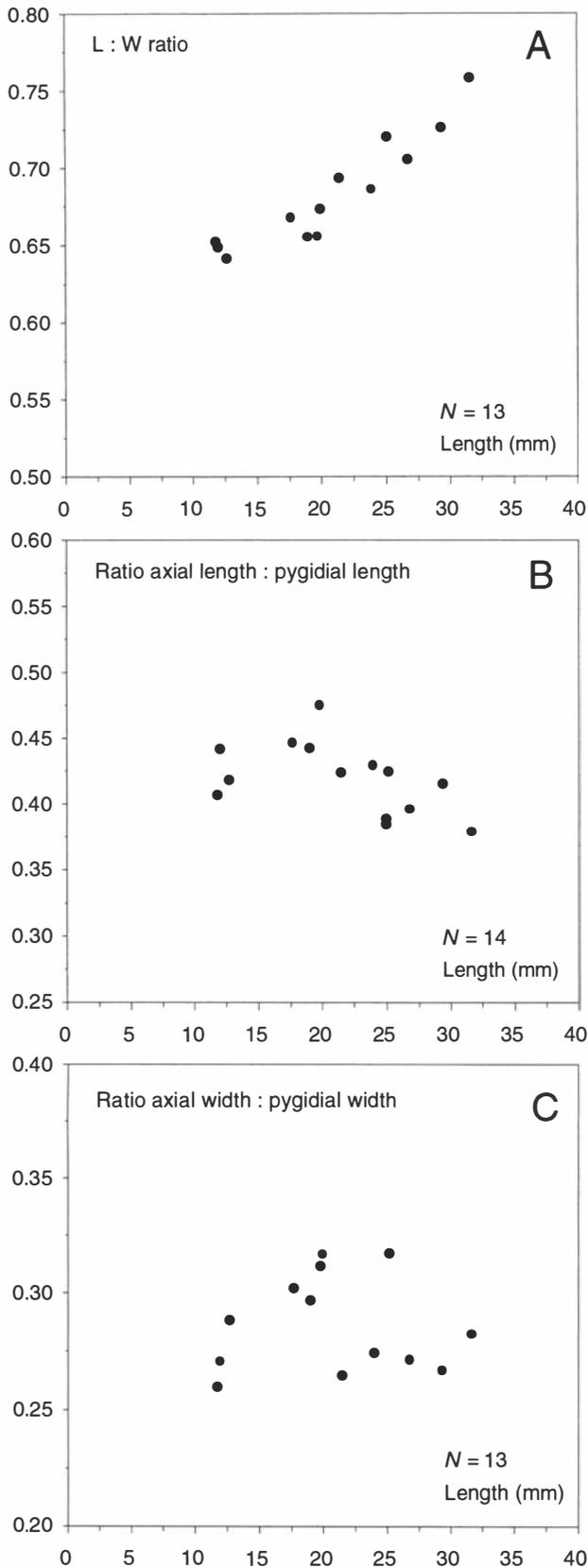
moulds; the pattern is apparent from Fig. 238. Palpebral area, including lobes and main inner part of posterior fixigenae, is presumably smooth. The anterior transverse lines continue onto anterior part of librigena, while the posterior part of librigena presumably is smooth (specimens corroded). The terrace-line density of the holotype cranidium, 26 mm long, is about 2 lines/mm on the anterior part. No punctuation of test (or internal moulds) has been seen in any specimen. Cephalic doublure not exposed in the material at hand.

Hypostome unknown.

Ten thoracic segments. Axis quite arched, occupying less than half of the pleural width on anterior segment (in the size order of about 0.45), tapering backwards to about 0.75 of the anterior axial width. The inner, flat portion of the pleura correspondingly becomes progressively wider in posterior direction. No pleural furrows. Single transverse terrace lines occur on axis, no terrace lines have been seen on the inner part of pleural fields, and no punctuation of test surface has been observed, but this may relate to preservation.

Pygidium semicircular to slightly parabolic in outline, L:W ratio 0.64–0.75 (mean 0.68; $N = 13$); the ratio is clearly influenced by size, the largest specimens being the most elongate (Fig. 239A). Sagittal convexity moderate for an *Iliaemus*, and the pygidia appear elongate. Axis funnel-shaped, comparatively long and narrow, stretches for 0.38–0.47 of the pygidial length (mean 0.42; $N = 14$), and occupies 0.26–0.32 of the pygidial width at anterior margin (mean 0.29; $N = 13$). Axis tends to be relatively shortest in the largest specimens (Fig. 239B), whereas the relative width is not influenced by size (Fig. 239C). Axis tapers backwards, clearly less so behind the third or fourth axial ring (Fig. 240C); terminal piece evenly rounded. Articulating half-ring ill-defined, separated by a shallow furrow; remaining axial segmentation indistinct, but internal moulds show traces of about seven segments, incl. the terminal piece. Axis fairly convex anteriorly, but descends in posterior direction, and the terminal part is only slightly elevated above adjacent pleural fields. Axial furrows wide and moderately impressed on internal moulds, effaced on testaceous material. Internal moulds show a slender postaxial ridge, running to posterior margin (Fig. 240H); the ridge is absent on outside of test. Pleural fields gently convex, almost flat, showing a weakly developed half rib delimited by a shallow, rather wide furrow, the distinctness of which varies from vaguely to moderately impressed on internal moulds; it is effaced on testaceous material. Segmentation of pleural fields effaced when the test is intact; internal moulds exhibit five indistinct pleural ribs, terminating at paradoublural line (Fig. 240F). A faint paradoublural furrow is occasionally developed on internal moulds; on testaceous specimens the pleural fields smoothly pass into the convex 'border area', descending to outer margin. 'Border area' widest postaxially, accounting for about half of the pygidial length. Articulating facets small, triangular in outline, steeply downsloping anterolaterally; the bend between facet and 'border area' strikes at an angle of

Fig. 238. □A–C, G–L. *Iliaemus fornicatus* n.sp. □A–C. Holotype. Largely exfoliated large cranidium, side view, $\times 1.5$, dorsal view, stereo-pair, $\times 1.5$, and frontal view, stereo-pair, $\times 1.5$. MGUH 22.998 (S 1735), bed +13, Skelbro. □B. As A, □C. As A, □G–I. Exfoliated cranidium, dorsal, frontal and side views, $\times 2$. MGUH 22.999 (GM 1878.1546), Duegård, Bornholm. □J–L. Exfoliated small cranidium showing sagittal furrows; side view, dorsal view (stereo-pair) and frontal view, $\times 3$. MGUH 23.000 (S 1497), bed +13, Skelbro. □D–F. *Iliaemus* cf. *fornicatus* n.sp. Partly exfoliated cranidium, side, dorsal (stereo-pair) and frontal (stereo-pair) views, $\times 2$. MGUH 23.001 (A 371), bed A-25, Slemmestad.



about 40–45° to sagittal line. Well-impressed, roughly transverse external terrace lines are present on the pleural fields, entering the lateral parts of axis (Fig. 240B). A few forward curving lines even crosses the anterior part of axis, but its main postero-central part is smooth; no lines present on the convex 'border area'. Three to four lines per millimetre were counted on the pleural fields close to axis in a pygidium, 20 mm long. Test punctate, not only on the pleural fields, but also on the entire 'border'; the punctation is almost absent on axis. Well-preserved internal moulds also reveal this punctation (Fig. 240G), whereas terrace lines rarely are impressed. The evenly distributed punctation consists of numerous small and fewer larger pits. Pygidial doublure is, as typical for illaenids, very broad, postaxially stretching for more than half of the pygidial length; combined width (tr., both sides incl.) behind articulating facets approximately half of post-axial doublure length. The convex doublure is very closely reflexed against dorsal test. A mesial furrow runs from inner margin of doublure to stop short off posterior margin. Inner margin of 'sarsi type' (cf. Jaanusson 1954, p. 561) with a median, falciform incision, flanked by small acuminations (Fig. 240E). Doublure covered with coarse, rather continuous terrace lines; the lines on the main posterior part are approximately transverse, and therefore meet the outer margin discordantly. The lines are gently disturbed in the inner axial area, curving backwards. There is a total of about 18–20 lines postaxially. The terrace lines are indicated on the dorsal side of doublure by rows of minute tubercles; rather densely spaced tubercles also occur in between the 'lines'.

Affinities. – *Illaeus fornicatus* n.sp. belongs to the *I. sarsi* species group (see Jaanusson 1957, p. 110), also holding the Scandinavian species *I. sarsi* Jaanusson, *I. aduncus* Jaanusson, *I. incisus* Jaanusson and *I. schuberti* n.sp. Compared to the three first mentioned, the cephalon of *I. fornicatus* n.sp. is distinguished by the strongly arched and narrow (tr.) glabella, the relatively long axial furrows, the moderate sagittal curvature, the generally more extensive terrace-line ornamentation, and by being overall comparatively more elongate. The thorax has a relatively narrow and strongly vaulted axis. The pygidium of *I. fornicatus* n.sp. is more general in outline, but internal moulds may be identified by the comparatively strongly vaulted, narrow axis, which at anterior margin typically accounts for about 0.3 of the pygidial width, whereas for instance the contemporaneous *I. sarsi* shows values around 0.35–0.40. The terrace-line patterns of *I. ad-*

Fig. 239. Pygidia of *Illaeus fornicatus* n.sp. □A. Ratio between maximum width and sagittal length plotted against length. □B. Ratio between axial length and pygidial length (sag.) plotted against pygidial length. □C. Ratio between anterior axial width and maximum pygidial width plotted against pygidial length.

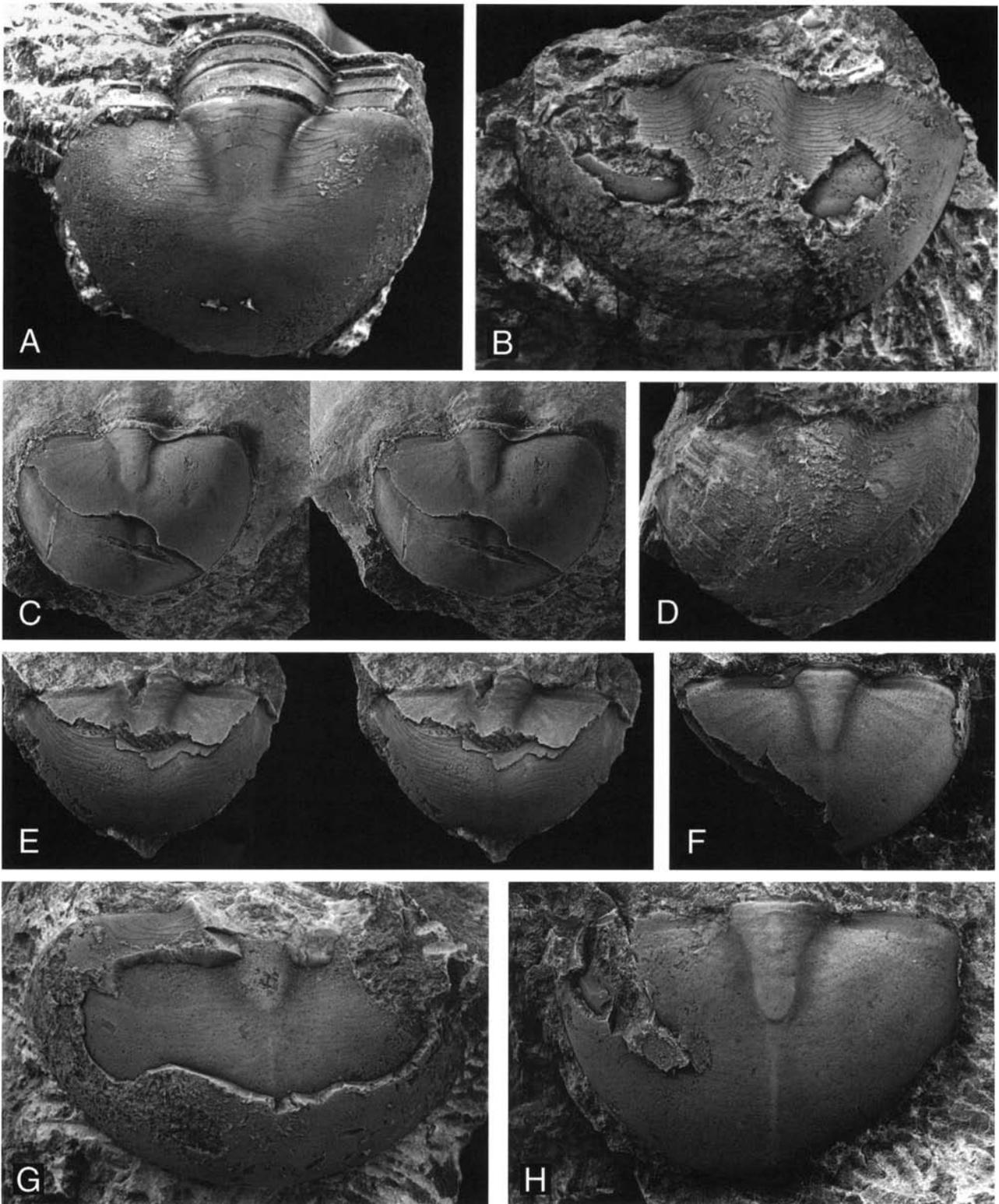


Fig. 240. □A. *Illaeus cf. fornicatus* n.sp. Pygidium showing few, well-impressed terrace lines, $\times 3$. Complete specimen MGUH 23.002 (A 498), bed A-41, Slemmestad. □B–H. *Illaeus fornicatus* n.sp. □B. Somewhat corroded pygidium showing comparatively dense terrace-line pattern, $\times 2.5$. MGUH 23.003 (K 1297), bed 15, Killeröd site b. □C. Paratype. Internal mould of pygidium showing part of doublure, stereo-pair, $\times 1$. MGUH 23.004 (S 1746), bed +13, Skelbro. □D. Somewhat corroded pygidium showing comparatively dense terrace-line pattern, $\times 2$. Complete specimen MGUH 23.005 (K 328), bed +22, Killeröd. □E. Internal mould of pygidium showing doublure, stereo-pair, $\times 1.5$. MGUH 23.006 (K 363), bed +32, Killeröd. □F. Exfoliated pygidium showing segmentation of pleural fields, $\times 3$. MGUH 23.007 (S 1575), bed +13, Skelbro. □G. Partly exfoliated pygidium showing pitted mould surface with imprints from external terrace lines, oblique dorsal view, $\times 3$. MGUH 23.008 (K 1315), bed 19, Killeröd site b. □H. Exfoliated pygidium showing axis and postaxial ridge, $\times 2.5$. MGUH 23.009 (S 1714), bed +13, Skelbro.

uncus and *I. incisus* pygidia are clearly different from that of *I. fornicatus* n.sp., while the terrace-line patterns of *I. sarsi* and *I. fornicatus* n.sp. are of similar type, but the lines are commonly more numerous and more densely spaced in *I. fornicatus* n.sp. The terrace-line pattern is, however, more variable in *I. sarsi* than hitherto recognized (see section on *I. sarsi*), and it is suspected that the line densities reflect environment. The *I. fornicatus* n.sp. pygidium has markedly higher number of terrace lines on the doublure than any other Scandinavian species of the *I. sarsi* group, and, besides, the lines appear to be more distinctly impressed.

I. schuberti n.sp. is the most *fornicatus*-like member of the *I. sarsi* group, showing a very similar glabellar outline, but *I. fornicatus* n.sp. differs by being significantly larger, markedly more elongate, the glabella is even more arched, the pygidial surface sculpture is more extensive and the pygidial doublure shows denser terrace lines.

I. polymitus Ancigin, 1977 from the Lower Ordovician of the southern Urals also has a strongly vaulted glabella, but apparently less so than *I. fornicatus* n.sp., and the adjacent lateral pits are less distinctly impressed; it cannot be ascertained which species group the Russian species belongs to.

The coeval *I. oscitatus* Fortey, 1980 from Spitsbergen (member of the *sarsi* group), has a much less vaulted glabella, flanked by less distinct lateral pits, a different surface sculpture of cranidium and pygidium, and does not seem close to *I. fornicatus* n.sp. None of the approximately coeval North American illaenid species described by Hintze (1953), Whittington (1963, 1965), or Ross (1967) resemble *I. fornicatus* n.sp., for instance they all have a less inflated glabella.

The Upper Arenigian illaenid material from the Sobova Formation, Turkey, referred to as *I. cf. herculeus* Gortani by Dean (1973), resemble *I. fornicatus* n.sp. and, even more so, *I. schuberti* n.sp. (*q.v.*).

Remarks. – A few specimens from the Lysaker Member, treated as *I. cf. fornicatus* n.sp., are strongly similar to the material from the Komstad Limestone and should either be included in *I. fornicatus* n.sp. or separated at the subspecies level only. The Norwegian specimens differ by having slightly less arched glabellas (Fig. 238D vs. A), the lateral impressions in the axial furrows are faint, and almost do not affect their course, the posterior branches of axial furrows are nearly straight, and the cranidial terrace-line pattern is less dense (e.g., Fig. 238F vs. C). The pygidia are basically like those from the Komstad Limestone; one Norwegian specimen has a less dense terrace-line pattern (Fig. 240A vs. B), but the variability of this character remains to be documented. The Norwegian material is clearly different from the associated *I. sarsi*, separated by the same features as listed for *I. fornicatus* n.sp. versus *I. sarsi*, i.e. a strongly convex glabella, elongate cranidium and pygidium, a narrow pygidial axis, and more numerous terrace lines on the pygidial doublure.

C. Poulsen (1936) listed *Illaeus revaliensis* Holm [= *I. wahlenbergi* (Eichwald, 1825)] from Bornholm. The mate-

rial (comprising cranidia MGUH 22.999 (Fig. 238G–I) and GM 1878.1547) was examined by Jaanusson (1957, p. 141), who remarked that they belong to a new species in the *I. excellens* group. However, the associated pygidia clearly prove that this new species belongs to the *I. sarsi* group.

Illaeus schuberti n.sp.

Figs. 241–242

Derivation of name. – In honour of the Austrian composer Franz Schubert (1797–1828). The species was conceived while I was listening to Schubert's quintet 'The Trout'.

Holotype. – Exfoliated cranidium MGUH 23.011 (F 270) (Fig. 241D–F) from 2–6 cm below top of bed 28, Fågelsång, A. 'raniceps' Zone.

Additional material. – Nine cranidia and 18 pygidia.

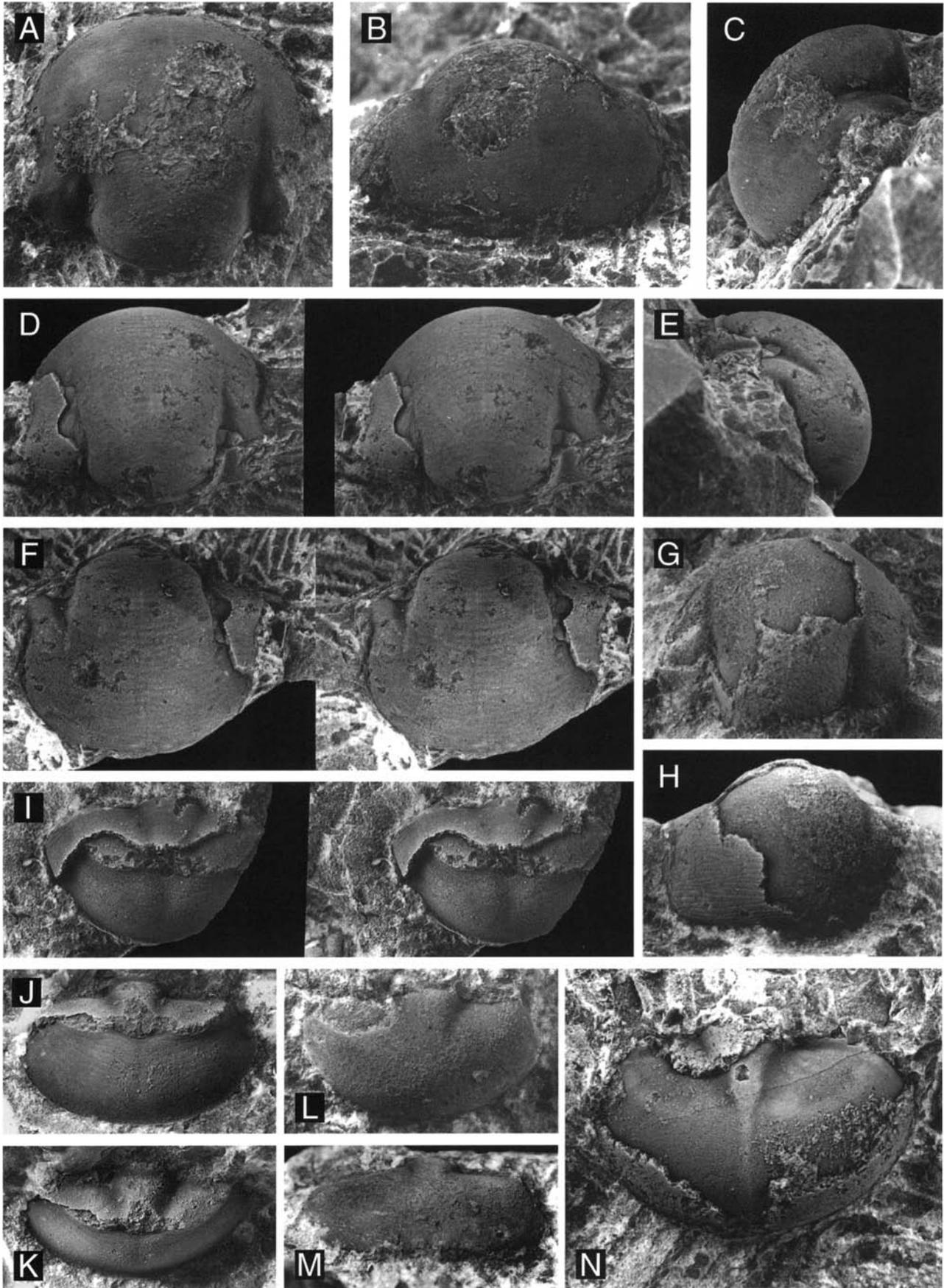
List of additional material. – □Cranidia K 886 (im) [MGUH 23.010], K 1103 (pim), K 1106 (pim), K 1110 (pim) [MGUH 23.012], K 1111 (im), K 1167 (t), K 1204 (im), K 1206 (t), LU 159 (im). □Pygidia K 825 (im) [MGUH 23.013], K 826 (pim), K 859 (im and is), K 868 (im), K 876 (pim), K 889 (pim), K 1011 (im), K 1031 (im), K 1043 (im), K 1116 (im), K 1164 (t) [MGUH 23.015], K 1172 (im) [MGUH 23.014], K 1179a (t), K 1179b (im), K 1180 (im), K 1192 (pim) [MGUH 23.016], K 1207 (im), K 1210 (im).

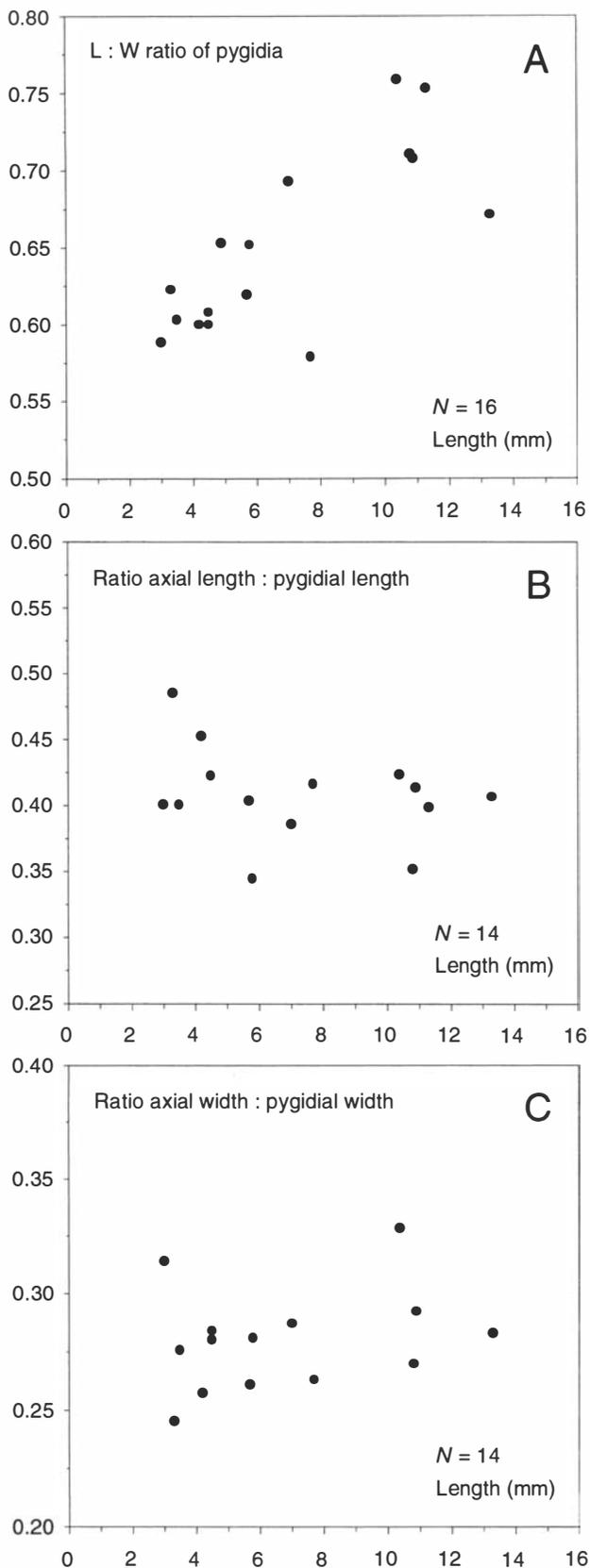
Occurrence. – The bulk of the material is from Killeröd site b, bed interval 0–8, representing the A. 'raniceps' Zone. A few specimens are from beds 26–28 at Fågelsång, also belonging to the A. 'raniceps' Zone. Cranidium LU 159 is from Fågelsång, and may originate from the same interval, but a positive identification of level is not possible.

