

Trilobites of the Hagastrand Member (Tøyen Formation, lowermost Arenig) from the Oslo Region, Norway. Part II: Remaining non-asaphid groups

OLE A. HOEL

Hoel, O. A.: Trilobites of the Hagastrand Member (Tøyen Formation, lowermost Arenig) from the Oslo Region, Norway. Part II: remaining non-asaphid groups. *Norsk Geologisk Tidsskrift*, Vol. 79, pp. 259–280. Oslo 1999. ISSN 0029-196X.

This is Part II of a two-part description of the trilobite fauna of the Hagastrand Member (Tøyen Formation) in the Oslo, Eiker-Sandsvør, Modum and Mjøsa areas. In this part, the non-asaphid trilobites are described, while the asaphid species have been described previously. The history and status of the Tremadoc–Arenig Boundary problem is also reviewed, and I have found no reason to insert a Hunnebergian Series between the Tremadoc and the Arenig series, as has been suggested by some workers. Descriptions of the localities yielding this special trilobite fauna are provided. Most of the 22 trilobite species found in the Hagastrand Member also occur in Sweden. The 12 non-asaphid trilobites described herein belong to the families Metagnostidae, Shumardiidae, Remopleuridae, Nileidae, Cyclopygidae, Raphiophoridae, Alsataspidae and Plimeridae. One new species is described; *Robergiella tjernviki* n. sp.

Ole A. Hoel, Paleontologisk Museum, Sars gate 1, N-0562 Oslo, Norway.

Introduction

The Tremadoc–Arenig Boundary interval is a crucial point in the evolution of several invertebrate groups, especially among the graptolites and the trilobites. In the graptolites, this change consisted most significantly in the loss of bithekae and a strong increase in diversity. For the trilobites, this interval saw the final disappearance of most of the typical Cambrian groups and the emergence of many of the main groups typical of the Ordovician. The Tremadoc–Arenig Boundary interval also saw a major global regression, which means that sediments from this time are not present in most areas, notably in the Welsh Basin, where the Tremadoc and Arenig Series was defined. Proposals on how to solve this problem are important discussion points in works dealing with areas where this boundary interval is represented. A study of the literature on the Tremadoc–Arenig Boundary is therefore included here.

The trilobites described in this monograph constitute the non-asaphid species that are present in the Hagastrand Member (Tøyen Formation) in the Oslo, Eiker-Sandsvør, Modum and Mjøsa areas of the Oslo Region. The asaphid species have already been described (Hoel 1999). The Tøyen Formation (Owen et al. 1990) is a shale unit of latest Tremadoc–middle Arenig age deposited on the continental slope at the western edge of the epicontinental sea that covered most of the Baltic platform. It overlies limestones of the Bjørkåsholmen Formation, and occurs in all districts of the Oslo Region except Skien-Langesund, where there is a hiatus between the Upper Cambrian and Lower Llanvirn (Owen et al. 1990, pp. 8–9) (Fig. 1). It is also present in the Allochthons of the Scandinavian Caledonides to the northwest (Rasmussen & Bruton 1994). The

contemporaneous platform deposits in Sweden are dominated by a condensed limestone succession. In Norway, the Tøyen Formation is divided into two members: the lower