Diagnosis. – Small species of 'sarsi-type'. Posterior part of glabella highly vaulted, anterior part of cranidium short (sag.), sagittal convexity high, and cranidial angle is overturned. Pygidium of moderate convexity (sag.); axis triangular, long postaxial ridge defined on internal moulds; surface sculpture sparse.

Description. – Small species, largest cranidium 15.8 mm long, largest pygidium 13.0 mm long. The cranidium is rather

Fig. 241. Illaeus schuberti n.sp. □A–C. Exfoliated cranidium showing imprints of external terrace lines; dorsal, frontal and side views, $\times 3$. MGUH 23.010 (K 886), bed 6, Killeröd site b. □D–F. Holotype. Exfoliated cranidium showing imprints of external terrace lines; dorsal (stereo-pair), side and frontal (stereo-pair) views, $\times 2.5$. MGUH 23.011 (F 270), bed 28, Fågelsång. □G–H. Partly exfoliated small cranidium, dorsal and frontal views, $\times 5$. MGUH 23.012 (K 1110), bed 6, Killeröd site b. □I. Internal mould of pygidium showing axis and doublure, oblique dorsal view (stereo-pair), $\times 5$. MGUH 23.013 (K 825), bed 1, Killeröd site b. □J–K. Internal mould of small pygidium showing doublure, posterior and dorsal views, $\times 6$. MGUH 23.014 (K 1172), bed 8, Killeröd site b. □L–M. Slightly corroded small pygidium, dorsal and posterior views, $\times 6$. MGUH 23.015 (K 1164), bed 8, Killeröd site b. □N. Partly exfoliated pygidium showing postaxial ridge, oblique posterior view, $\times 5$. MGUH 23.016 (K 1192), bed 8, Killeröd site b.





similar to that of *I. fornicatus* n.sp., but has a markedly shorter anterior part. Because of this 'shortness' the width across palpebral lobes is equivalent to about 1.2 times the cranial length, the PW:L ratio is about 1.1, the sagittal convexity is stronger, and the cranial angle is overturned, reading at around 60° . Glabella is slightly wider than in *I. fornicatus* n.sp., so the convexity (tr.) appears less distinct; the posterior glabellar width is, nevertheless, equivalent to only about 0.55 times the width across palpebral lobes (ratio approximately the same as to the width across posterior fixigenae, but which are damaged in most specimens). This relatively low ratio reflects that the posterior branches of axial furrows are virtually straight, diverging only slightly backwards from lateral impressions, so glabella is approximately of the same width all the way, while the glabella of *I. fornicatus* n.sp. rapidly widens backwards from lateral impressions. The cranial terrace-line patterns are similar in *I. schuberti* n.sp. and *I. fornicatus* n.sp.

Pygidium subsemicircular in outline; L:W ratio 0.59–0.76, but changes during growth (Fig. 242A), so pygidia less than 4.5 mm long show L:W values between 0.59 and 0.62 (mean 0.60; $N = 6$) and pygidia more than 4.9 mm long show L:W values between 0.62 and 0.76 (mean 0.69; $N = 10$). Sagittal convexity comparatively moderate for the genus. Axis appears short with rounded terminal piece on testaceous material, longer and more triangular with pointed terminal piece on internal moulds, but the relative length is also influenced by size (Fig. 242B); pygidia less than 4.5 mm long have an axis stretching for 0.40–0.48 of the pygidial length (mean 0.43; $N = 5$), whereas this L:L ratio for pygidia more than 4.9 mm long varies between 0.34 and 0.42 (mean 0.39; $N = 9$); this change reflects the pygidial elongation relating to growth (Fig. 242A). Axial width at anterior margin equivalent to 0.25–0.33 of the pygidial width (mean 0.28; $N = 14$; Fig. 242C). Axis of rather low relief, moderately vaulted anteriorly, descending rearwards, delimited by wide and indistinct axial furrows, which shallow up posteriorly, and axis merges smoothly with postaxial area (Fig. 241L). Axial relief more pronounced on internal moulds, showing a well-defined axis all the way, continuing into a low postaxial ridge (effaced on outside of test), running almost to posterior margin of pygidium (Fig. 241N). An articulating half-ring is defined on internal moulds, delimited by a shallow furrow; remaining axial segmentation effaced. Pleural fields very slightly convex, almost flat; segmentation effaced, apart from an anterior

Fig. 242. Pygidia of *Illaeus schuberti* n.sp. □A. Ratio between maximum width and sagittal length plotted against length. □B. Ratio between axial length and pygidial length (sag.) plotted against pygidial length. □C. Ratio between anterior axial width and maximum pygidial width plotted against pygidial length.

half rib delimited by a shallow furrow, visible only on internal moulds. Paradoxical line not indicated; area above double convex, sloping strongly towards outer margin. Articulating facets fairly large, triangular in outline. A few fine terrace lines present anteriorly on pleural fields and on axis, but most of the test surface is smooth. The fine terrace lines may be very difficult to discern [and do not survive photographic reproduction], and no lines are impressed on internal moulds. The smallest pygidia seem to be smooth; it is possible, but not likely, that this is a preservational artefact. Double of pygidium convex, closely reflexed against dorsal test, stretching for slightly more than half of the pygidial length postaxially; it is only half as wide anteriorly behind the articulating facets. Double is of 'sarsi-type' with a median falciform incision in inner margin, flanked on both sides by small blunt projections (Fig. 241I–J); a mesial furrow runs from inner margin to stop short off posterior margin. Double terrace lines arranged roughly parallel to outer margin, but with some irregularities in the sagittal area. The lines are rather faint, best impressed on the inner half, indistinct on the outer half; there seems to be a total of about 12–13 lines adjacent to sagittal line.

Affinities. – *Illaeus schuberti* n.sp. is a member of the *I. sarsi* group (see Jaanusson 1957, p. 110). By comparison to the other Scandinavian members of this group (*I. sarsi* Jaanusson, *I. aduncus* Jaanusson, *I. incisus* Jaanusson and *I. fornicatus* n.sp.) *I. schuberti* n.sp. appears to be distinctly smaller, the glabella is quite arched (almost like in *I. fornicatus* n.sp.), and the pygidial terrace-line pattern is very restricted. It may relate to poor preservation, but none of the exfoliated pygidia show axial segmentation or indications of ribs on pleural fields, which are usually seen in well-preserved specimens of other species.

I. cf. herculeus Gortani *sensu* Dean (1973), described from the Sobova Formation (Upper Arenig) of Turkey, seems close to *I. schuberti* n.sp., but the Scandinavian species differs by showing no anterior divergence of axial furrows, and the sagittal convexity of the cranidium is less strong. The limited material originally separated as *I. herculeus* by Gortani (1934) appears to have a not quite as strongly vaulted glabella, and the cranidium is overall broader than that of *I. schuberti* n.sp. (cf. Gortani 1934, Pl. 19:1).

Remarks. – *I. schuberti* n.sp. may be identical or related to a new *Illaeus* species (of *I. excellens* group?), mentioned by Jaanusson (1957, p. 159) from the *Raniceps* Limestone of Öland.

Illaeus sarsi Jaanusson, 1954

Fig. 243

Synonymy. – (Key papers only, see Jaanusson 1957 for further references.) □1882 *Illaeus Dalmani*, v. Volborth, Holm – Brögger, p. 97 (occurrence). □1954 *Illaeus sarsi* n.sp. –

Jaanusson, pp. 575–576; Pl. 1:1–2, ?3 (definition of species, occurrence, illustrations of hypostome and cephalic test). □1957 *Illaeus sarsi* Jaanusson, 1954 – Jaanusson, pp. 114–123; Pl. 4:1–9; Textfigs. 2–6, 14–18 (description, discussion of taxonomy, occurrence, illustrations of holotype and additional complete specimens, pygidia). □1973 *Illaeus sarsi* Jaanusson – J. Bergström, Pl. 5:5–6 (illustrations of individual in supposed life position). □1976 *Illaeus sarsi* (Jaanusson) – Reymont, p. 10; Figs. 28a–b (illustrations of complete specimen). □1980 *Illaeus sarsi* Jaanusson – Tjernvik & Johansson, p. 194, Textfig. 2 (occurrence).

Holotype. – Entire specimen Ar 10343, figured by Jaanusson (1957, Pl. 4:1–3).

Material. – Nineteen complete specimens, 3 cephalae (incl. 1 with some thoracic segments), 7 cranidia and 16 pygidia.

List of material. – □Complete specimens K 313 (c), LU 154a (c), A 453 (im), A 465 (im) [MGUH 23.020], A 469 (im), A 475 (im), A 485 (im), A 486 (im), A 488 (im) [MGUH 23.019], A 494 (pim), A 500 (im), A 504 (im), A 531 (im), A 534 (im), A 543 (im), A 549 (im), A 556 (pim), A 1116 (im), A 1130 (im). □Cephalae K 331 (c), A 407 (pim) [MGUH 23.017], A 536 (im). □Cranidia K 908 (im), K 909 (im), A 393 (im), A 404a (pim), A 409 (im), A 532 (im), A 578 (im). □Pygidia A 398 (im), A 403? (im), A 414 (t) [MGUH 23.022], A 452 (im), A 464? (im), A 468a (im), A 468b? (im), A 474 (im), A 480 (im), A 481? (im), A 489 (t) [MGUH 23.021], A 516? (im), A 528 (im), A 550 (im), A 1113 (t) [MGUH 23.018], A 1141 (pim).

Occurrence. – The species is frequent in bed interval A-28–A-57 at Slemmestad, of which bed 28 is correlated with the top of the *M. limbata* Zone, whereas the remaining beds belong to the *A. expansus* Zone. A few specimens were found at Killeröd in beds +22 and +32, representing the *A. expansus* Zone. Complete specimen LU 154a is from Komstad, presumably from a level corresponding to bed +22 of Killeröd.

Illaeus sarsi is typical of the *A. expansus* Zone of Sweden (Jaanusson 1954, 1957; Tjernvik & Johansson 1980).

Remarks. – See Jaanusson (1957, pp. 117–123) for description. The material from the Komstad Limestone in all preserved features matches this description, but the important surface sculpture is not preserved, as the only testaceous specimens are somewhat corroded. The comparatively low glabellar convexity (tr.) and the cranidial broadness distinguish the specimens from the coeval *I. fornicatus* n.sp.. Furthermore, the thoracic axis is distinctly wider and less arched than in *I. fornicatus* n.sp., and the pygidia are less elongate and show a wider, less vaulted axis.

The material from Slemmestad has not been studied in detail, but closely matches Jaanusson's (1957) account of *Illaeus sarsi*, except that the pygidial terrace-line pattern is somewhat more variable. The majority of the early pygidia are exfoliated, but a single specimen from bed A-29 shows numerous terrace lines, covering almost the entire dorsal surface (Fig. 243H). Pygidia from about bed A-39 and upwards show coarse, openly spaced terrace lines on the pleural fields, and the steep 'border' is without lines (Fig. 243G).

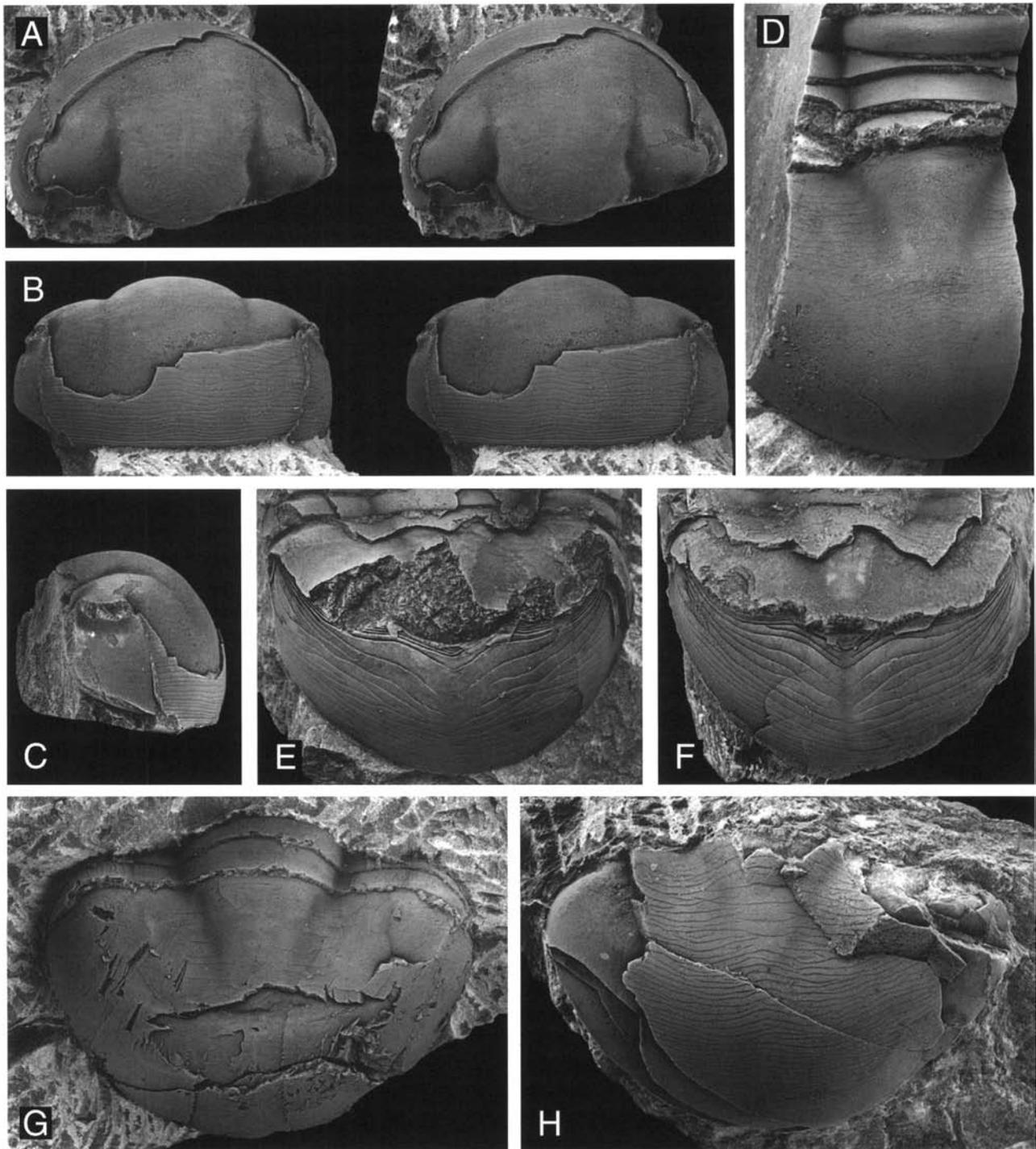


Fig. 243. *Illaenus sarsi* Jaanusson, 1954. □A–C. Partly exfoliated cranidium, dorsal (stereo-pair), frontal (stereo-pair) and side views, $\times 2$. MGUH 23.017 (A 407), bed A-29, Slemmestad. □D. Fragmentary pygidium showing moderately dense external terrace lines, $\times 3$. MGUH 23.018 (A 1113), bed A-45, Slemmestad. □E. Internal mould of pygidium showing double, $\times 2$. Complete specimen MGUH 23.019 (A 488), bed A-40, Slemmestad. □F. Internal mould of pygidium showing single, $\times 2$. Complete specimen MGUH 23.020 (A 465), bed A-36, Slemmestad. □G. Pygidium showing very sparse external terrace-line sculpture, $\times 2$. MGUH 23.021 (A 489), bed A-40, Slemmestad. □H. Pygidium showing comparatively dense external terrace-line pattern, $\times 3$. MGUH 23.022 (A 414), bed A-29, Slemmestad.

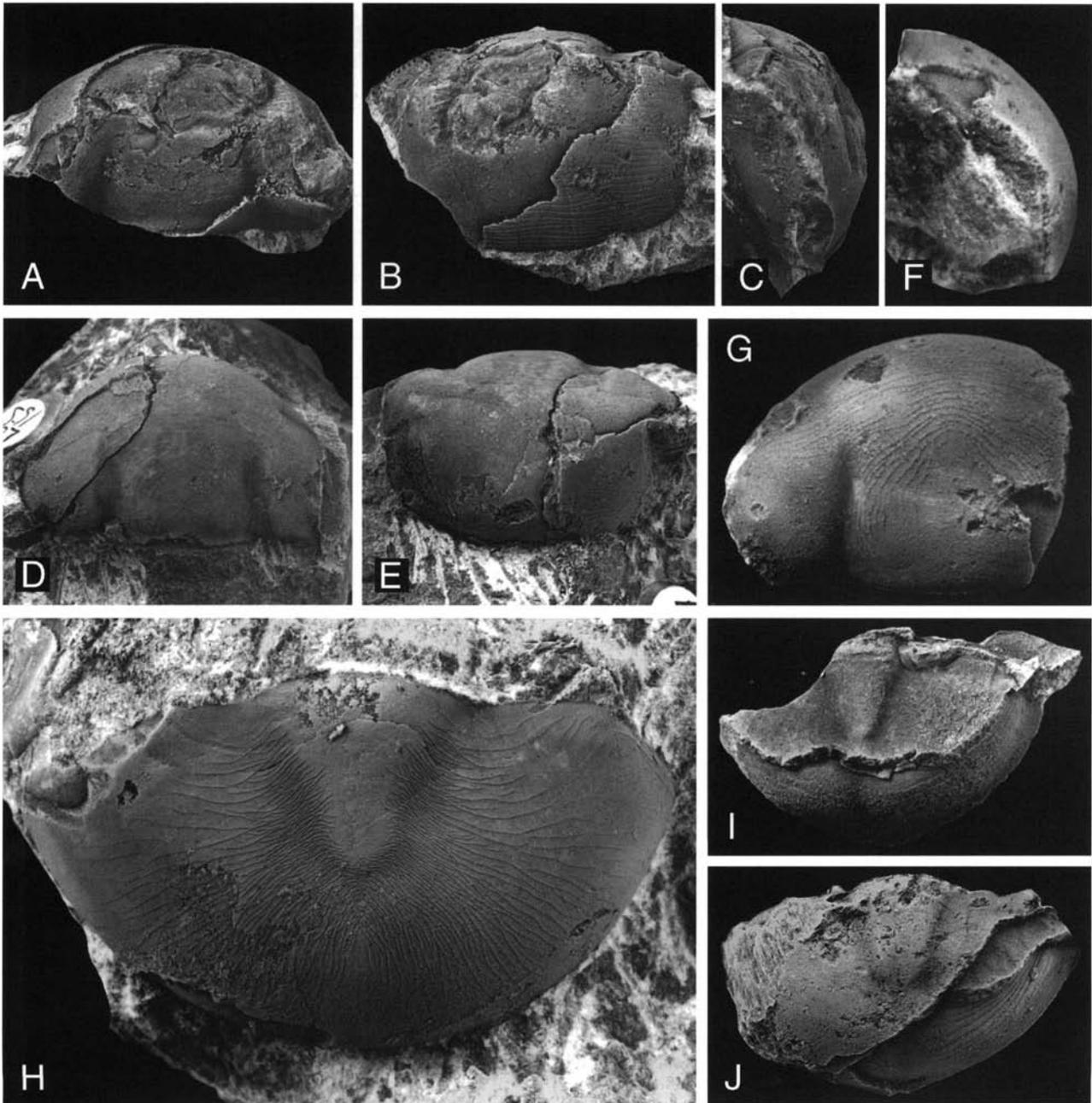


Fig. 244. *Illaeus aduncus* Jaanusson, 1957. □A–C. Corroded, partly exfoliated cranidium, dorsal, frontal and side views, $\times 2$. MGUH 23.023 (K 1104), bed 6, Killeröd site b. □D–E. Largely exfoliated cranidium showing imprints of external terrace lines on glabella, dorsal and frontal views, $\times 2$. LO 7125 (LU 155), Fågelsång. □F–G. Small cranidium showing external terrace-line pattern, side and dorsal views, $\times 8$. MGUH 23.024 (K 1093), bed 6, Killeröd site b. □H. Well-preserved pygidium showing external terrace-line pattern, $\times 5$. PMO 1745, Svartodden Limestone, Tollboden, Oslo (Bjørlykke coll.). □I. Internal mould of pygidium showing doublure and axis, $\times 3$. MGUH 23.025 (F 303), bed 27, Fågelsång. □J. Internal mould of pygidium showing part of doublure, oblique dorsal view, $\times 4$. MGUH 23.026 (K 876), bed 6, Killeröd site b.

Actually, none of the pygidia from the upper part of the *A. expansus* Zone have lines on the 'border', but in all other respects they (many of which are from articulated entire specimens) are indistinguishable from *I. sarsi*, and should not be separated from the species. The terrace-line pattern was most likely affected by the environment, which poten-

tially debases the separation of *I. sarsi* and *I. incisus*. The latter species(?) is characteristic of the *A. expansus* / *A. 'raniceps'* boundary interval (Tjernvik & Johansson 1980), which was a time of sea-level lowstand; the early, highly '*incisus*-like' pygidium from bed A-29 (base of *A. expansus* Zone) at Slemmestad is also from a shallow-water interval.

Illiaenus aduncus Jaanusson, 1957

Fig. 244

Synonymy. – (Key papers only, see Jaanusson 1957 for further references.) □1957 *Illiaenus aduncus* n.sp. – Jaanusson, pp. 123–129; Textfigs. 19–20; Pls. 5:1–8; 6:6 (description, occurrence, illustrations of complete specimen, cephalon and pygidia). □1980 *Illiaenus aduncus* Jaanusson – Tjernvik & Johansson, p. 194; Textfigs. 1, 10L (occurrence, illustration of pygidium). □1984 *Illiaenus aduncus* Jaanusson, 1957 – Wandås, p. 233; Pl. 11M–Q (occurrence, illustrations of cephalon and pygidia).

Holotype. – Entire specimen Ar 4207, figured by Jaanusson (1957, Pl. 5:1–3).

Material. – Four cranidia, and 2 tentatively assigned pygidia.

List of material. – □Cranidia K 1013 (t), K 1093 (pim) [MGUH 23.024], K 1104 (pim) [MGUH 23.023], LU 155 (im) [LO 7125]. □Pygidia K 876? (im) [MGUH 23.026], F 303? (d) [MGUH 23.025].

Occurrence. – Sample LU 155 is from Fågelsång; the lithology suggests a provenance from a level above bed 23. This may be the *A. expansus* Zone or, more likely, the *A. 'raniceps'* Zone. The remaining material is from Killeröd site b, beds 0 and 6, which are correlated with the *A. 'raniceps'* Zone.

I. aduncus is typical of the *A. 'raniceps'* Zone of Sweden (see Jaanusson 1957, pp. 156–160; Tjernvik & Johansson 1980). The species also occurs in the Svartodden Limestone of the Oslo area (Fig. 244H), and Wandås (1984) reported it from the base of the succeeding Elnes Formation, i.e. *M. gigas-M. obtusicauda* Zone.

Remarks. – The available cranidia are in gross outline 'sarsi-like', but the glabella is even flatter, and the anterior cranial part is comparatively steeper and more sharply downflexed. Transverse lines cross the anterior part, being most distinct anteriorly and rather faint just below the cranial flexure; U-shaped lines bend around the middle part of glabella. All of these characters, and especially the terrace-line pattern, conform to Jaanusson's (1957) description of *I. aduncus*.

By comparison to *I. incisus* the cranidia at hand are relatively broader, have a marginally less convex (tr.) glabella, and are covered with more densely spaced terrace lines. The *aduncus* cranidia are readily separated from those of the associated *I. schuberti* n.sp., which have a much more strongly vaulted glabella, and a less 'sarsi-like' outline.

The available pygidium is exfoliated, but most likely matches the more readily identified cranidia. It differs from the associated pygidia of *I. schuberti* n.sp. by having a different axial outline, and the sagittal convexity is stronger.

Family *Raphiophoridae* Angelin, 1854

Raphiophorid material. – Four complete specimens, 338 cranidia and 72 pygidia, of which 29 cranidia and 4 pygidia were too poorly preserved to be identified at the species level.

Remarks on Early Ordovician Baltoscandian species

These introductory remarks are kept at the family level in order to avoid recapitulations, since the individual raphiophorid species often have been variously assigned to different genera during the passage of time. *Ampyx*, *Rhombampyx*, *Lonchodomas*, *Cnemidopyge* and *Globampyx* are represented in the available material. For a general discussion of the family, see Harrington *et al.* (1959), Whittington (1959) and Fortey (1975a).

Ampyx costatus 'Boeck' was firstly described by Angelin (1854), and the authorship is here attributed to him (cf. Størmer 1941, pp. 131–132). 'A.' *costatus* was originally included in *Ampyx mammilatus* by Sars (1835), see discussion and figures by Størmer (1941, pp. 131–132; Pl. 2:13–18). It is characteristic of the Llandeilo-Caradoc of Scandinavia, but Brögger (1887) listed 'A.' *costatus* also from the 'Fragment Limestone' [Killingen Member] of the Oslo area; however, Wandås (1984) did not find the species in this interval. Schmidt (1894) tentatively assigned a few specimens to *A. costatus*, originating either from the upper part of BIII or from CI (compare Schmidt 1894 vs. 1907). 'A.' *costatus* (s.str.), which was transferred to *Cnemidopyge* by Whittard (1955), thus occurs at levels well above the Komstad Limestone (Størmer 1941; Hadding 1913), but a closely related form, referred to as *Cnemidopyge costatus* n.subsp. A, has been collected from the base of the *A. expansus* Zone of the Komstad Limestone.

Lonchodomas domatus Angelin, 1854 was originally reported from the *Ceratopyge* beds of Hunneberg and Oslo; the species has not been found since then (cf. Linnarsson 1869; Brögger 1882; Moberg & Segerberg 1906; Tjernvik 1956). The material referred to as *L. cf. domatus* by Weber (1948) was separated as *L. karakanensis* by Chugaeva (1958). Balashova (1966) remarked that the cephalon of *L. domatus* resembles *Ampyx simonkovensis*, while it was suggested that the pygidium of *L. domatus* might be an incorrect reconstruction including too many segments. There is no valid basis for the latter assumption, but the cephalon of *L. domatus* is actually strikingly similar to the 'Ampyx' *paterglaber-frater* species group, characterized by a highly vaulted and smooth glabella (diagnostic characters of *L. domatus* according to Angelin 1854, p. 83). The prominent spine drawn by Angelin (1854, Pl. 40:16) is clearly indicated as a reconstruction, which is possibly incorrect. The pygidium, on the other hand, resembles the pygidium of *Globampyx obtusus* (compare Moberg & Segerberg 1906, Pl. 7:7b vs. 7:10). Hence it is possible that the enigmatic *L. domatus* is a hybrid pieced together of two species, and its cephalon may eventually prove conspecific with *Ampyx cf. pater sensu* Tjernvik (1956, 1980; see below). This suggestion remains speculative, though, and, pending retrieval of the type material, which appears to be lost, *Lonchodomas domatus* Angelin, 1854 must be regarded a *nomen dubium* (see also comments by Moberg & Segerberg 1906, p. 100).

A supplementary description of *Ampyx pater* Holm, 1882 was presented by Törnquist (1884) and Tjernvik (1956); a lectotype was designated by Skjeseth (1952) (figured by Holm 1882, Figs. 13–14, 16). The species, which here is transferred to *Rhombampyx*, occurs in the *M. dalecarlicus* and *M. estonica* Zones (Tjernvik 1956, 1980). A similar form, referred to as *Ampyx* cf. *pater* by Tjernvik (1956, 1980), occurs in the *M. armata* and *M. planilimbata* Zones, and it may be close to or conspecific with *Lonchodomas domatus* Angelin and/or '*Ampyx*' [*Rhombampyx*] *simonkovensis* Balashova, occurring around the Tremadoc–Arenig boundary (see above remarks). Another form, referred to as *Ampyx* aff. *pater*, was listed from the *M. polyphemus* Zone of Sweden by Tjernvik (1980); the relationship to the coeval *Rhombampyx glaber* (Poulsen, 1965) is uncertain. The *R. pater-glaber-frater* n.sp. species group has a long stratigraphic range, occurring from the base of the Hunneberg Stage (or even from the *A. serratus* Zone) to the middle of the Volkhov Stage. The strong similarity of these species suggests that they are closely related and presumably represent a single, or, at least, a simple evolutionary line.

Ampyx linmarssoni Schmidt, 1894, occurs in the Hukodden Limestone at Slemmestad; it or a closely related form also occurs in the *M. polyphemus* Zone of Sweden (Tjernvik 1980). The species is now transferred to *Globampyx* Fortey, 1975. *G. linmarssoni* resembles the older '*Ampyx*' *obtusus* (see Moberg & Segerberg 1906, pp. 100–101, and Tjernvik 1956, pp. 271–272), which occurs throughout the Billingen Stage (Tjernvik 1980), and the two species are probably closely related. A possible third member of this species group is the still older '*Ampyx*' *brevicauda* Wiman, 1905, occurring in the Hunneberg Stage (Tjernvik 1980).

Ampyx volborthi Schmidt, 1894, now assigned to *Lonchodomas*, is here subdivided into two subspecies, *L. volborthi volborthi*, occurring in the *M. (M.) limbata* Zone, and *L. volborthi schmidtii* n.subsp., occurring in the *A. expansus* Zone. *Ampyx knyrkoi* Schmidt, 1907, is possibly a junior synonym of *L. v. volborthi*. *L. balticus* Modliński, 1973 seems near the *L. volborthi* group, but the species is insufficiently known, and, besides, the name is probably a secondary homonym of *L. balticus* (Kummerov, 1928). The material identified with *Lonchodomas volborthi* by Skjeseth (1952) (see also Fortey 1975a, p. 69) is related to *Lonchodomas tenuis* n.sp., found in the lower half of the *M. polyphemus* Zone on Bornholm.

Ampyx nasutoides Regnéll, 1940 is insufficiently known, but presumably belongs to *Lonchodomas*, and it may be close to *L. tenuis* n.sp. The species occurs around the *M. estonica*–*M. polyphemus* zonal boundary.

Genus *Ampyx* Dalman, 1827

Type species. – *Ampyx nasutus* Dalman, 1827 (by monotypy).

Ampyx nasutus (Dalman, 1827)

Figs. 245–247

Synonymy. – □1827 *Asaphus* (*Ampyx*) *nasutus*–Dalman, pp. 68–69; Pl. 5:3a–c (description, occurrence, illustrations of entire specimen). □v 1882 *Ampyx nasutus*, Dalm. – Brögger, p. 58; Pl. 5:15, 15a, 15b (occurrence, illustrations of complete specimen). □1894 *Ampyx nasutus* Dalm. – Schmidt, pp. 77–80; Pl. 6:1–10 (description, occurrence, illustrations of cephalia, pygidia, complete specimens). □v 1936 *Ampyx nasutus* Dalm. [*partim*] – C. Poulsen, p. 48 (listed). □1950 *Ampyx nasutus* Dalman, 1827 – Whittington, pp. 554–556; Textfig. 6A–B; Pl. 74:3–9 (description of neotype, illustrations of cranidia, pygidia, complete specimens). □1973 *Ampyx nasutus* Dalman, 1827 – Modliński, p. 57; Pl. 5:1 (description and illustration of cranidium). □1973 *Lonchodomas volborthi* (Schmidt, 1894) – Modliński, Pl. 5:2 (illustrations of pygidium). □1973 *Ampyx nasutus* Dalman – J. Bergström, Pl. 5:2. □1980 *Ampyx nasutus* – Tjernvik & Johansson, pp. 176–177, 194 (occurrence). □1980 *Ampyx nasutus* Dalman – Reymont, Fig. 1a–b (designation and illustrations of lectotype). □v 1984 *Ampyx nasutus* Dalman, 1827 – Wandås, p. 235; Pl. 12D–F, I (occurrence, illustrations of cranidium, cranidia).

Lectotype. – Enrolled specimen Ög 110, figured by Dalman (1827, Pl. 5:3), designated by Reymont (1980), and replacing the neotype chosen by Whittington (1950).

Material. – Three complete specimen, 51 cranidia, and 16 pygidia.

List of material. – (Internal moulds if not otherwise stated). □Complete specimens A 1164, LU 126 (pim), K 905 (c). □Cranidia S 1510, S 1531, S 1538, S 1595, S 1610 [MGUH 23.028], S 1619, S 1685a [MGUH 23.029], S 1685c, S 1694, S 1708, S 1709, S 1722, S 1729 [MGUH 23.030], K 368 (t), K 877, K 878 (pim), K 882 (pim), K 893 (t), K 1004 (t), K 1036a? (t), K 1036b (t), K 1042 (t), K 1091 (t), K 1093b, K 1099?, K 1100?, K 1108a?, K 1108b, K 1109a, K 1110a, K 1110b (t), K 1111a? (t), K 1117? (pim), K 1125a (pim), K 1125b (t), K 1131a, K 1131b, K 1133, K 1134?, K 1138?, K 1146 (t), K 1176 (pim), K 1223?, K 1239 (pim), K 1253 (t), A 538, GM 1987.21, GM 1987.22 (pim) [MGUH 23.027], LU 100a [LO 7109], LU 100b, LU 146 (c). □Pygidia S 1541 [MGUH 23.031], S 1575, S 1721, S 1759 (t), K 881, K 1093a (pim), K 1108d?, K 1128 (t), K 1132 (t), K 1166 (t), K 1175 (pim), K 1179 (t) [MGUH 23.032], K 1227 (em), K 1340 (t), GM 1984.1804a, LU 34?.

Occurrence. – *A. nasutus* ranges from the base of the *Asaphus expansus* Zone and into the *A. 'raniceps'* Zone of the Komstad Limestone. The species is confined to the uppermost 6 cm of bed +13 at Skelbro, that is, the very base of the *A. expansus* Zone; the GM samples listed are from the same level at Vasegård. The species is frequent at Killeröd, and ranges from the basal part of the *A. expansus* Zone and upwards (beds +22, +35, 10–11), with an acme in the *A. 'raniceps'* Zone (beds 6–8 and 0, site b). *A. nasutus* occurs sparsely at Fågelsång, although I did not find any new material; museum specimens LU 100a, b are from the basal part of the *A. expansus* Zone; complete specimen LU 126 is from another, presumably higher level. Additional LU-samples are from erratic boulders of Komstad Limestone at Andrarum.

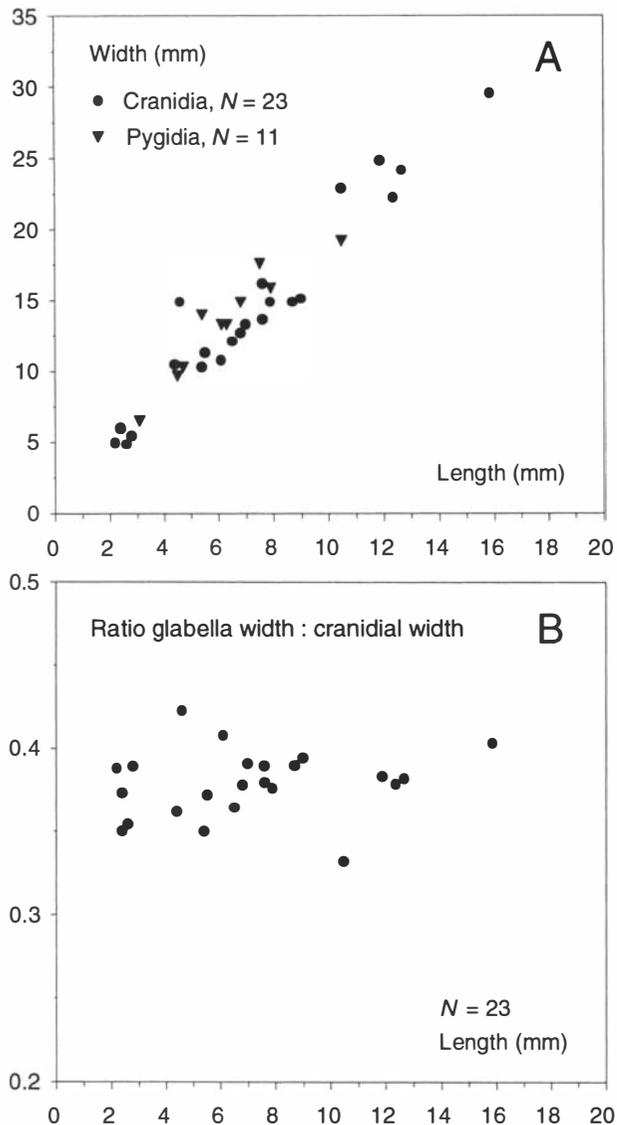


Fig. 245. *Ampyx nasutus* (Dalman, 1827). □A. Maximum width plotted against sagittal length of cranidia and pygidia. □B. Ratio between maximum glabella width and cranial length (sag.) plotted against cranial length.

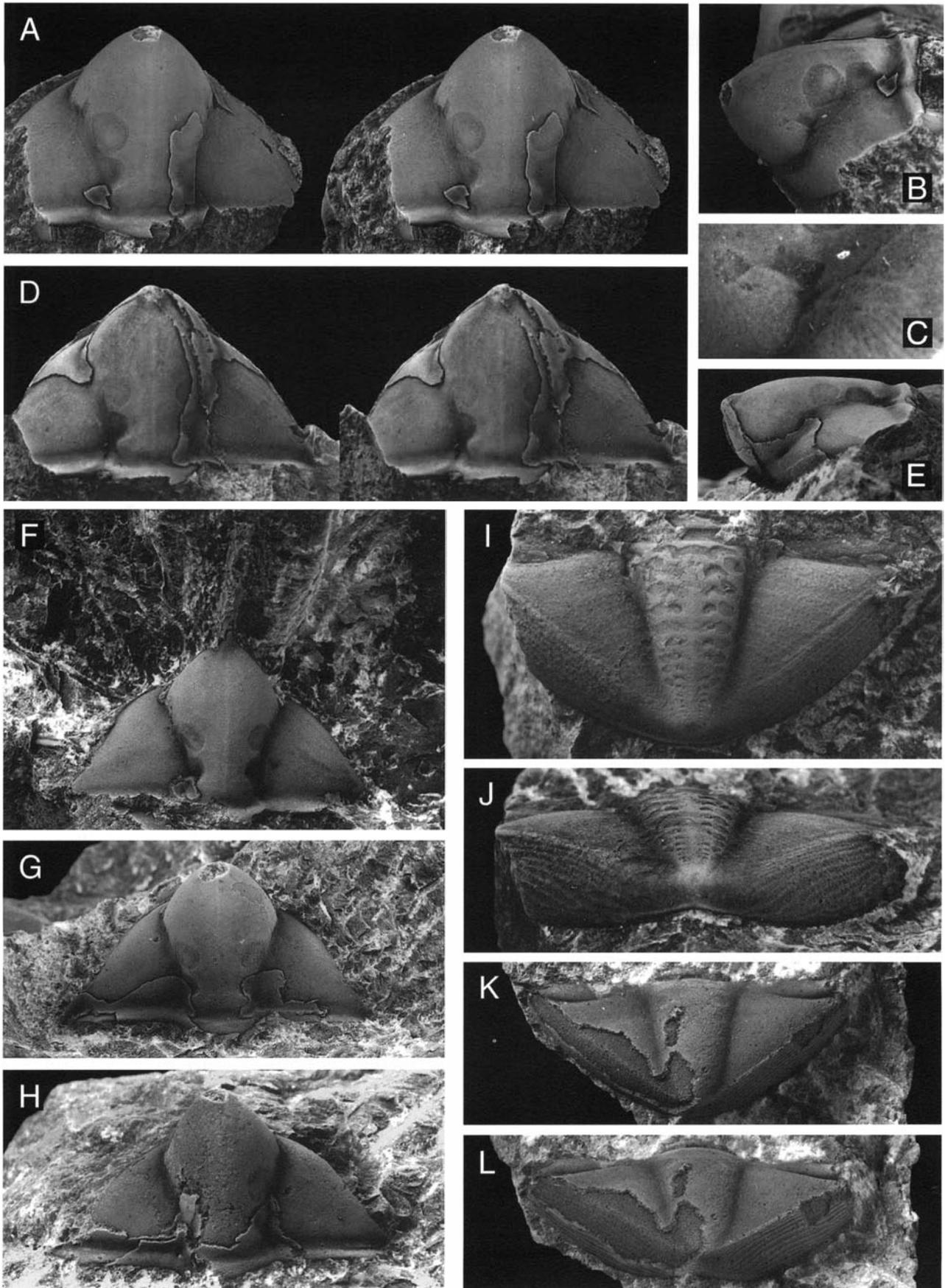
Single specimens have been found in the Lysaker Member at Slemmestad, complete specimen A 1164 was not sampled *in situ*, cranidium A 538 is from bed 55, Zone of *A. expansus*.

Ampyx nasutus is a typical element of the fauna in the *A. expansus* and *A. 'raniceps'* Zones of Sweden (see, e.g., Tjernvik & Johansson 1980), and it also occurs in the same interval of the eastern Baltic area (Schmidt 1894, 1907). At least in Norway it ranges upwards into the *M. obtusicauda / gigas* Zones (Wandås 1984). Schmidt (1907) also listed it from the top of the Volkhov Stage, which, though, remains to be documented.

Description. – See Schmidt (1894) and Whittington (1950); the present remarks are supplementary to those descrip-

tions. Whittington (1950) described three pairs of glabellar muscle areas (Whittington 1950, p. 554 and Textfig. 6A). The material at hand shows that the anterior pair is composite, consisting of a main posterior impression and a minute anterior impression situated just above the axial furrow, so that F3 is grossly rounded L-shaped in outline (right lateral view; cf. Fig. 246C). The lectotype specimen, illustrated by Reyment (1980), has a clearly bicomposite F3. Glabellar spine subcircular in cross-section, curving upwards; spine length 0.8–1.0 times the length of glabella. Wandås (1984, Pl. 12E) figured a cranidium with a spine approaching 1.5 times the length of glabella. It appears that Schmidt (1894) was of the impression that some specimens of *A. nasutus* lack a spine, and the longest preserved spine in the eastern Baltic material was half as long as glabella (Schmidt 1894, p. 78). It cannot be excluded that spine length relates to environment, with a short spine in specimens that lived on coarser substrate and a long spine in individuals that lived on a muddy substrate. Alternatively there may be an evolutionary trend towards a longer spine. Faint, oblique genal ridges cross the fixigenae of internal moulds, running from a point level with F3 towards genal angles, but are cut by the facial suture shortly in front of the genal angles (Fig. 246D). The ridges, which are effaced on testaceous material, are double, and the two branches diverge gently away from axis in the adaxial part, but then run almost parallel. In exfoliated specimens the foremost part of the fixigenae, anterior to the genal ridges, is occasionally covered with a rather coarse punctation, sometimes arranged in 'reticulate' rows, especially close to the genal ridges, and which generally radiate away from axis. The genal ridges and the radiating pattern are fairly distinct on internal moulds of large specimens, whereas smaller cranidia occasionally show a smooth mould surface. The reticulate pattern is not reflecting the external ornamentation. Whittington (1950, p. 555) described the cephalic posterior border as convex. In the specimens at hand the border is flat or gently concave, slanting forwards. It is characteristic for *A. nasutus* that the cephalic posterior border furrow is almost straight, with a posterior turn only in the extreme distal part. The minute impression in the distal part of the furrow is here described as weakly (adults)

Fig. 246. *Ampyx nasutus* (Dalman, 1827). □A–C. Largely exfoliated cranidium, dorsal (stereo pair) and side views, $\times 3$. Close up in C shows anterior glabellar muscle insertion site (F3), $\times 8$. LO 7109 (LU 100a), lower beds, Fågelsång, loc. E21b. □D–E. Partly exfoliated cranidium, dorsal (stereo pair) and side views, $\times 3$. MGUH 23.027 (GM 1987.22), Vasegård, Bornholm. □F. Exfoliated cranidium showing proximal part of glabellar spine, $\times 5$. MGUH 23.028 (S 1610), bed +13, Skelbro. □G. Largely exfoliated cranidium, $\times 3$. MGUH 23.029 (S 1685a), bed +13, Skelbro. □H. Largely exfoliated small cranidium, $\times 6$. MGUH 23.030 (S 1729), bed +13, Skelbro. □I–J. Exfoliated pygidium showing axis and border, dorsal and posterior views, $\times 5$. MGUH 23.031 (S 1541), bed +13, Skelbro. □K–L. Partly exfoliated pygidium showing curved pleural furrow, dorsal and oblique posterior views, $\times 6$. MGUH 23.032 (K 1179), bed 8, Killeröd site b.



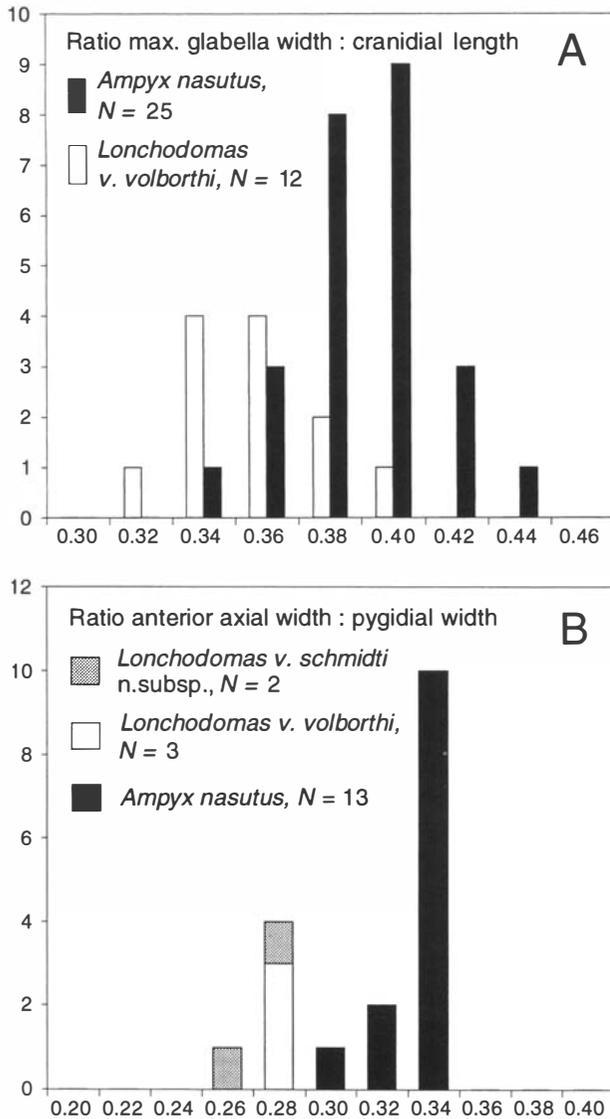


Fig. 247. *Ampyx nasutus* versus *Lonchodomas volborthi volborthi*. □A. Cranidia. Comparison of ratios between maximum glabella width and cranial length (sag.). □B. Pygidia. Comparison between ratios of anterior axial width and pygidial length (sag.).

to moderately (juveniles) impressed (cf. Whittington 1950, p. 555); it is much more distinct on internal moulds. When the test is intact the pit is somewhat elongate, whereas internal moulds show a simple round shape. An additional shallow impression is developed in the proximal part of the posterior border furrow, close to the triple junction between the border furrow, the axial furrow and the occipital furrow. The slightly elongate impression, which is visible also on outside of test, continues onto the anterior part of the posterior border.

The test surface of cranidium is finely punctate; the sculpture, however, is distinctly coarser than in the coeval *Loncho-*

domas volborthi (Schmidt, 1894), especially on glabella; it is less distinct on the posterior half of fixigenae, and the glabellar muscle areas are smooth.

Affinities. – *A. nasutus* (Dalman) is superficially quite similar to *Lonchodomas volborthi* (Schmidt, 1894), and isolated skeletal parts, notably cranidia and juveniles, may be difficult to assign, despite the circumstance that the two species belong to different genera. By comparison the cranidium of *A. nasutus* is slightly less convex (exsag.), the glabella is less pointed, broader (Fig. 247A), without preoccipital lobes, F3 is less obviously composite, the spine base is positioned at a relatively lower level above anterior border, the posterior border is narrower, delimited by an almost straight border furrow, the minute impression in the posterior border furrow near genal angle is indistinct (or nearly effaced), when the test is intact, and developed as a simple round hole (not slit-like) on internal moulds, and the test surface is more coarsely pitted, especially on glabella. Specimens of *L. volborthi* with intact test show an angular glabellar spine, not round as in *A. nasutus*; the spine is, however, almost round in internal moulds of *L. volborthi*. The pygidium of *A. nasutus* is readily separated from *L. volborthi* by showing no distinct edge or sharp bend between the pleural fields and the border, the axis is broader (tr.) (see Fig. 247B), and the terrace lines of the border region typically continue onto the outer part of the pleural fields. It is also characteristic that the anterior furrow, delimiting the anterior half rib, is curved, not straight as in *L. volborthi*.

Compared to adults the juvenile cranidium of *Ampyx nasutus* is more convex (exsag.), the glabella tend to be relatively narrower (tr.), the pit in posterior border furrow near genal angle is better defined, so the overall appearance is quite 'volborthi-like'. Juvenile cranidia of *A. nasutus* are separated from *L. volborthi* by the lack of preoccipital lobes, the narrower posterior border, the round frontal spine, and the different test ornamentation. The juvenile pygidia of *A. nasutus* have a 'volborthi-like' marked edge between the border and pleural fields, and which may even be rim-like, but the pygidia are identified by the broad axis (tr.) and the curved anterior pleural furrow.

A. nasutus is distinguished from other species of *Ampyx* by its large size, the broad, virtually non-carinate, glabella with distinct F1–F2, the broad pygidial axis, the curved anterior pleural furrow of pygidium, and a few terrace lines often continues from pygidial border onto outer part of pleural fields.

Remarks. – *Lonchodomas volborthi* is the dominant raphiophorid species in the Lysaker Member at Slemmestad, and it is likely that material was identified with *A. nasutus* by Brøgger (1882). However, the complete specimen figured by Brøgger (1882, Pl. 5:15, a, b; refigured by Wandås 1984, Pl. 12I) does represent *A. nasutus*, and the collections at the Paleontological Museum, Oslo, contain surprisingly few *L. volborthi*, but several specimens of *A. nasutus*. This bias is

presumably reflecting the different size of these species. The pygidium figured by Modliński (1973, Pl. 5:2), identified with *L. volborthi*, has a curved anterior pleural furrow, and appears to belong to *A. nasutus*.

Genus *Rhombampyx* Fortey, 1975

Type species. – (OD) *Rhombampyx rhombos* Fortey, 1975.

Remarks. – *Rhombampyx* was erected to accommodate two Spitsbergen species, *R. rhombos* and *R. tragula*, and the South American *Raphiophorus? lamasi* Harrington & Leanza, 1957 (Fortey, 1975a). The pygidium of *R. tragula* is unknown, and I strongly doubt that it truly belongs to *Rhombampyx*, as the glabella appears rather specialized, and the backward protrusion of the occipital region is a unique feature. Typical representatives of *Rhombampyx* are smallish, characterized by a highly inflated glabella with effaced or faintly impressed muscle areas, and a salient feature is the unusually short pygidium with a high border, delimited from the pleural fields by a narrow rim. The Chinese species *Ampyx yui* Lu in Lu *et al.*, 1965 (Arenig) complies with these characteristics and should be transferred to *Rhombampyx* as indicated by Zhou *et al.* (1984) (see especially Lu 1975, Pl. 40:12, 14). These authors also compared *R. yui* to *Ampyx priscus* Thoral, 1935, but that species has a typical long *Ampyx* pygidium, and should not be included in *Rhombampyx*. The Spitsbergen species *Ampyxoides inermis* Fortey, 1975 has a rather *Rhombampyx*-like pygidium, but the indicated absence of a glabellar spine (cf. Fortey 1975a) would be unusual for the genus. The North American material referred to as *Ampyx* sp. by Ross (1967 p. 22, Pl. 7:20–21) almost certainly represents *Rhombampyx*.

The Baltoscandian species *Ampyx pater* Holm, 1882, *Ampyx simonkovensis* Balashova, 1966, and *Ampyx glaber* Poulsen, 1965 are here assigned to *Rhombampyx*, together with a new species, *R. frater* n.sp., as they are characterized by a highly inflated, smooth glabella, and a short, very characteristic pygidium with high border. The inadequately known *Lonchodomas domatus* Angelin, 1854 may also belong to this group, see introductory remarks on family above.

Rhombampyx glaber (Poulsen, 1965)

Figs. 248–250

Synonymy. – □v 1936 *Ampyx volborthi* Schm. – C. Poulsen, p. 48 (listed). □v 1936 *Ampyx* n.sp. – C. Poulsen, p. 48 (listed). □v cf. 1952 *Ampyx pater* Holm [*partim*] – Skjeseth, pp. 176–178; Pl. 5:4b, 7; non Pl. 5:2, 12–16 [= *Rhombampyx pater* (Holm)] (illustrations of cranidium). □v 1965 *Ampyx glaber* n.sp. [*partim*] – V. Poulsen, pp. 98–101; Pl. 8:5–7, 11; non Figs. 8–10 [= *Lonchodomas tenuis* n.sp.] (description, occurrence, illustrations of cephalon and cranidium).

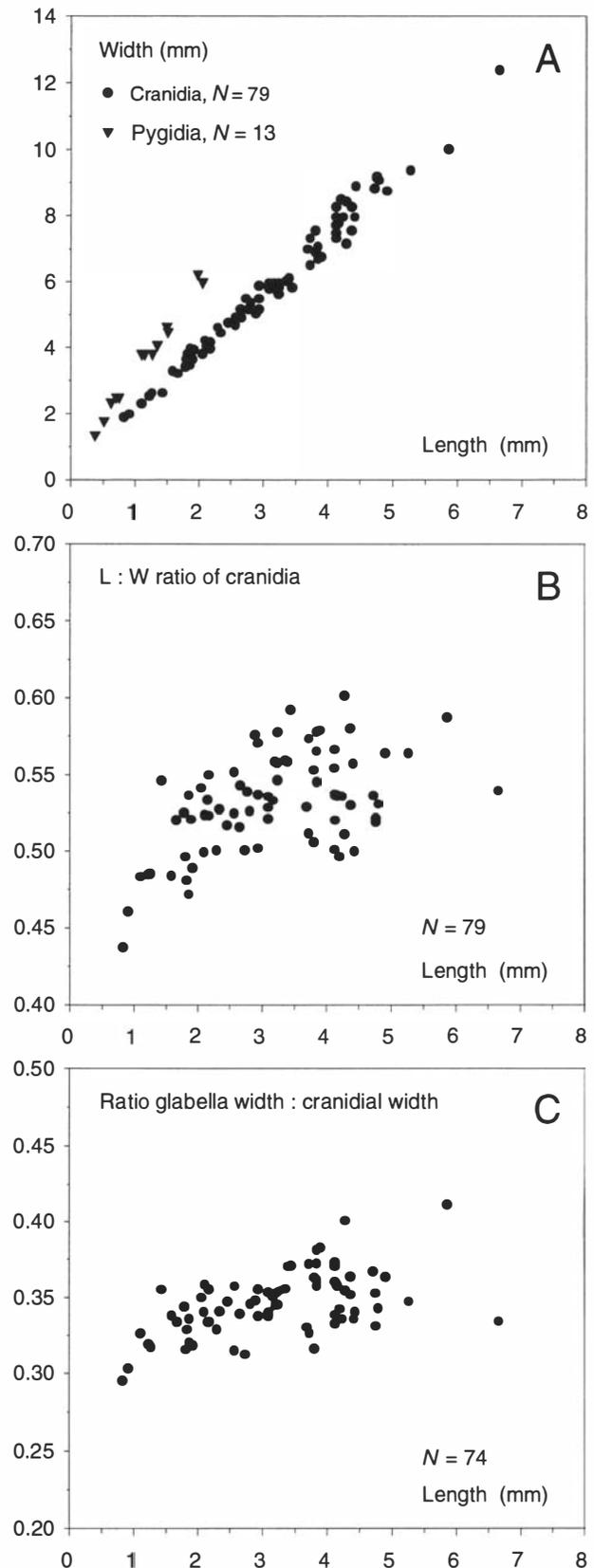


Fig. 248. *Rhombampyx glaber* (Poulsen, 1965). □A. Maximum width plotted against sagittal length of cranidia and pygidia. □B. Cranidia. Ratio between maximum width and sagittal length plotted against length. □C. Cranidia. Ratio between maximum glabella width and cranial length (sag.) plotted against cranial length.

Holotype. – Cranidium MGUH 9463 from the Skelbro beds, Skelbro, figured by V. Poulsen (1965, Pl. 8:5–7).

Material. – 166 cranidia and 19 pygidia, plus cranidium A 609c (im) and pygidium A 633 (im) [MGUH 23.044], referred to as *R. cf. glaber*.

List of material. – □Cranidia S 4 (im), S 7 (im) [MGUH 23.033], S 12 (im), S 16 (t), S 18a (im), S 21 (im), S 30 (im), S 40 (pim), S 45a (im), S 51 (t), S 63a (im), S 63b (im), S 81a (t), S 83 (im), S 94 (t), S 105 (im), S 107 (pim), S 130a (im), S 130b (im), S 136a (im), S 136b (im), S 139 (im), S 140 (t), S 146 (im), S 151a (im), S 151b (im), S 161 (im), S 173 (im), S 179 (im), S 185a (im), S 185b (im), S 186 (im), S 206a (im), S 206b (im), S 207 (im) [MGUH 23.034], S 210 (im), S 212 (im), S 216 (im), S 238b (c), S 244 (im), S 250 (im), S 253 (im), S 256 (im), S 257 (im), S 260 (im), S 269 (c), S 276a (im), S 276b (im), S 276c? (im), S 295 (pim), S 296 (pim), S 298 (im), S 300 (pim), S 302 (t), S 305 (pim), S 310? (im), S 318 (im), S 322 (t), S 346 (im), S 351 (pim), S 353 (pim), S 394 (pim), S 415 (im), S 416 (pim), S 421 (im), S 426? (im), S 440 (im), S 458 (im), S 465 (pim), S 468 (im), S 483a (im), S 483b (im), S 486 (im), S 488 (im), S 501a (im) [MGUH 23.036], S 501b (t), S 501c (t), S 504a (im), S 504b (im), S 504c (im), S 505a (t), S 505b (im), S 507a (t) [MGUH 23.035], S 507b (im), S 518 (pim), S 520a (im), S 520b (pim), S 532a (im), S 532b (im), S 533a (im), S 533b (t), S 533c (im), S 544b (im), S 552b (pim), S 553a (pim), S 553b (im), S 558 (im), S 588a (pim), S 588b (pim), S 588c (im), S 588d (im), S 588e (t), S 588f (im), S 588g (im), S 588h (im), S 588i (im), S 594a (im), S 594b (pim), S 594c (im), S 595a (im), S 595b (im), S 595c (im), S 595d (im), S 595e (im), S 595f (pim), S 595g (im), S 595h (im), S 595i (im), S 595k (im), S 595l (im), S 597 (t), S 598 (im), S 606 (t), S 607a (im), S 607b (im), S 611a (im), S 611b (im), S 612a (im), S 612b (im), S 614 (t), S 617 (im), S 618 (pim), S 619 (im), S 628a (im), S 628b (im), S 632? (im), S 633 (im), S 635a (im), S 639a (im), S 639b (t), S 639c (t), S 639d (t), S 639e (pim), S 639f (t), S 639g (t), S 639h (pim), S 639j (im), S 642a (im), S 642b (im), S 647a (t), S 647b (pim), S 650 (im), S 654a (pim), S 654b (t), S 654c (im), S 661 (im), S 693 (im), S 700 (t), S 1678 (im), GM 1987.5 (im), GM 1987.6 (im), GM 1987.8 (im), GM 1987.10 (im), GM 1987.12 (im), GM 1987.18a (im), GM 1987.18b (im). □Pygidia S 18b (im), S 25 (t), S 28 (t) [MGUH 23.038], S 45b (pim) [MGUH 23.039], S 81b? (t) [MGUH 23.041], S 106 (em), S 164 (im), S 187 (im) [MGUH 23.040], S 208b (im) [MGUH 23.043], S 297 (im), S 345 (im), S 380 (t) [MGUH 23.037], S 544a (t), S 552c (im), S 595j (im), S 596 (c), S 635b (t) [MGUH 23.042], S 639i (im), GM 1871.1025 (im).

Occurrence. – The species occurs in great abundance in beds interval –21 to –18 at Skelbro, single specimens have been found in bed –16. The entire interval belongs to the lower half of the *M. polyphemus* Zone.

The material referred to as *Rhombampyx cf. glaber* is from bed M-1 at Slemmestad, representing the upper part of the *M. polyphemus* Zone. *R. glaber*, or a closely related form, also occurs in the Herramb Member at Ringsaker (*M. polyphemus* or *M. estonica* Zone), see discussion below.

Rhombampyx glaber has not been reported from Sweden or the eastern Baltic area, but it is unknown what *Ampyx aff. pater sensu* Tjernvik (1980), listed from the *M. polyphemus* Zone of Sweden, encompasses.

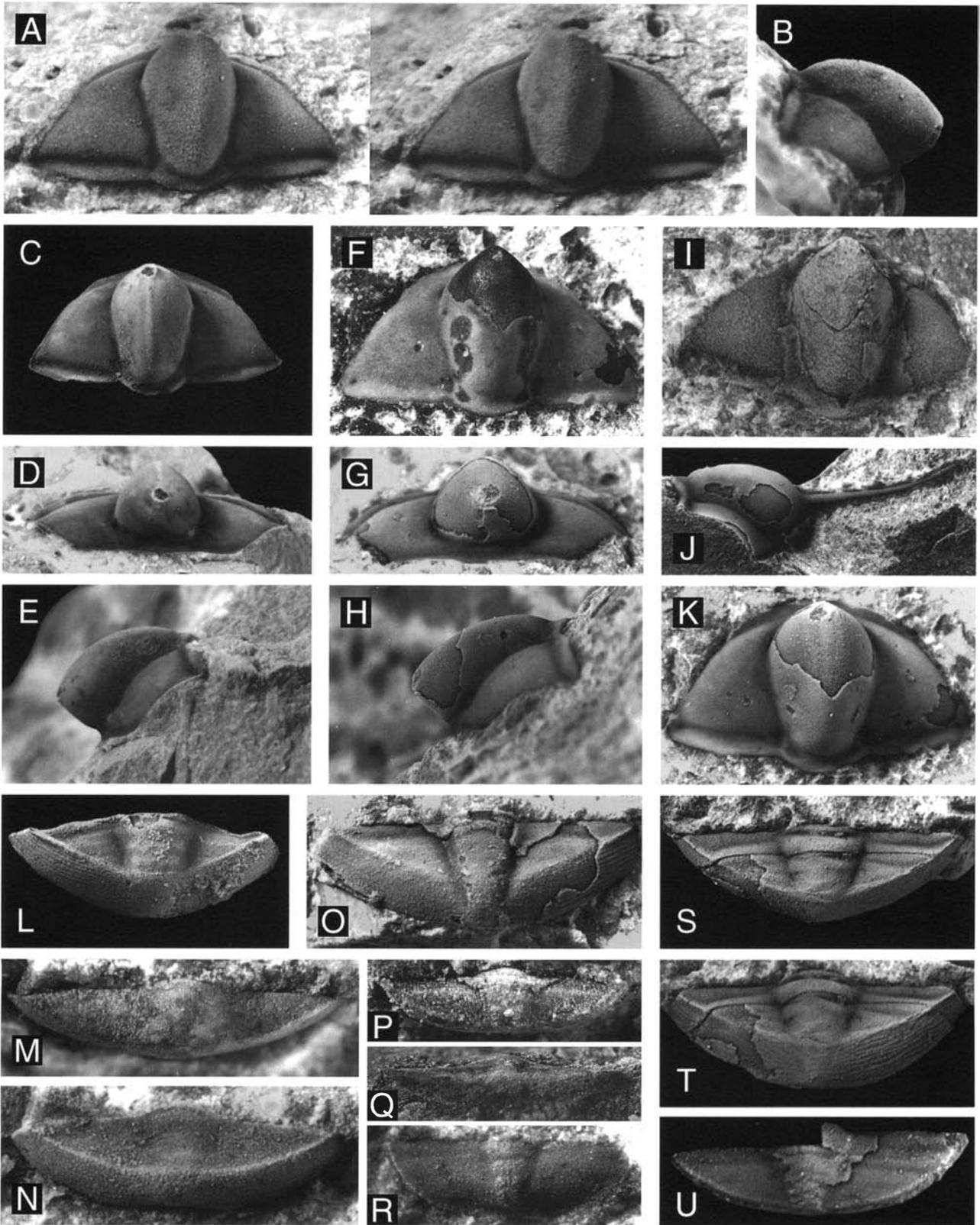
Diagnosis. – Cranidium strongly convex (exsag.), glabella distinctly vaulted, pointed, overhanging anterior margin; glabellar muscle scars almost effaced; posterior border narrow, delimited by nearly straight border furrow; cephalic test surface smooth. Pygidium short with high border; axis continues onto border, although with a very low relief. [Emended from V. Poulsen 1965.]

Description. – Small for a raphiophorid, largest cranidium 6.7 mm long, largest pygidium 2.1 mm long. The cephalon is exhaustively described by V. Poulsen (1965, p. 99). Maximum glabella width equivalent to 0.29–0.41 of the cranidial width (mean 0.35; $N = 78$, see Fig. 248C).

Hypostome and thorax unknown.

The pygidia originally described as *Ampyx glaber* by V. Poulsen (1965, pp. 99–100) are here identified with *Lonchodomastenus* n.sp., and another group of pygidia is attributed to *Rhombampyx glaber*. Pygidium subfalcate in outline with straight anterior margin and acute anterolateral corners; L:W ratio 0.32–0.35 in specimens longer than 1.2 mm, and 0.27–0.31 in shorter ones (Fig. 250A). Axis moderately vaulted and roughly of the same height all the way back; it is comparatively narrow, the width at anterior margin accounts for 0.24–0.27 of the pygidial width in most specimens, but those from bed –18 have a ratio of about 0.3. Axis delimited by shallow, wide axial furrows, which are more distinct on internal moulds; it tapers evenly backwards, but even specimens with intact test show an indistinct axial extension onto the border, which terminates short off posterior margin (Fig. 249T). Anterior portion of axis comprises three faint axial rings in addition to the anterior, well-separated, short (sag.), articulating half-ring; no rings are discernible in the axial part on the border. Two rows of dark-coloured muscle markings are occasionally present in the ring furrows. The markings consist of subround, comparatively large and distinct distal spots situated close to the axial furrows, and small, more indistinct spots positioned close to sagittal line. The inner spots are often joined across midline by a narrow band. Three such double pairs of markings are situated on the axis between anterior margin and border; in one instance four additional single pairs occur on the posterior part of the axis in the border region, where only the inner pair is present. Pleural fields virtually flat, with indistinct segmentation, apart from the anterior half rib, separated by a shallow, indistinct furrow. Border gently convex, steeply down-sloping, in juvenile specimens subvertical; border area is well set off by a marked change of slope, and a narrow rim is developed in some specimens at the edge of the pleural fields. In a minute juvenile pygidium (Fig. 249R), 0.4 mm

Fig. 249. □A–H, J–T. *Rhombampyx glaber* (Poulsen, 1965). □A–B. Exfoliated small cranidium, dorsal (stereo-pair) and side views, $\times 14$. MGUH 23.033 (S 7), bed –21, Skelbro. □C–E. Exfoliated cranidium, dorsal, frontal and side views, $\times 9$. MGUH 23.034 (S 207), bed –21, Skelbro. □F–H. Partly exfoliated cranidium with transparent cuticle showing dark coloured glabellar muscle insertion sites, dorsal (non-whitened), frontal and side views, $\times 9$. See also K. MGUH 23.035 (S 507a), bed –21, Skelbro. □I. Partly exfoliated cranidium, side view showing upturned glabellar spine, $\times 6$. MGUH 23.036 (S 501a), bed –18, Skelbro. □J. Same specimen as F–H, dorsal view, $\times 9$. □K. Pygidium showing terrace-line pattern on border, $\times 9$. MGUH 23.037 (S 380), bed –19, Skelbro. □M–N. Tiny juvenile pygidium, dorsal and oblique posterior views, $\times 25$. MGUH 23.038 (S 28), bed –21, Skelbro. □O. Largely exfoliated pygidium showing axis continuing onto



border, oblique posterior view, $\times 9$. MGUH 23.039 (S 45b), bed -21, Skelbro. □P-Q. Exfoliated tiny juvenile pygidium, dorsal and posterior views, the latter showing distinct mesial arch, $\times 20$. MGUH 23.040 (S 187), bed -21, Skelbro. □R. Exfoliated tiny juvenile pygidium, dorsal view, $\times 15$. MGUH 23.041 (S 81), bed -21, Skelbro. □S-T. Pygidium showing undetached thoracic segment, dorsal and oblique posterior views, the latter showing axial continuation onto border, $\times 12$. MGUH 23.042 (S 635b), bed -18, Skelbro. □U. Exfoliated tinypygidium, $\times 25$. MGUH 23.043 (S 208), bed -21, Skelbro. □I. *Rhombampyx* cf. *glaber* (Poulsen, 1965). Exfoliated cranidium, $\times 8$. MGUH 23.044 (A 609), bed M-1, Slemmestad.

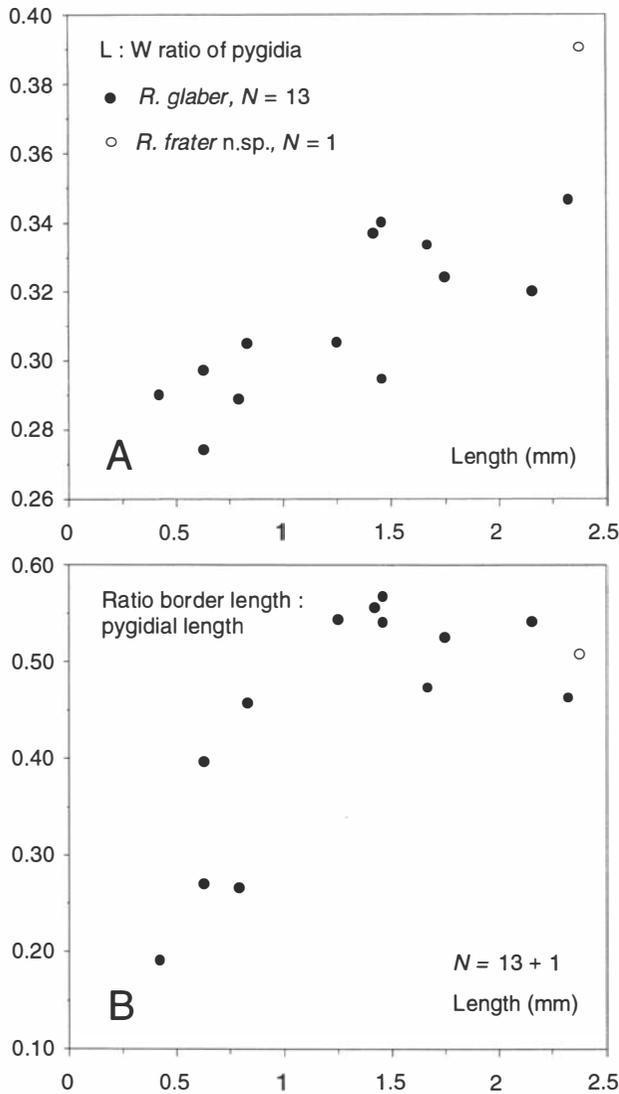


Fig. 250. Pygidia of *Rhombampyx glaber* (Poulsen, 1965) (●) and *Rhombampyx frater* n.sp. (○). □A. Pygidial L:W ratio plotted against pygidial length. □B. Ratio between maximum border width (adjacent to mesial arch) and pygidial length plotted against pygidial length.

long, the border is bent down only posteriorly, while the anterolateral parts are confluent with the pleural fields without change of slope. Maximum border width is attained adjacent to the gentle mesial arch; the relative border width increases markedly with size up to a pygidial length of 1 mm and then remains largely constant (Fig. 250B). In small specimens the mesial arch even creates an incision in the margin when viewed dorsally (Fig. 249P). Articulating facets very small, pointed triangular, subvertical, situated roughly at an angle of 45° to sagittal line. Test surface of pleural fields smooth; border area covered with fine, closely spaced terrace lines (Fig. 249L). The lines curve slightly forward-upwards mesially. Doublure not visible in the available material.

Affinities. – *R. glaber* is rather like *R. pater* (Holm), *R. simonkovensis* (Balashova), and *R. frater* n.sp., and these species are inferred to be closely related. Shared features are moderate size, a strongly inflated, almost smooth glabella, and a similar, very characteristic type of pygidium.

R. glaber is distinguished from *R. pater* by the more inflated glabella, clearly overhanging anterior margin, the cranium is more trapezoidal in outline owing to the wider anterior border (tr.), the cephalic posterior border furrow is almost straight, not curving forwards distally, the pygidium has a broader border, relatively smaller pleural fields and a wider axis with fewer axial rings.

R. simonkovensis is inadequately known (cf. Balashova 1966, pp. 21–22; Pl. 2:1–2), but *R. glaber* presumably has a more inflated glabella with a stronger sagittal curvature, slightly more convex fixigenae and a shorter pygidium with fewer axial rings.

Differences from *R. frater* n.sp. are enumerated in the section on that species. *R. glaber* is readily distinguished from species of *Ampyx* by the prominently vaulted glabella, clearly pointing forwards and overhanging anterior margin, the lack of glabellar muscle impressions, the almost straight posterior cephalic border furrow, the smooth cephalic test, and the remarkable, short (sag.) pygidium with a steep, wide border showing a vestigial continuation of axis.

Remarks. – A slightly damaged cranium and pygidium from bed M-1 at Slemmestad match the Bornholm material in all preserved features, except that the anterior glabellar overhang is minimal. It is preferred to treat the sparse Norwegian material as *R. cf. glaber* awaiting recovery of better preserved specimens, but it certainly more closely resembles *R. glaber* than *R. frater* n.sp.

One of the crania identified with *Ampyx pater* by Skjeseth (1952, Pl. 5:4b, 7) was assigned to *A. glaber* by V. Poulsen (1965, p. 10). The specimen has been studied, and such an identification is possible, but owing to the lack of preparation the anterior glabellar overhang is exaggerated, and the glabella falsely appears more slender than it is in reality. However, the posterior border furrow does not curve forwards distally, which is a very characteristic feature of *R. pater*, and an assignment to that species cannot be upheld. The cranium is tentatively allocated to *R. glaber*.

For remarks on *Ampyx volborthi sensu* Regnéll (1942), tentatively assigned to *R. glaber* by V. Poulsen (1965), see *Lonchodomas volborthi volborthi* (Schmidt, 1894).

Rhombampyx frater n. sp.

Figs. 250–252

Synonymy. – □? 1980 *Ampyx pater nasutus* Dalman – Tjernvik & Johansson, p. 192 (listed).

Derivation of name. – Latin *frater* = brother.

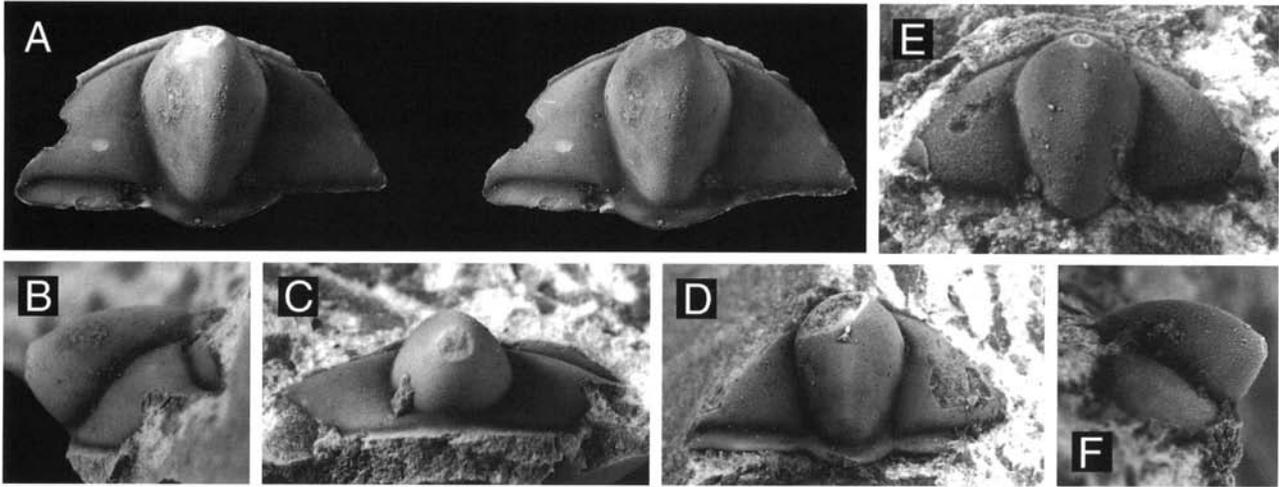


Fig. 251. *Rhombampyx frater* n.sp. □A–C. Holotype. Cranidium, dorsal view (stereo-pair), side view and frontal views, $\times 8$. MGUH 23.045 (S 974), bed –4, Skelbro. □D. Paratype. Cranidium, $\times 5$. MGUH 23.046 (S 944), bed –4, Skelbro. □E–F. Small cranidium, dorsal and side views, $\times 8$. LO 7082 (LU 25b), Tommarp.

Holotype. – Cranidium MGUH 23.045 (S 974) (Fig. 251A–C) from 2 cm below top of bed –4, Skelbro, Zone of *M. simon*.

Paratypes. – Cranidium MGUH 23.046 (S 944) (Fig. 251D) from 3 cm below top of bed –4, Skelbro; pygidium LO 7083 (LU 25c) (Fig. 252) from an unknown level at Tommarp.

Additional material. – Twenty-four cranidia and 3 pygidia.

List of additional material. – □Crania S 857 (t), S 870 (t), S 880 (c), S 943 (t), S 952 (t), S 985 (t), S 992 (t), S 999 (t), S 1077? (t), S 1145 (im), S 1162? (c), S 1181 (c), S 1223 (c), S 1235 (c), 1257? (c), S 1657 (t), S 1257? (im), K 26 (t), K 647a? (c), K 647b? (c), LU 25b (t) [LO 7082], LU 27a (t), LU 27b (t), LU 27c? (t). □Pygidia S 869 (c), S 1027 (c), LU 25d? (em).

Occurrence. – *Rhombampyx frater* n.sp. occurs in bed interval –7 to +6 at Skelbro, representing the upper part of the *M. simon* Zone and the lower part of the *M. limbata* Zone (infrequent). A few specimens have been found within the *M. simon* Zone of SE Scania at Gårdlösa-2 (bed L) and Gårdlösa-4a (beds 4, 7). The museum specimens examined are from an unknown level at Tommarp.

Diagnosis. – As *R. glaber*, but glabella is just slightly more inflated, posterior border of cranidium is wider, and raised higher above fixigenae; glabellar muscle scars vestigial; pygidium relatively narrower, with less vaulted axis.

Description. – Small for a raphiophorid, largest cranidium ca. 7.2 mm long, largest pygidium 2.1 mm long. Cranidium subtrapezoidal in outline, about twice as wide as long, with strongly inflated glabella, and is basically alike the cranidium of *R. glaber*, described by V. Poulsen (1965 p. 99); the following remarks supplement that account. Glabella occupies about one third of the cranidial width, maximum glabella width attained at about one third of the cranidial length from front; it is round-arched in frontal view, posteriorly pseudo-

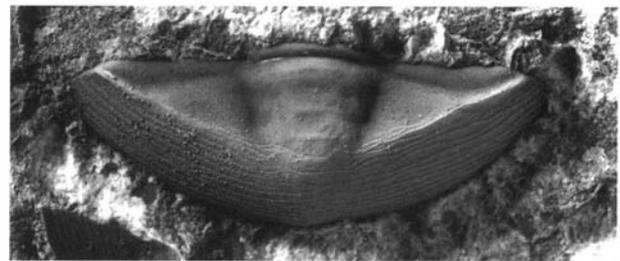


Fig. 252. *Rhombampyx frater* n.sp. Paratype. Pygidium, $\times 12$. LO 7083 (LU 25c), Tommarp.

carinate. F1 and F2 occasionally very faintly impressed, but normally glabellar muscle areas are not indicated on testaceous specimens; no internal moulds have been available for study. A small depression, possibly corresponding to F0, occurs at the triple junction of axial, occipital, and posterior border furrows. Occipital ring somewhat raised above the rear of glabella. Anterior border of cranidium gently forward sloping, almost horizontal, about twice as wide (tr.) as glabella (maximum width). Anterior margin gently and broadly arched in frontal view. Genal ridges not observed (no internal moulds available). Posterior border somewhat raised above fixigenae, especially in the distal half; adaxial part slopes moderately forward, abaxial part steeper. Cranidial test surface smooth.

Librigena, hypostome and thorax unknown.

Pygidium exceedingly alike *R. glaber*, but is relatively narrower, about 2.5 times as wide as long, and for the same reason the axis accounts for 0.3 of the pygidial width at anterior margin; it is slightly less vaulted than in *R. glaber*. It cannot be excluded, however, that the low pygidial W:L

ratio is due to the comparatively large size of the specimen (cf. Fig. 250A).

Affinities. – *Rhombampyx frater* n.sp. is rather like *R. glaber* Poulsen, *R. pater* (Holm), and *R. simonkovensis* (Balashova), and is almost certainly related to these species.

R. frater n.sp. is distinguished from *R. glaber* by the slightly wider (exsag.) anterior and posterior cranial border (the latter is also raised higher above the fixigenae), the less vaulted pygidial axis and the wider pygidial border. Besides, it is believed that *R. frater* attains larger sizes than *R. glaber*. Because of the pronounced convexity of *R. frater* n.sp., the glabella of this species also gives the impression of being relatively wider and higher raised above the fixigenae. The separating characters for *R. glaber* versus *R. pater* and *R. simonkovensis* also apply to *R. frater* n.sp. compared to these species.

The new species is separated from the Spitsbergian *R. rhombos* Fortey by its more strongly inflated, broader glabella, the wider posterior cephalic border, the shorter pygidial axis, and the unsegmented pleural fields of pygidium.

The Chinese material of *R. yui* (Lu), figured by Lu (1975, Pl. 40:8–14) is somewhat compacted, hence the prominence of the glabella is difficult to evaluate. The new Baltoscandian species seems, at least, to have a broader posterior cephalic border, but the glabella is also surmised to be more strongly inflated.

Remarks. – It is possible that *R. frater* n. sp. is identical to *Ampyx pater nasutus sensu* Tjernvik (1980, p. 192), reported from the *M. simon* Zone of mainland Sweden. In some respects the cranidium of the new species looks intermediate between *R. pater* and *A. nasutus*, but the designation *A. pater nasutus* is invalid, and the respective pygidia are much different. It is unlikely that the two species are closely related.

Genus *Cnemidopyge* Whittard, 1955

Type species. – (OD) *Trinucleus nudus* Murchison, 1839.

Cnemidopyge costatus n.subsp. A

Fig. 253

Material. – Four cranidia and 1 pygidium.

List of material. – □Cranidia S 1685 (im) [MGUH 23.047], F 190? (c) [MGUH 23.048], LU 139 (im), LU 151 (im) [LO 7124]. □Pygidium F 166 (im) [MGUH 23.049].

Occurrence. – *C. costatus* subsp. A occurs in the basal part of the *A. expansus* Zone at Skelbro (top of bed +13) and Fågel-sång (beds 19–20). Museum specimens from Röstånga (LU 139) and Fågel-sång (LU 151) are most likely from a similar level.

The upper Arenigian *C. costatus* n.subsp. A appears to be the earliest known representative of *Cnemidopyge*. For a discussion of British species of *Cnemidopyge*, see Hughes (1969) and Kennedy (1989).

Description. – Largest confidently identified cranidium 9.4 mm long (Fig. 253A); the tentatively assigned cranidium F 190 is about 12 mm long (Fig. 253B–C). Pygidium F166 is about 8 mm long. Cranidium roughly triangular in outline, about twice as wide as long. Glabella pyriform, distinctly vaulted, with a gentle convex sagittal curvature; it is pronouncedly triangular in frontal view, profile highest at about midline. Glabella fairly slender (tr.), occupying less than 0.3 of the maximum cranial width, greatest glabella width is attained about 0.2 of the cranial length from anterior margin. Glabellar front, which overhangs cranial margin, is drawn into a broad-based, carinate spine, triangular in cross-section, length unknown. Spine base rather lowered, height above anterior cranial margin equal to about one third of the maximum glabella width. Proximal part of the stout spine presumably approximately horizontal; distal part unknown. F1 and F2 large and very deeply impressed, giving a characteristic double constricted appearance to the posterior part of glabella; F3 obscure. Preoccipital lobes faintly inflated. All specimens, including F 190, show an elongate, narrow (tr.), gently convex glabellar portion between the lower limit of the well-impressed muscle areas and the axial furrow, extending to the anterior, obscurely indicated muscle area (F3). The axial furrows are actually bulging slightly outwards at level with F1–F2 (Fig. 253A, D). Occipital furrow rather shallow and wide throughout, curving faintly backward mesially, joining the axial furrows laterally. Occipital ring narrow (sag.), convex, slightly elevated above rear part of glabella, not separated from posterior border by axial furrows; posterior margin slightly arcuate backwards. Axial furrows and preglabellar furrow narrow and shallow, but better defined than in the other raphio-phorid species described here. Small, comparatively indistinct fossulae situated in the axial furrows just in front of maximum glabellar width. Anterior border of cranidium flat, uniformly very narrow throughout (sag., exsag.), and rather long (tr.) being almost twice as long as maximum glabellar width. Anterior margin of cranidium is broadly, evenly and gently arched in frontal view (Fig. 253F). Fixigenae gently convex, sloping moderately forwards; internal moulds show very faint genal ridges extending from a level adjacent to glabellar F3 towards genal angle; the ridges are not likely to be visible when the test is intact. Posterior border narrow (exsag.), barely concave, slanting forwards, especially so in the distal half, while the proximal part is nearly confluent with fixigenae. Posterior border furrow almost effaced and the border is defined just by a slight change of slope. Patches of intact test anteriorly on glabella and on fixigenae covered with a fine, dense punctation.

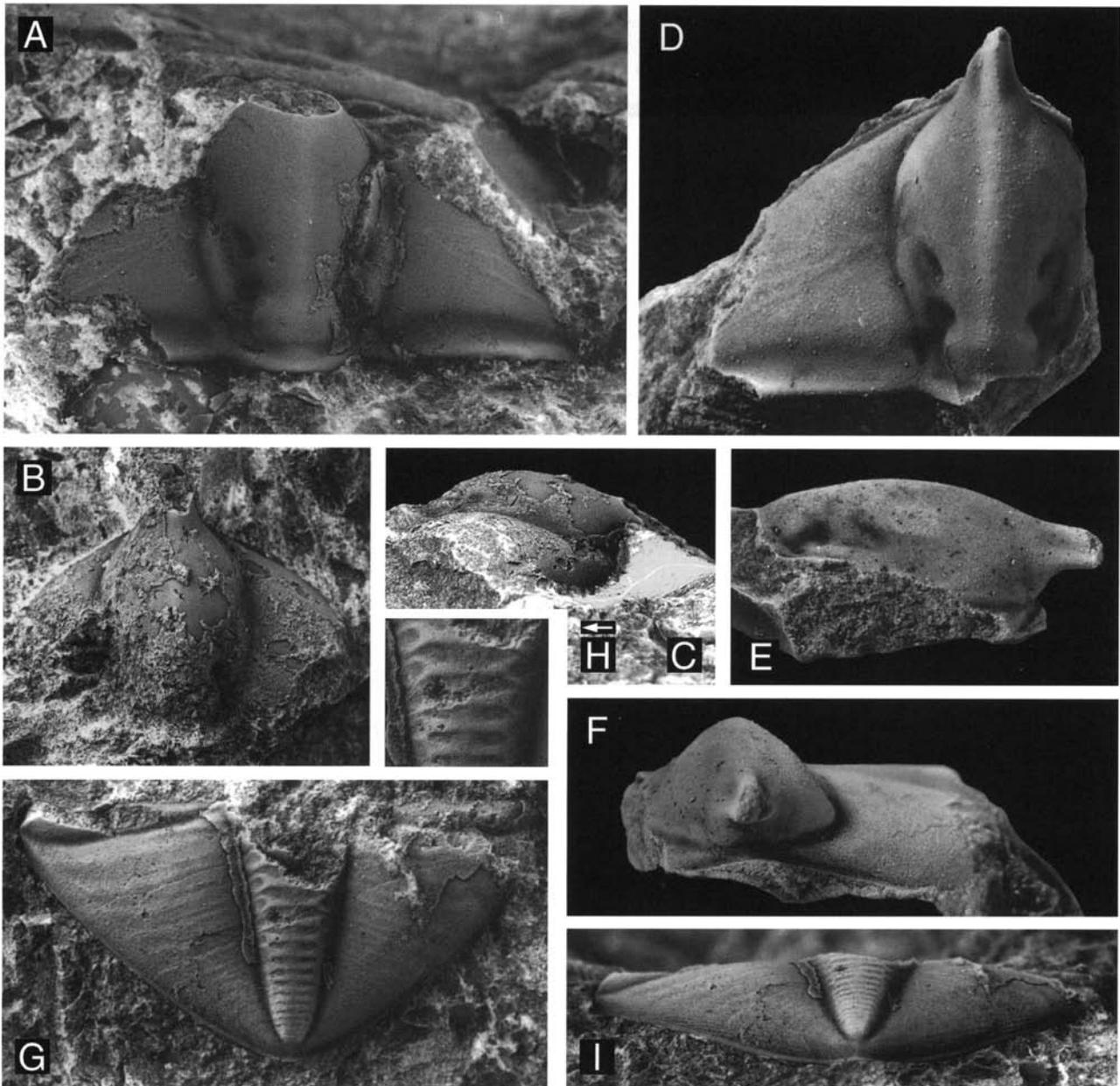


Fig. 253. *Cnemidopyge costatus* n. subsp. A. □A. Fragmentary, exfoliated cranidium, $\times 5$. MGUH 23.047 (S 1685), bed +13, Skelbro. □B–C. Corroded, large, tentatively assigned cranidium, dorsal and side views, $\times 3$. MGUH 23.048 (F 190), bed 20, Fågelsång. □D–F. Fragmentary exfoliated small cranidium, dorsal, side and frontal views, $\times 10$. LO 7124 (LU 151), Röstånga. □G–I. Exfoliated pygidium, dorsal and posterior views, $\times 5$, and close-up of axis, $\times 10$. MGUH 23.049 (F 166), bed 19, Fågelsång.

Pygidium F 166 (Fig. 253G–I), most likely matching the cranidia described above, is triangular in outline, almost twice as wide as long, anterior margin impaired but appears straight, anterolateral corners acute. Axis gently vaulted; the width at anterior margin accounts for about 0.25 of the pygidial width; it is long, tapering evenly backwards to terminate shortly in front of posterior margin; terminal piece acutely rounded. Axis consists of 16 or 17 rings, separated by shallow transverse furrows, even less deep mesially, plus

terminal piece and anterior half-ring. The lateral parts of each of the anterior five axial rings are divided into two crests encircling a shallow central impression (Fig. 253H). The crests of adjacent rings are closely set, and the anterior transverse furrows are therefore very narrow laterally. Pleural fields gently convex. Eight or nine faint pleural ribs are indicated, each consisting of two ridges of about equal height, running outwards, slightly backwards, distally curving in anterolateral direction, terminating short off margin.

Anterior half rib raised above pleural fields, from which it is delimited by a moderately impressed, narrow furrow running outwards-backwards, to curve forwards distally. A narrow border area is vaguely defined by termination of the faint pleural ribs and by a change of surface ornamentation. Pygidial margin thickened, particularly so in the posterior half; mesial arch indistinct. A few patches of test preserved on the pleural fields show a very fine, dense punctation. Impressions of fine terrace lines are visible on the mould surface in the border area; they are roughly parallel to but join the outer margin at a low angle. The lines fade out posteriorly, close to sagittal line.

Affinities. – *Cnemidopyge costatus* n.subsp. A closely resembles *C. costatus costatus*, but differs by having a slightly narrower glabella (tr.), the inflated basal glabellar areas are marginally smaller, and the pygidium has a less inclined, comparatively ill-defined border. The shared similarities are so obvious, however, that the Komstad Limestone material is separated only at the subspecies level, and it represents a probable ancestor of *C. costatus costatus*.

Cnemidopyge mammilatus (Sars) is separated from *C. costatus* by having a plump glabella not overhanging anterior margin, and it presumably lacks a spine (possibly rudimentary); the pygidium shows a better-defined border and differently shaped pleural ribs.

Remarks. – The large, poorly preserved cranidium F 190 is suspected to have been compacted, so the carinate appearance of glabella is lost. The glabellar spine, on the other hand, is very prominent, situated at a low level, which in combination with the elongate, convex small areas beneath the posterior muscle scars on glabella, suggest that the specimen presumably is conspecific with the better preserved museum material from the locality.

Whittard (1955) allocated '*Ampyx*' *costatus* to *Cnemidopyge*. This genus apparently evolved in Baltoscandia during the Arenigian, and subsequently migrated to Great Britain (during the Llandeilo) and to North America (during the Caradoc) (Hughes 1969, p. 63).

The 'mid' Arenigian *Ampyx salteri* was allocated to *Cnemidopyge* by Fortey & Owens (1987); in my opinion the pygidial structure of that species (as well as the not so well-impressed glabellar muscle areas) are more *Ampyx*-like.

Genus *Lonchodomas* Angelin, 1854

Type species. – *Ampyx rostratus* Sars, 1835 (SD Bassler 1915).

Lonchodomas volborthi (Schmidt, 1894)

Remarks. – The species was described in some detail by Schmidt (1894), but confusion later arose with regard to the limits of this taxon (e.g., Skjeseth 1952; V. Poulsen 1965). It

is here suggested to recognize two subspecies, *L. volborthi volborthi* (Schmidt, 1894), occurring in the *M. limbata* Zone, and *L. volborthi schmidti* n. subsp., ranging from the upper part of the *M. limbata* Zone and into the *A. expansus* Zone. It appears, however, that the former subspecies has a longer range in the eastern Baltic area (see below), and it is possible that the two forms merely represent ecophenotypes.

Lonchodomas volborthi volborthi (Schmidt, 1894)

Fig. 254–255

Synonymy. – □v 1882 *Ampyx nasutus* Dalm. [*partim*] – Brögger, p. 58 (occurrence). □1894 *Ampyx Volborthi* n.sp. – Schmidt, pp. 80–83; Pl. 6:11–20 (description, occurrence, illustrations of complete specimens, cephalo, pygidia). □1905 *Ampyx Volborthi* F.S. – Lamansky, p. 170 (listed). □1907 *Ampyx Volborthi* m. – Schmidt, pp. 64, 95 (listed). □? 1907 *Ampyx Knyrkoi* m. – Schmidt, pp. 65, 95; Pl. 3:11, 12, 12a (short description of cephalon, occurrence, illustrations of cephalo). □v non 1936 *Ampyx volborthi* Schm. – C. Poulsen, p. 48 [= *Rhombampyx glaber* Poulsen and *Lonchodomas tenuis* n.sp.]. □1942 *Ampyx volborthi* F. Schmidt – Regnéll, pp. 3–4; Textfig. 4 (occurrence, illustration of pygidium). □v non 1952 *Lonchodomas volborthi* (Schmidt, 1894) – Skjeseth, pp. 178–179; Pl. 5:1, 3, 5, 8, 9, 11. [= *L. cf. tenuis* n.sp.]. □non 1973 *Lonchodomas volborthi* (Schmidt, 1894) – Modliński, Pl. 5:2 [= *Ampyx nasutus*]. □v non 1975a *Ampyx volborthi* Schmidt, 1894 (*sensu* Skjeseth 1952) – Fortey, p. 69; Pl. 23:2. [= *L. cf. tenuis* n.sp.]. □v cf. 1980 *Ampyx* spp. – Tjernvik, p. 192, Textfig. 3 (occurrence).

Lectotype. – Here designated, complete specimen figured by Schmidt (1894, Pl. 6:11).

Material. – Fifteen cranidia and 4 pygidia.

List of material. – (Internal moulds if not otherwise stated). □Cranidia F 49 (t), F 62, LU 75 (t) [LO 7105], A 745, A 806 [MGUH 23.050], A 823, A 870, A 940, A 947, A 949 (pim), A 955, A 966 (pim) [MGUH 23.051], A 995?, A 1054? (t), PMO S 3247 (pim). □Pygidia A 813 [MGUH 23.052], A 854 (compacted), A 910 (pim) [MGUH 23.054], A 1064 [MGUH 23.053].

Occurrence. – *Lonchodomas volborthi volborthi* (Schmidt) occurs fairly frequently in bed interval M-6–M-10 at Slemmestad, and sparsely in bed interval M-11–M-14; except for bed M-6, belonging to the *M. simon* Zone, both intervals represent the lower subzone of the *M. limbata* Zone. Museum specimen PMO S 3247 is most likely from the upper part of the Hukodden Limestone. *L. volborthi volborthi* also occurs infrequently in the upper part of the *M. limbata* Zone at Fågelsång, whereas the subspecies has been found neither on Bornholm nor in SE Scania.

L. v. volborthi (Schmidt) has been reported from the eastern Baltic BIII α Zone (Schmidt 1894, 1907; Lamansky 1905) and also from the upper part of BII (Schmidt 1907, p. 95).

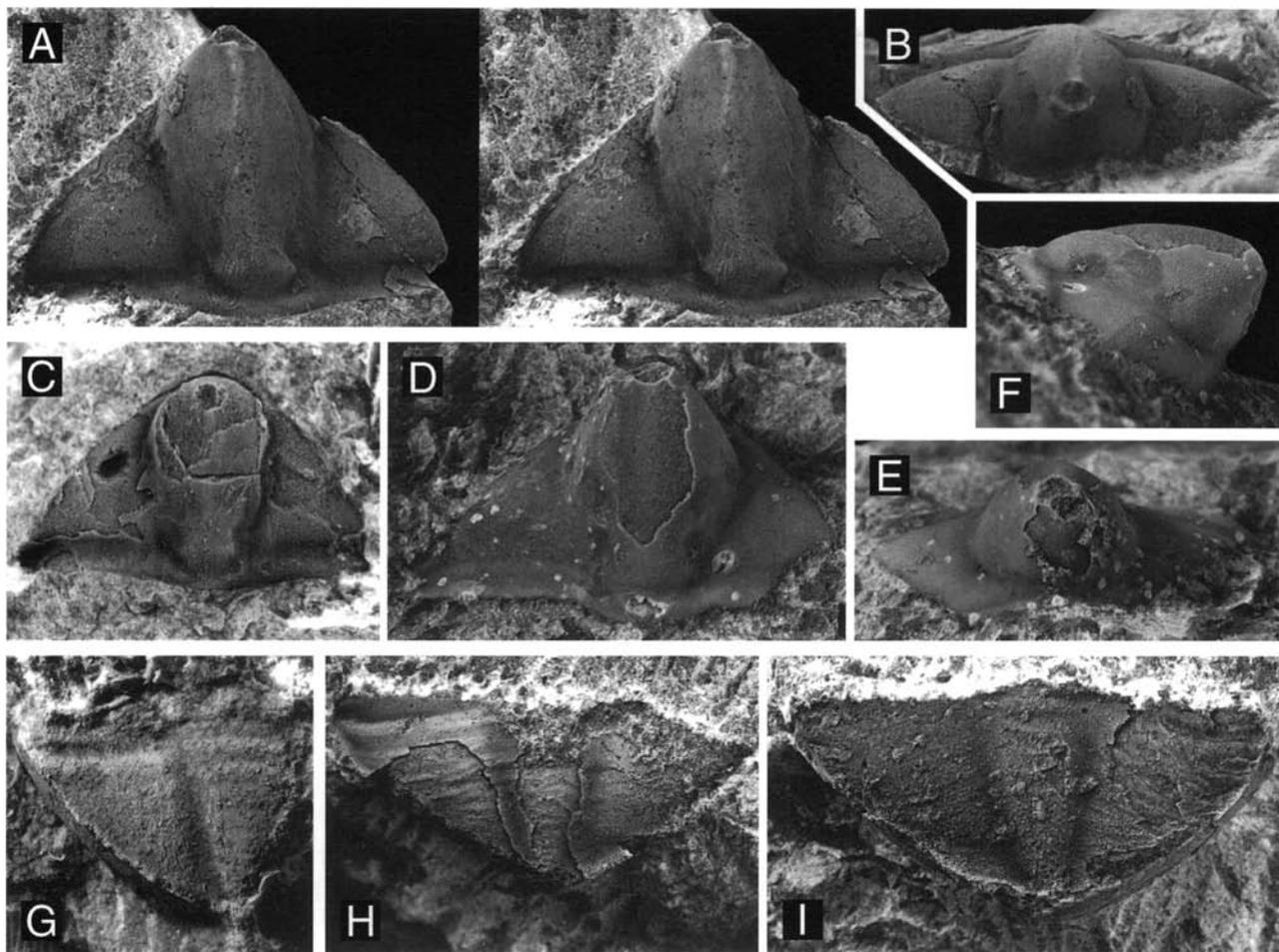


Fig. 254. *Lonchodomas volborthi volborthi* (Schmidt, 1894). □A–B. Exfoliated cranidium, dorsal view (stereo-pair) and frontal view, $\times 4$. MGUH 23.050 (A 806), bed M-7, Slemmestad. □C. Partly exfoliated, somewhat compacted cranidium, dorsal view, $\times 4$. MGUH 23.051 (A 966), bed M-10, Slemmestad. □D–F. Partly exfoliated cranidium with transparent cuticle showing coloured glabellar muscle insertion sites, dorsal, frontal and side views, $\times 6$. LO 7105 (LU 75), Fågelsång, loc. E21. □G. Fragmentary, exfoliated pygidium, $\times 6$. MGUH 23.052 (A 813), bed M-7, Slemmestad. □H. Partly exfoliated, compacted pygidium, $\times 4$. MGUH 23.053 (A 1064), bed M-14, Slemmestad. □I. Corroded pygidium, $\times 4$. MGUH 23.054 (A 910), bed M-9, Slemmestad.

The latter occurrence is possibly an error, as the extended range appears only from a list and is not discussed in the text, but also *A. knyrkoi* Schmidt, 1907 (a possible synonym of *L. volborthi*), was stated to occur in the upper part of BII (Schmidt 1907). *L. volborthi*, described by Regnéll (1942), presumably originated from the *A. lepidurus* Zone of northern Öland. *Ampyx* 'spp.' sensu Tjernvik (1980), here identified with *L. volborthi*, ranges through the middle third of the *M. limbata* Zone in the Finngrundet core.

Diagnosis. – Glabella distinctly inflated, pointed, glabellar spine angulate; glabella with well-impressed F1, composite F3, and preoccipital lobes; fixigenae pronouncedly convex (exsag.); anterior and posterior borders of cranidium wide (exsag.), posterior border furrow curved slightly backwards distally; surface sculpture of fine pits typically present only on anterior half of glabella. Pygidium with raised rim, separating pleural fields from steeply sloping border; anterior

furrow on pleural fields straight, test surface of pleural fields smooth. [Emended from Schmidt 1894.]

Description. – Medium-sized for a *Lonchodomas*, largest cranidium 11.3 mm long, largest pygidium 7.9 mm long. Cranidium triangular to subtrapezoidal in outline, cranidial L:W ratio 0.5–0.6 ($N = 9$). Glabella distinctly inflated and raised well above fixigenae, basal circumference pyriform; it is faintly triangular in frontal view, posteriorly weakly carinate, with a very gentle sagittal convex curvature; profile highest at base of spine or slightly behind. Glabella moderately narrow (tr.), occupying 0.3–0.4 of the cranidial width (tr.) (mean 0.35; $N = 9$) (Fig. 255B); maximum width attained at about 0.2 of the cranidial length from anterior margin. Glabellar front overhanging cranidial margin; summit drawn into a long forward-upward pointing spine, pentagonal in cross-section. Height of spine base above preglabellar furrow corresponds to 0.4–0.5 ($N = 10$) of the

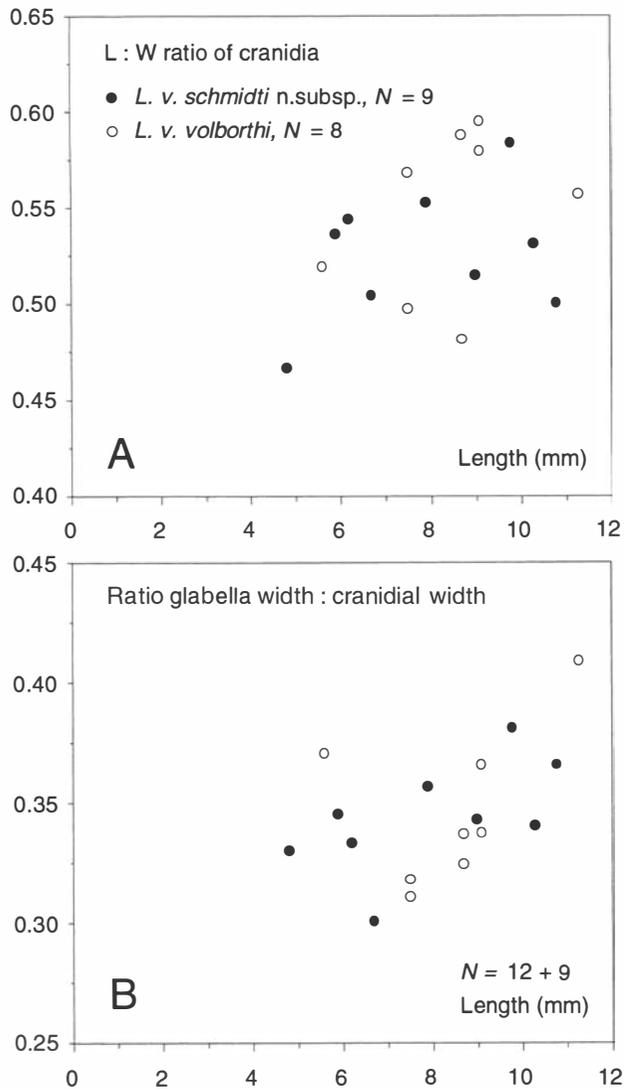


Fig. 255. Crania of *Lonchodomas volborthi volborthi* (Schmidt, 1894) (○) and *L. v. schmidti* n. subsp. (●). □A. Cranial L:W ratio plotted against cranial length. □B. Ratio between maximum glabella width and cranial width plotted against cranial length.

maximum glabella width. Spine definitely more than 0.3 times as long as cranium (excl. spine), presumably about 0.8, but it is broken in all specimens at hand. Four pairs of round to ovoid muscle areas on glabella, of which the anterior (F3) and posterior (F0) pairs are visible only in specimens showing coloured muscle markings. The following description is based primarily on specimen LO 7105 (Fig. 254D–F). F0 small, situated in occipital furrow and on anterior part of occipital ring; it is V-shaped with apex pointing adaxially, the posterior branch of the V is situated anteriorly on occipital ring, the anterior branch is pointing obliquely forward-outward into occipital furrow; both branches terminate close to base of axis. F1 is the most conspicuous of

the muscle areas, being just slightly smaller than F2, but better impressed; F1 situated adjacent to axial furrows in front of occipital furrow, from which it is separated by the gently inflated preoccipital lobes, accentuating the impressed appearance of F1, which therefore is fairly distinct also on internal moulds (Fig. 254A). F2, the largest of the four pairs, is situated roughly at midline some way up glabella, though still in the lower part of glabella; it is ovoid in outline, and generally visible also on internal moulds as obscure shallow impressions. F3 small, situated very close to axial furrows about one third of glabella length from front. It actually consists of two, partly fused coloured areas, of which the lower one adjacent to axial furrow is the largest, rather irregular in shape, presumably indicating a cluster of several small fused spots, while the upper one is smaller, situated slightly anterior to the lower marking, to which it is connected by a narrow band. The double or even triple nature of the anterior muscle area was considered an important diagnostic feature by Schmidt (1894, p. 81). Occipital furrow moderately impressed and wide throughout, curving slightly backwards mesially, laterally joining posterior border furrows. Occipital ring narrow (sag.), convex, slightly arcuate backwardly and not separated from posterior border by axial furrows. Axial and preglabellar furrows narrow and shallow, but glabella is well set off by a distinct change of slope; deep elongate fossulae situated anteriorly in axial furrows just in front of maximum glabella width. Anterior cranial border somewhat variable. The Norwegian specimens show a short (tr.) border, the transversal length is about 0.6 times the maximum width of glabella (Fig. 254C); the border is flat, fairly wide (sag.), sloping in abaxial direction owing to the mesial arch. The Scanian specimens show a transversely longer border (Fig. 254E), of about the same length (tr.) as maximum glabella width, so the crania assume a subtrapezoidal outline. The Norwegian crania have a mesial arch (frontal view), but it is suspected that the arch is less obvious in cephalae. The Scanian specimens show a more gently and broadly arched anterior margin. Fixigenae triangular in outline, convex, sloping anterolaterally. Eyes absent. Genal ridges weakly indicated on some internal moulds; they are of very low relief, straight, apparently single, running from a position level with anterior muscle area (F3) towards genal angles. Posterior border comparatively wide (exsag.), almost flat, sloping forwards, moderately so in the adaxial half, more steeply so in the abaxial half; it is delimited by a wide, fairly impressed border furrow, distally turning backwards towards genal angle. Elongate pit situated in the furrow just inside genal angle. The material shows some variation with regard to the steepness of posterior border, particularly the distal part. Facial suture marginal only in front of glabella, then crosses the gena, running almost straight to genal angle. Test surface covered with small, weakly impressed, densely spaced pits on the anterior half of glabella, remaining parts of cranium smooth; an exception is the large

Scanian specimen F 49, in which also the fixigenae are covered with small pits. The general lack of ornament is probably real and not depending on imperfect preservation. Schmidt (1894, p. 82) mentioned that a fine ornamentation *maybe* present on the cephalon. No librigenae available, see Schmidt (1894) for a brief description.

Hypostome unknown.

Thorax consists of five segments according to Schmidt (1894, p. 81) (see remarks below); there are no articulated specimens in the material at hand.

Pygidium broadly triangular in outline, about 2.0–2.3 ($N = 3$) times as wide as long, anterior margin straight, anterolateral corners acute. Axis gently vaulted, only slightly raised above pleural fields; width at anterior margin accounts for 0.26–0.27 ($N = 2$) of the pygidial width. It tapers evenly backwards, but reaches posterior border, terminal piece acutely rounded. Twelve to thirteen axial segments were counted on an internal mould in addition to the articulating half-ring, but this is a minimum number; only articulating half-ring and anterior two axial rings are fairly defined, separated by moderately impressed ring furrows. Axial furrows shallow and axis is essentially defined by a change of slope. Pleural fields slightly convex, sloping gently down posterolaterally; pleural region may show up to five indistinct pleural ribs in addition to anterior half rib, which is delimited by a moderately well-impressed, rather wide, straight furrow. The faint pleural ribs are visible on internal moulds as well as on testaceous material. On internal moulds the adaxial half of each rib is double, consisting of two low crests; these crests are united in the abaxial half. Border delimited by a thickened, narrow, raised rim at outer edge of the pleural fields, which actually slightly overhangs border; rim most conspicuous when the test is intact. Border very steep, almost vertical, and roughly of equal width throughout. It is unknown if a median arch is present. Surface sculpture of border consists of fine, closely spaced terrace lines, running parallel to outer margin, whereas pleural fields and axis are smooth. A single specimen with intact test shows, however, the presence of peculiar, narrow ridges of very low relief on the crests of the pleural ribs, two on each, running almost from axis to border. Doublure not visible in the specimens at hand.

Affinities. – *L. volborthi volborthi* and *L. v. schmidtii* n.subsp. are separated as chronosubspecies; the differences are discussed in the section on *L. v. schmidtii* n.subsp.

Lonchodomas v. volborthi is superficially rather like *Ampyx nasutus*, and identification of isolated skeletal parts may occasionally be troublesome as already mentioned by Schmidt (1894, p. 79); differences are enumerated in the section on *A. nasutus* (see also remarks below).

L. v. volborthi may be compared to the North American *L. normalis* (Billings, 1865) (see Whittington 1965), but the Baltoscandian species has a more strongly inflated glabella, and the anterior border is narrower (tr.).

The relation to *Ampyx knyrkoi* Schmidt, 1907 is discussed below. *L. v. volborthi* is distinguished from other species of *Lonchodomas* by the more convex cranidium (exsag.), the markedly inflated and only inconspicuously carinate glabella, and by the sharp edge between border and pleural fields of the pygidium.

Remarks. – The material identified with *Lonchodomas volborthi* by Skjeseth (1952, pp. 178–179) has been examined, and although the generic assignment appears correct, it seems to represent a new taxon, which presumably should be ranked as a subspecies of *L. tenuis* n.sp. Skjeseth (1952) assigned *volborthi* to *Lonchodomas*, partly because ‘*Ampyx volborthi*’ in the original description is stated to have only five thoracic segments. V. Poulsen (1965, pp. 100–101) remarked that the number of thoracic segments in *A. volborthi* actually may be six and not five, as the position of the cephalon in the complete specimen figured by Schmidt (1894, Pl. 6:11) is such that the anterior segment may be covered. However, Schmidt had additional complete specimens at his disposal (cf. Schmidt 1894, Pl. 6:17, 17a, 18), and he stated that thorax clearly consists of five segments (Schmidt 1894, p. 81). The presence of a four-edged glabellar spine and only five thoracic segments suggest an assignment to *Lonchodomas*.

Schmidt (1894) emphasized the close resemblance to *A. nasutus* (Dalman), but by comparison the following characters were regarded diagnostic of *L. volborthi*: The double or even triple nature of the anterior cephalic muscle area, the more elongate glabella with impressed posterior muscle pair, the outline of the anterior cephalic border, the moderately sloping posterior cephalic border, the posteriorly directed genal angles, the finer cephalic surface sculpture, the presence of only five thoracic segments and the development of a distinct, or even raised edge delimiting the pygidial pleural fields from the border, the lack of surface ornamentation on the pygidial pleural fields and the occasional presence of vague pygidial pleural ribs. The Scanian and Norwegian specimens are in accordance with these characteristics, although the former have an anterior cranial border which is longer (tr.) than typical. In this respect the Scanian specimens may be described as transitional to *Lonchodomas volborthi schmidtii* n.subsp.

The shape of the glabellar spine was not referred to by Schmidt (1894, pp. 80–82), but from the context it may be assumed round. This is supported by the short description of *Ampyx knyrkoi* (see Schmidt 1907, p. 65), as this species is stated to be entirely identical to *A. volborthi* except that the glabellar spine is distinctly four-edged with a longitudinal furrow on each side. The material at hand (particularly of *L. volborthi schmidtii* n.subsp.) shows, however, that it is essential to distinguish between testaceous and exfoliated specimens. Internal moulds show an almost round glabellar spine, whereas specimens with preserved test have a distinctly angulate spine. It is therefore suspected that the

indicated difference between *A. knyrkoi* and *A. volborthi* is a matter of preservation, and *A. knyrkoi* Schmidt, 1907 may eventually turn out to be a synonym of *A. volborthi* Schmidt, 1894.

Ampyx nasutus, listed from the entire Huk Formation of the Oslo area by Brögger (1882), probably included *Lonchodomas v. volborthi*. A single cranidium from the collections of Paleontological Museum, Oslo (PMO S 3247; old number: 52), was labelled *Ampyx*, but belongs to *L. volborthi volborthi*.

Regnéll (1942, pp. 3–4) figured and shortly described a pygidium of '*A. volborthi*' from the 'Lower *Asaphus* Limestone' of northern Öland; the validity of this identification was later questioned by V. Poulsen (1965, p. 100). However, the figured pygidium (Regnéll 1942, Textfig. 4) undoubtedly belongs to *Lonchodomas volborthi*, and presumably to *L. v. volborthi*, as indicated particularly by the distinctive raised edge of pleural fields towards the border area, but it also appears from the figure that vague pleural ribs are present and that the anterior furrow is straight.

Modliński (1973, Pl. 5:2) identified a ca. 6 mm long pygidium as *Lonchodomas volborthi*. The slight development of a rim, separating the pleural fields from the border, must be due to its small size, as the curved anterior furrow, separating the half rib, and the relatively broad axis (occupying ca. 0.30 of pygidial width) clearly points to an identification with *Ampyx nasutus*.

The poorly preserved material from the *M. limbata* Zone of the Finngrundet core, referred to as *Ampyx* spp. by Tjernvik (1980), has been examined; it belongs to *Lonchodomas volborthi*, and no evidence suggests that more than one species is present (but the material is admittedly rather fragmentary). A couple of fairly preserved pygidia (from 40.64 and 41.69 m in the core) have a distinctly raised rim between the pleural fields and border, and this feature points to an identification with *L. v. volborthi*.

Lonchodomas volborthi schmidtii n. subsp.

Fig. 255–256

Synonymy. – □? 1882 *Ampyx nasutus* Dalm. [*partim?*] – Brögger, p. 58 (occurrence). □cf. 1973 *Lonchodomas balticus* n. sp. – Modliński, pp. 57–58; Pl. 5:3 (diagnosis, description and figure of one cranidium).

Derivation of name. – In honour of academician F. Schmidt, who made an outstanding pioneering work on the eastern Baltic Ordovician trilobites.

Holotype. – Cranidium MGUH 23.057 (A 382a) (Fig. 256D) from bed A-26½, Lysaker Member, Slemmestad, uppermost part of the *M. limbata* Zone.

Paratypes. – Complete specimen MGUH 23.055 (A 443) (Fig. 256A–G) (bed A-34), cranidium MGUH 23.056 (A 383) (Fig. 256B–C) (bed A-26½) and pygidia MGUH 23.060 (A 233) (Fig. 256H) (bed A-13) and MGUH 23.061 (A 314)

(Fig. 256I–J) (bed A-19), all from the Lysaker Member at Slemmestad. Except for specimen MGUH 23.055, which is from the lower part of *A. expansus* Zone, the specimens are from the upper part of the *M. limbata* Zone.

Additional material. – Thirteen cranidia and 1 pygidium.

List of additional material. – □Cranidia A 242a (t), A 242b (t), A 242c (pim), A 246 (pim), A 247 (c), A 251 (pim), A 255 (im), A 283 (im), A 289 (pim), A 305 (pim) [MGUH 23.058], A 382b (pim) [MGUH 23.059], A 402 (pim), A 409? (pim). □Pygidium A 319 (im).

Occurrence. – *Lonchodomas volborthi schmidtii* n. subsp. is common in bed interval A-13–A-34 of the Lysaker Member at Slemmestad, representing the upper part of the *M. limbata* Zone and the lower part of the *A. expansus* Zone. The subspecies has not been found in the Komstad Limestone, but perhaps occurs in Poland (see discussion below).

Diagnosis. – As for *L. volborthi volborthi* (Schmidt, 1894) but the test surface of cranidium and pygidium (pleural fields) is finely pitted except from on muscle areas and in depressions; anterior cranial border is shorter (tr.), so the cranial outline is trapezoidal, glabellar overhang is more pronounced, and the pygidial border is less steep, and separated by a less distinct rim.

Description. – Largest cranidium about 11 mm long, largest pygidium 5.4 mm long. Cranial L:W ratio and relative glabella width are shown in Fig. 255. By comparison to *L. volborthi volborthi* the cranidium is more trapezoidal in outline, and glabellar front is more pronouncedly overhanging cranial margin in most specimens. It is also suspected, but not satisfactorily proven by the material, that the glabellar spine is slightly more prominent in *L. volborthi schmidtii* n. subsp. Configuration of muscle areas as in *L. volborthi volborthi*, but individual muscle areas of the composite F3 are larger and F3 is overall more distinct; F0 is difficult to discern in all specimens available. Anterior cranial border typically flat, gently forward sloping or almost horizontal, transversal length equivalent to 1 to 1.5 times the maximum glabellar width. Although slightly variable the border is typically comparatively broad (exsag.); anterior margin gently and broadly arched in frontal view in most specimens, a few cranidia show a more distinct median arch, thus resembling *L. volborthi volborthi*. Posterior border as in *L. volborthi volborthi*, but the distal bend of the bounding border furrow is more pronounced, and the elongate pit situated in the furrow just inside genal angle is more distinct, deeper. Facial suture differs from *L. volborthi volborthi* by being marginal anteriorly for a longer stretch before crossing the gena. The different outline influences the transversal width of the anterior cranial border, and thereby the general outline of cranidium. Genal angle continued into an oblique spine, diverging backwards at an angle of about 45°; spine at least as long as cranidium, but presumably longer. Posterior border furrow continues onto the spine. Test surface typically covered with small densely spaced pits except on glabellar

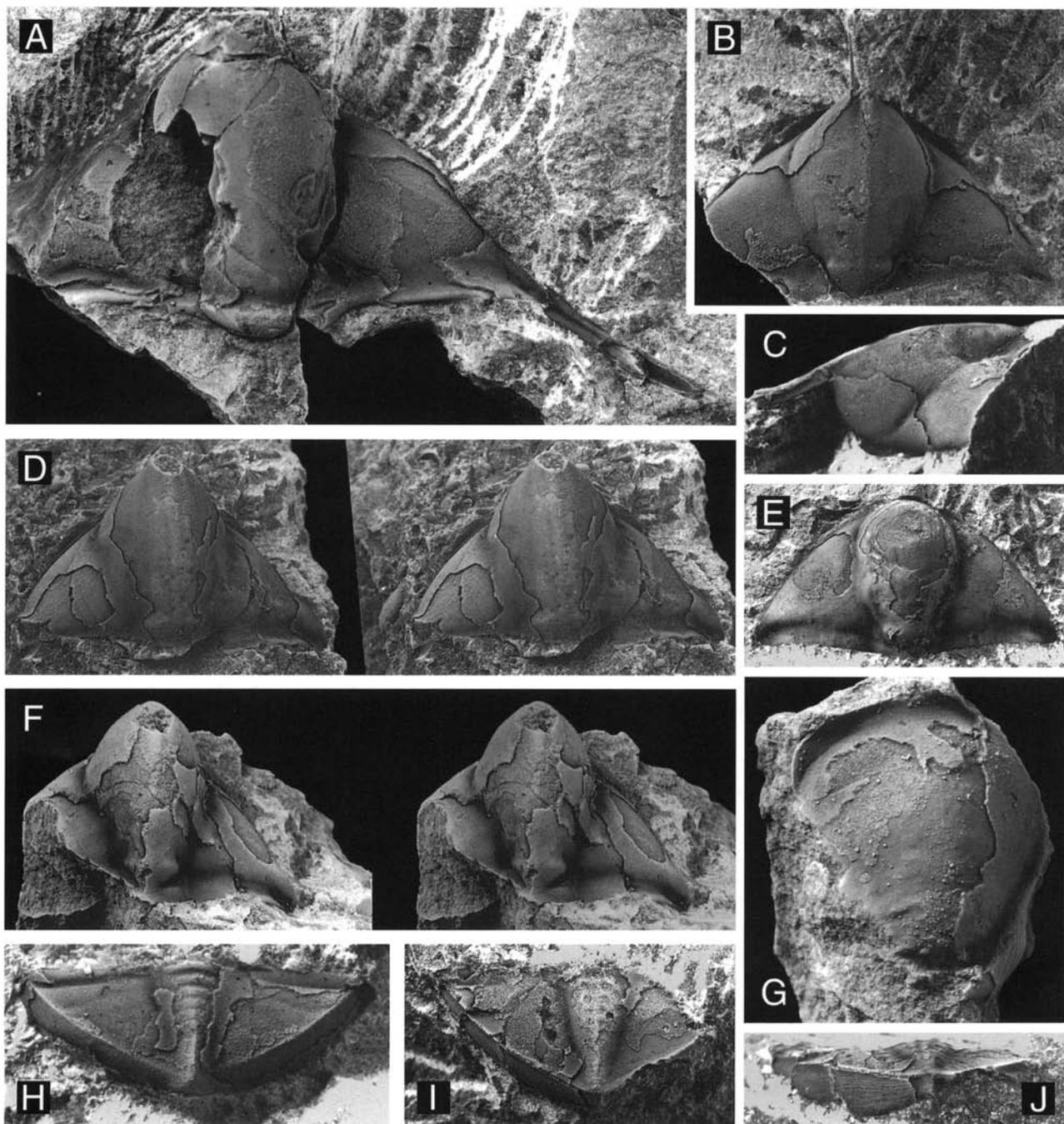


Fig. 256. *Lonchodomas volborthi schmidti* n. subsp. □A. Paratype. Largely exfoliated, fragmentary cephalon, showing genal spine, $\times 4$. Complete specimen MGUH 23.055 (A 443), bed A-34, Slemmestad. See also G. □B–C. Paratype. Largely exfoliated cranidium showing edged glabellar spine, side and dorsal views, $\times 6$. MGUH 23.056 (A 383), bed A-26½, Slemmestad. □D. Holotype. Partly exfoliated cranidium, dorsal view, stereo-pair, $\times 3$. MGUH 23.057 (A 382a), bed A-26½, Slemmestad. □E. Partly exfoliated, somewhat compacted cranidium showing posterior border, $\times 2.5$. MGUH 23.058 (A 305), bed A-19, Slemmestad. □F. Partly exfoliated cranidium, dorsal view, stereo-pair, $\times 4$. MGUH 23.059 (A 382b), bed A-26½, Slemmestad. □G. Paratype. Largely exfoliated, fragmentary hypostome, $\times 9$. Complete specimen MGUH 23.055 (A 443), bed A-34, Slemmestad. □H. Paratype. Largely exfoliated small pygidium, $\times 8$. MGUH 23.060 (A 233), bed M-13, Slemmestad. □I–J. Paratype. Partly exfoliated fragmentary pygidium showing axis and raised inner edge of border, dorsal and posterior views, $\times 4$. MGUH 23.061 (A 314), bed A-19, Slemmestad.

muscle areas, but some cranidia show ornamentation only on the anterior part of glabella like *L. volborthi volborthi*. Ornamentation weakly impressed. A few terrace lines present along outer margin of the genal spine.

A damaged hypostome was found inside enrolled specimen MGUH 23.055 (Fig. 256G). It is slightly longer than broad, presumably roughly pyriform in outline (margins partly injured). Anterior margin curved; edge distinctly

flexed in ventral direction. Anterior wings, if any, not preserved. Median body shield-shaped, gently inflated. A narrow, shallow, but distinct border furrow separates median body posterolaterally and posteriorly from the border area, which is raised (ventral view) adjacent to the furrow, sloping strongly outwards. Broad triangular projection situated on the lateral margin one third of the hypostomal length from posterior end, but the margin is injured anterior to the projection and the outline may be incidental. Posterior margin straight, truncate, continuing laterally into short and narrow (exsag.) posterior wings pointing in dorsal direction. Test preserved on one half of the hypostome. Very shallow elongate macula indicated on the exfoliated half close to posterior end of median body; the corresponding macula in the test-covered part is effaced. Test surface of median body finely pitted, except close to the border furrow (smooth); border area carries terrace lines on the raised edge adjacent to border furrow, the lines fan out on the triangle leading to posterior wing; outer part of border area smooth.

Thorax presumably consists of five segments (see remarks on *L. volborthi volborthi*); only four segments are preserved in the specimen at hand. Articulating half-ring well-developed, accounting for about 0.4 of the segmental length (sag.), separated by a deep, well-defined articulating furrow. Axis fairly wide (tr.), at most occupying about one third of total segmental width, probably somewhat less; it is moderately raised above pleural region, separated by shallow, wide axial furrows. Proximal part of pleura flat, cut by an oblique, shallow pleural furrow, which, however, appears fairly distinct as the pleural part behind the furrow is slightly raised with a concave forward-slope, very gentle in the proximal part, but with an increased steepness abaxially. Distal parts of thorax not preserved. Test surface of thorax shows a fine punctation, except on articulating half-rings and in articulating furrows, which are smooth. The punctation is arranged in rows on axis, resembling terrace lines, running obliquely backward-downwards; obscure radiating rows of pits are also present on the pleurae, arranged roughly parallel with and close to the pleural furrows.

Pygidium as described for *L. volborthi volborthi*, W:L ratio 2.2–2.5 ($N = 4$). Axis possibly stronger vaulted, and seems to have a better defined segmentation, but both characters may relate to preservational differences; axial width at anterior margin accounts for 0.27 ($N = 4$) of the pygidial width. Fifteen axial segments were counted on an internal mould in addition to articulating half-ring, but the true number of segments is presumably higher. Pleural fields slightly convex, especially in small specimens; segmentation effaced. Border separated by a narrow raised rim, less prominent than in *L. volborthi volborthi*; it is subvertical anterolaterally, though overall slightly less steep than in *L. volborthi volborthi*; maximum border width attained just next to the median arch. Surface sculpture of border consisting of fine, closely spaced terrace lines, whereas the pleural fields exhibit a fine punctation. A very faint punctation also occurs on the axis, at least rearwards.

Affinities. – *Lonchodomas volborthi schmidti* n.subsp. is considered a subspecies of *L. volborthi volborthi*, but it cannot be excluded that it merely represents an ecophenotype. Differences are highlighted in the description above.

L. volborthi schmidti n.subsp. may be compared to the North American *L. clavulus* Whittington, 1965, showing the same basic outline of all skeletal parts, including hypostome (cf. Whittington 1965, Pl. 11:11). The Baltoscandian form has, however, a well-defined anterior cephalic border, the hypostome is relatively elongate, and the pygidial axis appears to be but slightly narrower (cf. Whittington 1965, Pl. 11:4).

The relation to *Ampyx knyrkoi* Schmidt, 1907 is discussed in the section on *L. volborthi volborthi*. The distinction from other raphiophorid species is based on the same characters as stated for *L. volborthi volborthi*.

Remarks. – Schmidt (1894) particularly emphasized the morphology of the anterior cephalic border and the absence of ornamentation on the pygidial pleural fields of '*Ampyx volborthi*'. The above described material has a different outline of the anterior border, and the pleural fields are finely pitted. The new subspecies is known only from the Oslo region so far; it appears to be contemporaneous with *L. volborthi volborthi* (Schmidt, 1894) in the eastern Baltic area (cf. Schmidt 1894, 1907; Lamansky 1905), and presumably also in the Swedish area (Tjernvik 1980; Regnéll 1942; see section on *L. volborthi volborthi*).

The new subspecies is the most common raphiophorid in the Lysaker Member at Slemmestad, and was in all probability included in *A. nasutus* by Brögger (1882). However, no specimens of *L. volborthi schmidti* n.subsp. have been seen in the collections of the Paleontological Museum, Oslo.

Ampyx balticus Kummerov, 1928 looks close to *L. rostratus* and should rather likely be allocated to *Lonchodomas*. This entails that *L. balticus* Modliński, 1973, based on a single cranidium from the Goldap-1 drill-core, Poland, becomes a secondary homonym and ought to be renamed. This should not be done without a redescription of the holotype, as the species is inadequately characterized, and the original figure is rather poor (cf. Modliński 1973, pp. 57–58; Pl. 5:2); it has proved impossible to retrieve the original specimen. Judging from the published information, it apparently belongs to the *L. volborthi* group, and it may correspond to *L. volborthi schmidti* n.subsp., as the test surface is finely pitted (Modliński 1973, p. 58).

Lonchodomas tenuis n.sp.

Fig. 257A–J

Synonymy. – □v 1936 *Ampyx volborthi* Schm. [*partim*] – C. Poulsen, p. 48 (listed). □v 1965 *Ampyx glaber* n.sp. [*partim*] – V. Poulsen, pp. 98–101; Pl. 8:8–10 (description and figures of two pygidia).

Derivation of name. – Latin *tenuis* = narrow or slender, alluding to the comparatively narrow glabella of the new species.

Holotype. – Cranidium MGUH 23.065 (S 108) (Fig. 257H–I) from 1 cm below top of bed –21, Skelbro, Zone of *M. polyphemus*.

Paratype. – Pygidium MGUH 9461 from the Skelbro beds, Skelbro, Zone of *M. polyphemus*, figured by V. Poulsen (1965, Pl. 8:8–9).

Additional material. – Thirteen cranidia and 8 pygidia.

List of additional material. – □Cranidia S 186 (im), S 415 (im), S 466 (im), S 532 (em), S 552 (im), S 565 (im), S 570 (im), S 588 (pim), S 595 (im), S 631 (im), S 632 (im), S 634 (im), S 647 (im) [MGUH 23.062]. □Pygidia S 40 (pim) [MGUH 23.064], S 98 (t), S 210 (im), S 520 (em), S 553 (im) [MGUH 23.066], S 639 (em), GM 1987.7 (im) [MGUH 23.063], GM 1987.9 (em).

Occurrence. – *L. tenuis* n.sp. occurs in bed interval –21 to –18 at Skelbro, i.e. the lower half of the *M. polyphemus* Zone. The museum specimens studied undoubtedly originate from the same interval, as proven by the lithology of the samples. Similar material, treated as *L. cf. tenuis* n.sp., was found in bed M-1 at Slemmestad; it is described separately below.

L. tenuis n.sp. is among the earliest representatives of *Lonchodomas* in Scandinavia; the relationship to *Lonchodomas* sp. Tjernvik (1956, p. 272) from the *M. estonica* Zone is uncertain.

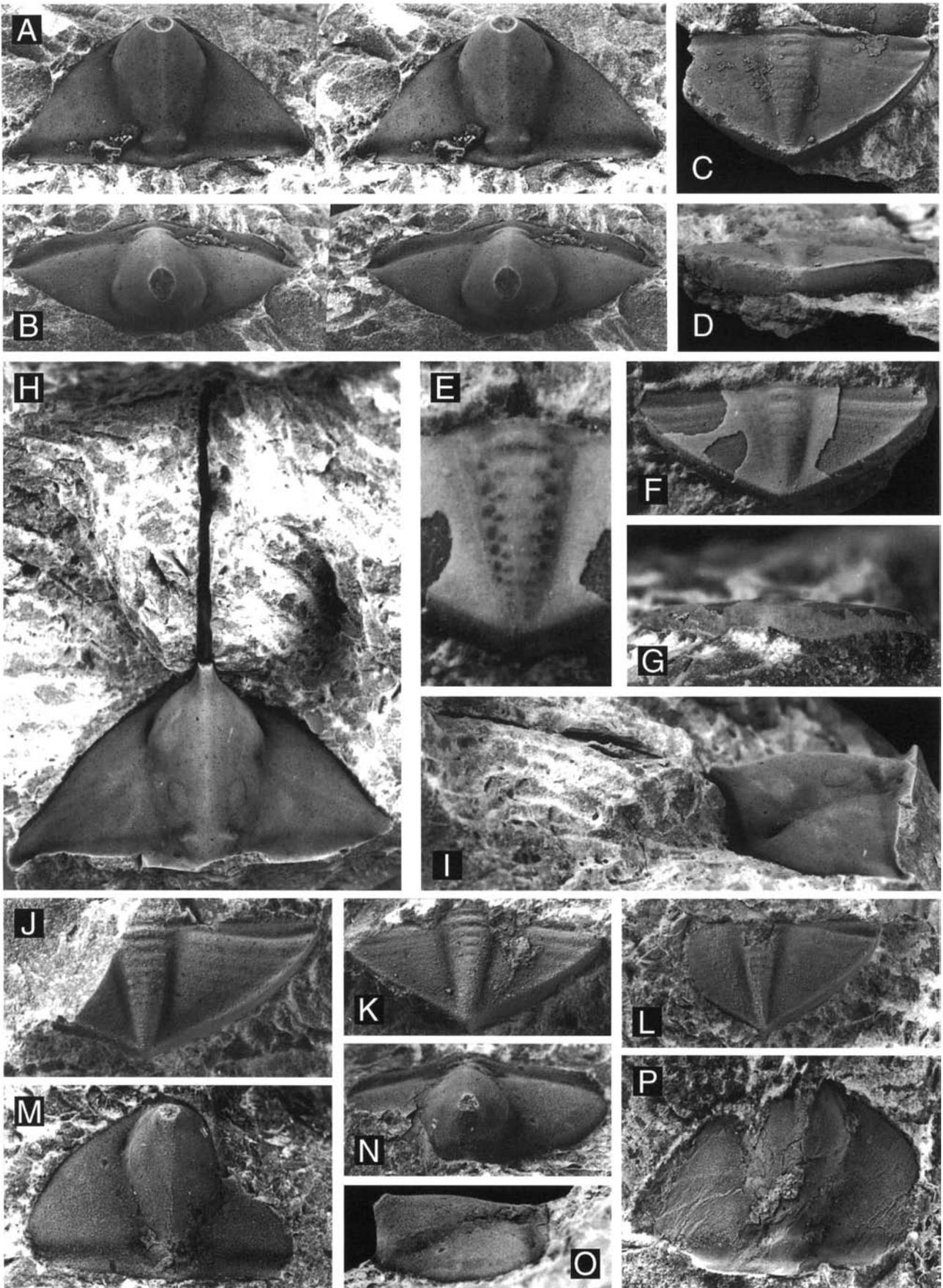
Diagnosis. – Cranidium distinctly triangular in outline with only a short (tr.) anterior border; glabella narrow (tr.), moderately inflated, with weakly impressed muscle scars; convexity (exsag.) of fixigenae low; pygidium with slender (tr.) axis, narrow, steep border and a restricted median arch; convexity overall low.

Description. – Medium-sized for a *Lonchodomas*, largest cranidium 8.7 mm long, largest pygidium 6.1 mm long. Cranidium triangular in outline, about twice as wide as long. Glabella moderately vaulted, slender (tr.), only slightly raised above fixigenae posteriorly; basal circumference approximately diamond-shaped, maximum width attained at about one third the length of cranidium from anterior end; front (excluding spine) level with or slightly overhangs anterior cranial margin. Glabella triangular in frontal view with highest profile at base of spine; it is faintly carinate on internal moulds (whether this also is the case, when the test is intact, is unknown). Summit of glabella drawn into a long forward-upward pointing spine, four-edged trapezoidal in cross-section, with the shortest side upwards. Longitudinal shallow furrows present on each side of the spine on testaceous material; these furrows are absent on internal moulds. Spine about 1.5 times as long as the cranidium, with a very slight downwards curvature (Fig. 257I). Four pairs of round to ovoid muscle areas of which F0, F2 and F3 are very faint and occasionally not discernible. F0 situated distally in the occipital furrow and abuts axial furrow; F1 moderately im-

pressed, situated just in front of occipital furrow, almost forming a shallow transverse glabellar furrow; F2 is the largest pair, situated midway between axial furrow and sagittal line; F3 small, situated on glabella very close to axial furrows shortly in front of F2. Elongate preoccipital lobes situated immediately behind F1; they are of moderate relief, but add to the distinctness of F1. Occipital furrow shallow, curving slightly backwards mesially and joins posterior border furrows laterally. Occipital ring narrow (sag.), not separated from posterior border by axial furrows; posterior margin slightly arcuate backwards. Axial and preglabellar furrows very shallow, indistinct, and glabella is defined essentially by a change of slope. Deep elongate fossulae situated anteriorly in the axial furrows, just in front of maximum glabellar width. Cranial anterior border flat, narrow (sag.) and short (tr.), not exceeding the width of glabella; border boomerang shaped in dorsal view. Border furrow effaced, and the anterior border is defined by a change of slope. Median arch moderately developed (frontal view). Fixigenae triangular in outline, gently convex, sloping anterolaterally. Faint, almost straight genal ridges of very low relief run from axial furrows immediately behind F3 to cranial margin just in front of genal angles on internal moulds. Rarely a second pair of faint ridges splits from the first ridges. It is unknown whether the genal ridges are visible on testaceous material. Posterior border narrow (exsag.), concave, somewhat raised above the level of fixigenae, especially distally, slanting moderately (inner half) to rather steeply (outer half) forwards, delimited by a wide, fairly impressed border furrow, which has a distinctive deep pit situated just inside genal angle. Suture marginal anteriorly for a short distance, then crosses gena in a faintly sigmoidal fashion, in the anterior half curving gently inwards, then gently outwards running to genal angle. All specimens exfoliated; well-preserved internal moulds are finely pitted on the fixigenal region; no ornamentation on glabella.

Librigena, hypostome and thorax unknown.

Pygidium broadly triangular in outline, about 2.1 to 2.5 times as wide as long; small specimens are widest. Anterior margin straight, anterolateral corners acute. Axis gently vaulted, only slightly raised above pleural fields; width at anterior margin accounts for 0.22–0.23 of the pygidial width. Axis tapers evenly backwards, but extends to posterior border; terminal piece rounded. Only about twelve rings are discernible on internal moulds, but at least fourteen, perhaps fifteen, axial segments in addition to the terminal piece can be counted in a specimen showing coloured muscle markings (Fig. 257E). In this pygidium the narrow (sag.) articulating half-ring is followed by eight fairly defined axial rings, separated by shallow furrows. Double pairs of round muscle markings are arranged in two rows in the anterior eight ring furrows; the largest and most distinct pair is situated close to axial furrows, the second, less conspicuous pair is situated slightly posterior to the first pair, roughly midway up the axis. The inner pair is joined across midline by a narrow band



in the first few segments. Behind axial furrow no. 9 the outer pair disappears and only the inner pair is visible in the posterior six or seven ring furrows. Axial furrows very shallow, and axis is defined mainly by a change of slope. Pleural fields very gently convex, almost horizontal, showing six pairs of obscure pleural ribs with interjacent furrows on internal moulds. Segmentation effaced in some specimens, and it is probably absent on testaceous material. Articulating half segment depressed below the level of pleural fields; it is delimited by a fairly deep furrow. This furrow and the faint interpleural furrows of the pleural fields terminate at the inner edge of border, demarcated by a narrow, raised rim. Border steep, subvertical, in posterior view showing a minor median arch; maximum border width attained adjacent to this arch. Border covered with fine, closely spaced terrace lines, arranged parallel to outer margin, whereas the surface of pleural fields appears smooth (see discussion below). The surface of the available internal moulds is smooth.

Affinities. – *Lonchodomas tenuis* n.sp. is separated from *L. volborthi* subsp. by the lower convexity of cranium, the less prominent glabella (narrower, less inflated), the shorter (tr.) anterior border, the presence of a median arch and by the comparatively narrower (exsag.) posterior border; the pygidium is distinctly longer, more triangular in outline, and the anterior half rib is less well-defined.

Lonchodomas 'volborthi' sensu Skjeseth (1952; see also Fortey 1975a, Pl. 23:2) is close to *L. tenuis* n.sp., but differs from the Bornholm material, for example in that the pygidium is relatively longer, with about nineteen axial segments, and the boundary between the pleural fields and border is less sharp.

L. tenuis n.sp. resembles '*Ampyx' nasutoides* Regnéll, which is insufficiently known, but the new species seems to be distinguished by a comparatively stronger vaulted and broader glabella and by a different outline of the cranium (triangular, not semicircular). See also *Lonchodomas* sp. I.

Remarks. – The assigned pygidia were identified with '*A. glaber*' by V. Poulsen (1965, Pl. 8:8–10). The lower number of axial segments stated by Poulsen reflects that he had mainly

internal and external moulds at his disposal. V. Poulsen (1965, p. 100) also described the pygidial test surface as finely punctate, and the apparent smoothness of the available single specimen with patches of intact test may relate to preservational shortcomings. It has not been possible to locate the testaceous pygidium studied by Poulsen.

Lonchodomas cf. tenuis n.sp.

Fig. 257K–P

Material. – Three cranidia and 3 pygidia, all internal moulds.

List of material. – □Cranidia A 603 [MGUH 23.070], A 608d [MGUH 23.069], A 608e (fragmentary). □Pygidia A 608c [MGUH 23.067], A 609e, A 645 [MGUH 23.068].

Occurrence. – All specimens are from bed M-1 at Slemmestad, Zone of *M. polyphemus*.

Remarks. – The material is quite like *Lonchodomas tenuis* n.sp., but the cranidia have a slightly narrower (tr.) glabella, fainter preoccipital lobes, and a slightly less raised posterior edge, and the pygidia have a comparatively broader and more prominent axis. The shared similarities are, however, so striking that the Norwegian material at most should be separated at the subspecies level from *L. tenuis* n.sp.

Lonchodomas sp. I

Fig. 258.

Synonymy. – □v 1936 *Ampyx nasutus* Dalm. [*partim*] – C. Poulsen, p. 48 (listed). □cf. 1940 *Ampyx nasutoides* n.sp. – Regnéll, pp. 4–5; Pl. 1:2–3 (short description, occurrence, illustrations of two cranidia).

Material. – Cranium GM 1987.23 (im) [MGUH 23.071].

Occurrence. – The cranium is from Vasegård, Bornholm. According to the label it was collected from the 'Lower *Asaphus* Limestone', and if so, it probably originates from bed interval –5 to –3 (Zone of *M. simon*). The lithology and associated fossils, however, point to a more likely provenance from beds –21 or –20 (*M. polyphemus* Zone).

Description. – Cranium exfoliated, 5.9 mm long, semicircular in outline, but the anterior border may be impaired; L:W ratio about 0.45. Glabella comparatively little vaulted (tr.), with nearly no sagittal curvature, and basically no anterior overhang. Axial muscle areas weakly impressed. Preoccipital lobes only gently inflated. Occipital ring narrow (sag.), slightly raised above the rear part of glabella, posterior margin curves gently backwards. Axial furrows not developed, the indistinct preglabellar furrow is narrow and shallow. No anterior cranial border, it may, however, be broken off. Posterior border faintly convex and raised above the fixigenae, in particular distally, sloping gently (inner half) to rather steeply (outer half) forwards; it is delimited by a wide,

Fig. 257. □A–J. *Lonchodomas tenuis* n.sp. □A–B. Exfoliated cranium, dorsal and frontal views (stereo-pairs), ×4. MGUH 23.062 (S 647), bed –18, Skelbro. □C–D. Exfoliated pygidium, dorsal and posterior views, ×4. MGUH 23.063 (GM 1987.7), Skelbro. □E–G. Partly exfoliated pygidium with transparent cuticle, dorsal and posterior views, ×9; non-whitened close-up of axis shows coloured muscle insertion sites, ×18. MGUH 23.064 (S 40), bed –21, Skelbro. □H–I. Holotype. Internal mould of cranium (test dissolved), dorsal and side views, ×4. MGUH 23.065 (S 108), bed –21, Skelbro. □J. Exfoliated pygidium, ×8. MGUH 23.066 (S 553), bed –18, Skelbro. □K–P. *Lonchodomas cf. tenuis* n.sp. □K. Exfoliated pygidium, ×8. MGUH 23.067 (A 608c), bed M-1, Slemmestad. □L. Exfoliated pygidium, ×4. MGUH 23.068 (A 645), bed M-1, Slemmestad. □M–O. Exfoliated cranium, dorsal, frontal and side views, ×4. MGUH 23.069 (A 608d), bed M-1, Slemmestad. □P. Compacted, exfoliated cranium, ×4. MGUH 23.070 (A 603), bed M-1, Slemmestad.

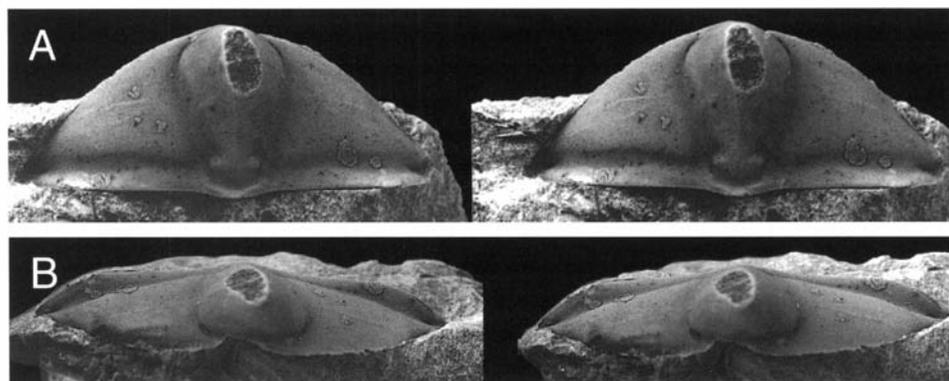


Fig. 258. *Lonchodomas* sp. I. □A–B. Exfoliated cranidium, dorsal and frontal views, stereo-pairs, $\times 4$. MGUH 23.071 (GM 1987.23), Vasegård, Bornholm.

shallow, border furrow, which has a pit situated just inside genal angle. Minute patches of intact test indicate that at least parts of fixigenae are finely pitted; the mould surface shows traces of a faint reticulate pattern posteriorly on fixigenae.

Affinities. – The cranidium resembles *Lonchodomas tenuis* n.sp., but is relatively shorter, semicircular (not triangular) in outline, and has a less vaulted glabella, and perhaps no anterior border. These features also separate *Lonchodomas* sp. I from the other species of *Lonchodomas* described here. The cranidium may be compared to that of *Ampyx cetsarum* Fortey & Owens, 1978, sharing a grossly similar outline, but *L.* sp. I has better defined preoccipital lobes and is likely to have a different cuticle ornamentation.

Lonchodomas sp. I may be identical to *Ampyx nasutooides* Regnéll. The original description and associated figures are, however, insufficient for a confident identification (cf. Regnéll 1940, p. 4; Pl. 1:2–3). The comparison is also hampered by the fact that the spine base is slightly damaged in the available specimen, obscuring the outline of glabella, which was emphasized as taxonomically important by Regnéll.

Lonchodomas sp. II

Fig. 259A

Material. – One partly exfoliated pygidium (A 510) [MGUH 23.072].

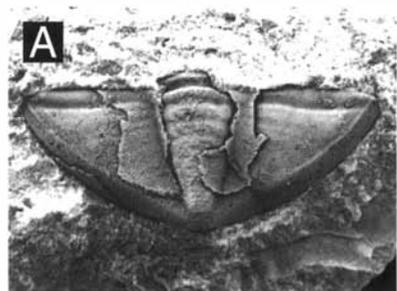


Fig. 259. □A. *Lonchodomas* sp. II. Largely exfoliated pygidium, $\times 5$. MGUH 23.072 (A 510), bed A-51, Slemmestad. □B. *Lonchodomas?* sp. III. Partly exfoliated cranidium, dorsal view, stereo-pair, $\times 4$. MGUH 23.073 (A 388), bed A-26½, Slemmestad.

Occurrence. – The specimen is from bed A-51 of the Lysaker Member, Slemmestad (upper part of the *A. expansus* Zone).

Remarks. – The isolated pygidium may represent a new subspecies of *L. volborthi*. Compared to *L. volborthi volborthi* and *L. volborthi schmidtii* n.subsp., the specimen is relatively shorter (sag.), the axis is more inflated, the mesial arch is better defined, and patches of preserved test on the pleural fields are densely pitted. Furthermore, the bend between pleural fields and border is sharp, but without thickened rim.

Lonchodomas? sp. III

Fig. 259B

Material. – Cranidium A 388 (t) [MGUH 23.073].

Occurrence. – The specimen is from bed A-26½ of the Lysaker Member, Slemmestad, i.e. uppermost part of the *M. limbata* Zone.

Description. – Cranidium ca. 7.3 mm long (excl. spine), pronouncedly triangular in outline, and about 1.5 to 1.6 times as wide as long (lateral parts damaged). Glabella narrow (tr.), occupying not more than one third of the maximum cranidial width; it is slightly to moderately vaulted, with a gently convex sagittal curvature; circumference pyri-

form. Glabellar front slightly overhanging margin of cranidium; spine very broad-based, and apparently trapezoidal in cross-section with the shortest side upwards. F1 and F2 weakly impressed, rounded and large, almost reaching from base to crest of glabella. Preoccipital lobes indistinct. Occipital furrow narrow, very shallow, but amplified by the preoccipital lobes and the raised occipital 'ring'. The latter is ill-defined, confluent with posterior border, and curves slightly backwards; like the border it is essentially flat, slanting moderately forwards. Axial and preglabellar furrows effaced. A pair of slit-like fossulae situated in the flexure ('axial furrow') just behind maximum glabellar width. Anterior border flat, almost horizontal, defined only by a change of slope. No median arch. Fixigenae slope very gently. Posterior border unusually wide (exsag.), virtually flat, defined only by a small change of slope. Distal part of border slightly narrower (exsag.), but with a similar slope as the proximal part. Test surface shows a faint punctation on glabella front, on posterior part of fixigenae, and on posterior borders; remaining surface seemingly smooth.

Remarks. – The cranidium exhibits a number of unique features, clearly separating it from the other raphiophorid species described here. It may represent a new genus.

Genus *Globampyx* Fortey, 1975

Type species. – (OD) *Globampyx trinucleoides* Fortey, 1975.

Remarks. – *Globampyx* was erected to accommodate *G. trinucleoides*, which occurs abundantly in the Profilbekken Member of Spitsbergen. The genus is characterized by a remarkably inflated, spineless glabella, no distal pit in the posterior cephalic border, five thoracic segments and faint pleural furrows on the pygidium (Fortey 1975a). A second species, *G. sinalae*, was described by Norford & Ross (1978) from the upper Arenig of western Canada.

Fortey (1975a, pp. 76, 79) suggested that the Scandinavian species *Ampyx obtusus* Moberg & Segerberg, 1906 and *Ampyx linnarssoni* Schmidt, 1894, may belong to *Globampyx*. It is evident that both species show points of resemblance to *G. trinucleoides*, and, pending a more thorough examination, they may conveniently be assigned to the same genus, as they definitely are not congeneric with *Ampyx* (*s.str.*) However, it is suspected that the apparent resemblance between the Scandinavian species and the genus from Spitsbergen may reflect convergent evolution and not a true close relationship (see also Tjernvik 1980, p. 186). It is for instance pointed out that the strongly inflated glabella is more keel-shaped in the Scandinavian species, whereas it is rounded in the Spitsbergenian as well as the Canadian species. The segmentation of the pygidial pleural fields also looks different.

The poorly known *Ampyx brevicauda* Wiman, 1905 is possibly an early member of the *Globampyx obtusus-linnarssoni* species group.

Globampyx linnarssoni (Schmidt, 1894)

Figs. 260–261

Synonymy. – □1885 *Hypocephalus Hauchecornei* gen. et spec. nov. – Remelé, p. 1032 (short description). [*Nomen nudum*]. [See Schmidt 1907, p. 64]. □1894 *Ampyx Linnarssoni* n.sp. – Schmidt, pp. 83–84; Pl. 6:21–23 (description, occurrence, illustrations of two cranidia and a pygidium). □1905 *Ampyx Linnarssoni* F.S. – Lamansky, p. 170 (listed). □1907 *Ampyx Linnarssoni* m. – Schmidt, p. 64 (listed). □1971 *Ampyx linnarssoni* Schmidt, 1894 – Neben & Krueger, Pls. 2:7–9; 3:9–10 (illustrations of cranidia and pygidium). □? 1980 *Ampyx?* cf. *linnarssoni* F. Schmidt – Tjernvik & Johansson, p. 191 (listed).

Lectotype. – Here designated, cranidium figured by Schmidt (1894, Pl. 6:21).

Material. – Six cranidia and 11 pygidia.

List of material. – (Internal moulds if not otherwise stated). □Cranidia A 583, A 584 (pim) [MGUH 23.075], A 590, A 608a [MGUH 23.074], A 609b [MGUH 23.076], A 609d. □Pygidia A 591, A 598a (pim), A 598b, A 607 [MGUH 23.080], A 608b (pim), A 609a, A 634a [MGUH 23.078], A 634b [MGUH 23.079], A 634c, A 637 [MGUH 23.077], A 644 (pim).

Occurrence. – All specimens are from the upper half of bed M-1 at Slemmestad, which belongs to the *M. polyphemus* Zone.

Globampyx linnarssoni (Schmidt, 1894) was originally reported from the BII α Zone of Estonia and eastern Russia (Schmidt 1894, 1907; Lamansky 1905) and *Ampyx?* cf. *linnarssoni* was listed by Tjernvik (1980, p. 191) from the *M. polyphemus* Zone of Sweden. *G. linnarssoni* is very frequent in the top bed of the Bruddestad Formation at Haget, northern Öland (unpublished data); the trilobite assemblage of this bed points to a correlation with the *M. polyphemus* Zone.

Diagnosis. – Glabella strongly inflated, keel-shaped, not overhanging anterior margin; a minute mesial tubercle is situated near summit of glabella, no spine; anterior border of cranidium wide (sag.). Pygidium with deeply impressed, wide axial and anterior pleural furrows, the latter delimiting a straight anterior half rib. No surface sculpture (both cranidium and pygidium), except on the border region of pygidium. No median arch (both cranidium and pygidium). [Emended from Schmidt 1894.]

Description. – Only the cranidium and pygidium are known (see also Schmidt 1894; Neben & Krueger 1971). Small to medium-sized raphiophorid, largest cranidium about 7.2 mm long, largest pygidium 7.0 mm long; Schmidt (1894, p. 84) listed a cranidium 8.5 mm long.

Cranidium subtrapezoidal in outline, and about half as long as wide. Glabella exceedingly inflated, and raised markedly above fixigenae, basal circumference pyriform; maximum height equivalent to just slightly less than maximum width, which is attained at about one third of the cranidial length from anterior margin, actually level with summit of

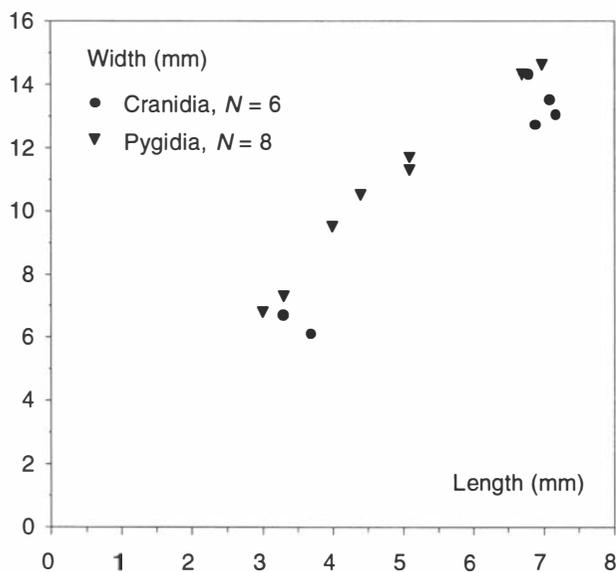


Fig. 260. *Globampyx linnarssoni*. Maximum width plotted against sagittal length of cranidia and pygidia.

glabella. Maximum glabella width corresponds to about one third of the maximum width of cranium, i.e. glabella is comparatively narrow (tr.). Front of glabella subvertical, with only a minimal overhang, and anterior margin of cranium is visible in dorsal view (Fig. 261A, C). Sagittal curvature gently convex posterior to glabella summit, almost straight, descending gradually rearwards. Glabellar outline like a Roman arch in frontal view, posteriorly slightly carinate; juvenile cranidia, about 3–4 mm long, show a more distinctly keel-shaped, rather carinate glabella (Fig. 261B). No frontal spine, but a minute glabellar tubercle is situated immediately in front of top point (all specimens are exfoliated). Obscure median keel, running almost to occipital furrow, indicated behind glabellar tubercle in a few specimens. The keel is not likely to show on testaceous material. Four pairs of round to ovoid muscle areas in the axial region, all of which are rather faint, and best defined in specimens showing coloured muscle markings. F0 situated anterolaterally on occipital ring, reaching down into occipital furrow; size moderate, only inconsiderably impressed and virtually effaced on internal moulds. F1 and F2 comparatively large and visible as shallow scars also on internal moulds. F1 situated shortly in front of occipital furrow, reaching from about one third up glabella and downwards, continuing obliquely backwards into axial furrow. F2, which is slightly larger than F1, situated a little in front of F1, reaching from one third up glabella and down to axial furrow. F3 small, bicomposite, consisting of a lower round area situated adjacent to axial furrow, shortly in front of F2, and an upper slightly smaller round area situated immediately above. F3 defined on internal moulds as shallow, inconspicuous impressions. Occipital furrow moderately impressed, curving

slightly backwards mesially; juvenile specimens show a more deeply impressed furrow. It shallows up laterally, and are replaced by small faintly inflated areas, situated adjacent to the axial furrow in the distal part of occipital 'furrow', immediately above posterior boundary of F1. Occipital ring narrow (sag.), convex, confluent with posterior border; it is somewhat raised above rear part of glabella, and occipital furrow is therefore defined also laterally despite the basal inflated areas. Axial furrow and preglabellar furrow narrow and shallow, but glabella is well set off by a marked change of slope. Minute, elongate, moderately deep fossulae situated in axial furrows just in front of maximum glabellar width. Anterior border of cranium comparatively wide (sag.) and long (tr.), rather flat, sloping gently forwards; no border furrow present and the border is essentially defined by a change of slope. Anterior margin gently and broadly arched in frontal view (Fig. 261D). Fixigenae triangular in outline, gently convex, sloping anteriorly. Genal ridges not seen. Posterior border of cranium slightly concave, almost straight, slanting forwards; adaxial half moderately elevated above fixigenae, abaxial half slightly more so; it is delimited by a shallow, though comparatively well-defined, straight border furrow. It is suspected that no pit is developed in the furrow near genal angle, but this cannot be verified (extreme distal part poorly preserved in all specimens available). Facial suture marginal anteriorly, then crosses the genae, being gently concave, almost straight, running to genal angle. A few patches of preserved test on anterior border and inner posterior portion of fixigenae and posterior border appears to be smooth; surface sculpture generally unknown as the available specimens are exfoliated; surface of internal moulds smooth.

Pygidium broadly triangular in outline, about 2.1 to 2.4 times as wide as long, anterior margin straight, anterolateral corners acute. Axis gently vaulted, gradually descending rearwards, and terminal piece levels with the adjacent pleural fields. Axial width at anterior margin equivalent to 0.26–0.30 of maximum pygidial width. Axis tapers evenly backwards, but reaches posterior border; terminal piece acutely rounded. Eight axial segments were counted on an internal mould in addition to the articulating half-ring, but the true number of axial segments may be slightly higher, as the indistinctly segmented posterior part possibly contains two to four rings. Only the articulating half-ring is well set off by a well-defined furrow; rearwards the ring furrows are very shallow, vaguely indicated laterally, effaced mesially. Axial furrows wide, deeply impressed, more distinctly so than in most raphiophorids. Pleural fields almost flat, horizontal; pleural region without segmentation apart from the anterior, moderately impressed, straight furrow, delimiting the anterior half rib; on external side of test this furrow is shallow. Three or four pleural ribs are vaguely indicated on a few internal moulds. The general absence of pleural furrows perhaps relates to poor preservation; the pygidia figured by Schmidt (1894, Pl. 6:23) and Neben & Krueger (1971, Pl. 2:9)

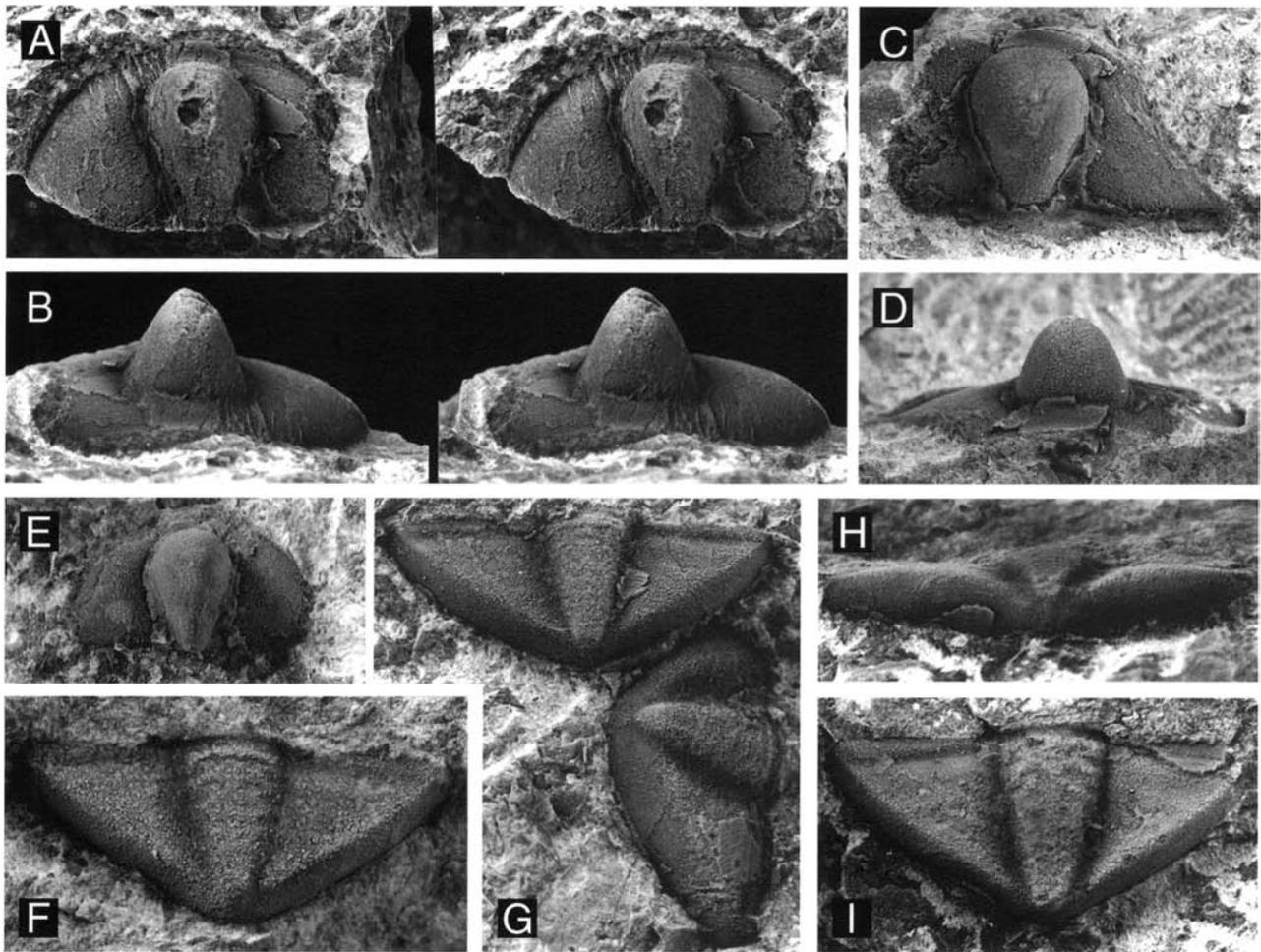


Fig. 261. *Globampyx linnarssoni* (Schmidt, 1894). All specimens are from bed M-1, Slemmestad. □A–B. Largely exfoliated cranidium, dorsal and frontal views, stereo-pairs, $\times 4$, MGUH 23.074 (A 608a). □C–D. Exfoliated, slightly fragmentary cranidium, dorsal and frontal views, $\times 4$, MGUH 23.075 (A 584). □E. Exfoliated small cranidium, $\times 6$, MGUH 23.076 (A 609b). □F. Exfoliated pygidium, $\times 4$, MGUH 23.077 (A 637). □G. Two exfoliated pygidia, $\times 5$, MGUH 23.078 and 23.079 (A 634a, b). □H–I. Exfoliated small pygidium, posterior and dorsal views, $\times 8$, MGUH 23.080 (A 607).

show such furrows. Border well set off by a marked change of slope; the flexure is gently rounded in adult specimens (all internal moulds), juveniles show sharper bend; it is inconclusively indicated by the material that the bend is most distinct on testaceous specimens. Border steep, sloping strongly in posterolateral direction, and of nearly uniform width all the way except at the intersection with axial furrows; the margin is slightly, broadly and evenly arched in posterior view. Border covered with closely spaced terrace lines arranged parallel to outer margin; pleural fields appear smooth (material badly preserved). Test is not preserved on the axis, and the doublure is not visible in the available material.

Affinities. – *Globampyx linnarssoni* is distinguished from *G. trinucleoides* by the stronger inflated, more carinate glabella with somewhat less deeply impressed F1 and F2, of which F1 enters the axial furrow, which does not seem to be the

case in *G. trinucleoides* (cf. Fortey 1975a, Pl. 29:1). The pygidium of *G. linnarssoni* differs by being relatively longer (sag.), the axial furrows are more impressed, pleural furrows are absent or vestigial, and a mesial arch is not developed. Although only partially known, the external ornamentation of *G. linnarssoni* appears quite different from that of *G. trinucleoides*.

G. linnarssoni must be closely related to the but slightly older *G. obtusus*, sharing the same inflated glabella, and the respective pygidia are also strongly similar. *G. obtusus* is distinguished by the characteristic elongate mesial keel on glabella, running backwards from a small tubercle, and from which a glabellar spine rises, pointing backwards. *Globampyx obtusus* is a potential candidate for an ancestor to *G. linnarssoni*, and the rudimentary glabellar keel of *G. linnarssoni* could be interpreted as another synapomorphy.

Ampyx brevicauda Wiman, 1905, was suggested closely related to '*Ampyx linnarssoni*' by Wiman (1905, p. 12), based

on the lack of a glabellar spine, and the presence of a faint mesial glabellar keel. Apart from the mentioned similarities, the two species seem rather different, but *Ampyx brevicauda* is insufficiently known, precluding a detailed comparison.

Globampyx linnarssoni is readily distinguished from most other raphiophorids by the characteristic strongly inflated, spine-less glabella. Schmidt (1894, p. 83) regarded *Ampyx linnarssoni* as the ancestor of *A. nasutus*, and he stressed the identical pattern of muscle areas on glabella, the short glabella (not overhanging anterior cranial margin), and the only faintly indicated glabellar spine as features in common. The pattern of muscle areas must be regarded as a plesiomorphic feature, shared with most other raphiophorids, the similar shape of glabella stated by Schmidt is not strikingly obvious, and a fairly well-developed glabellar spine seems generally to be present in *A. nasutus*. Accordingly, there is no evidence for a close relationship between the two species.

Remarks. – Schmidt (1894, p. 83) wrote that the glabella shows a mesial keel running forwards to a small tubercle from which the spine ('Horn') rises. No such spine is evident

from Schmidt's figures (1894, Pl. 6:21–22), but one of the specimens (Pl. 6:22) shows a fairly prominent median tubercle, and a vague sagittal keel is indicated on the other specimen (Pl. 6:21). The cranidia illustrated by Neben & Krueger (1971, Pls. 2:7–8; 3:9–10) exhibit a faint mesial keel, but no glabellar spine. It thus appears that there possibly are some variation with regard to this feature; Remelé (1885) actually also described two forms of *Hybocephalus hauchecornei*, a larger one with a glabellar spine, and a smaller one without. The lectotype of *G. linnarssoni* (Schmidt 1894, Pl. 6:21, 21a) has no spine, and this condition may be taken as characteristic of *G. linnarssoni* (*s.str.*)

Only a few of the specimens at hand exhibit a vestigial glabellar keel; it is normally absent. A better defined keel seems to be indicated in the material investigated by Schmidt (1894) and by Neben & Krueger (1971). Recognition of this feature may depend upon the state of preservation, but alternatively the differences in keel appearance may be phenotypic, reflecting environmental control, or it may relate to stratigraphic variation, where early specimens might show a less rudimentary keel.

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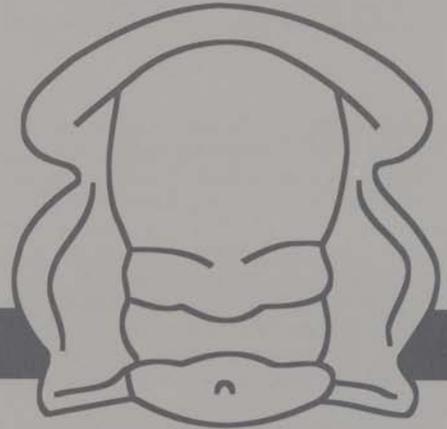
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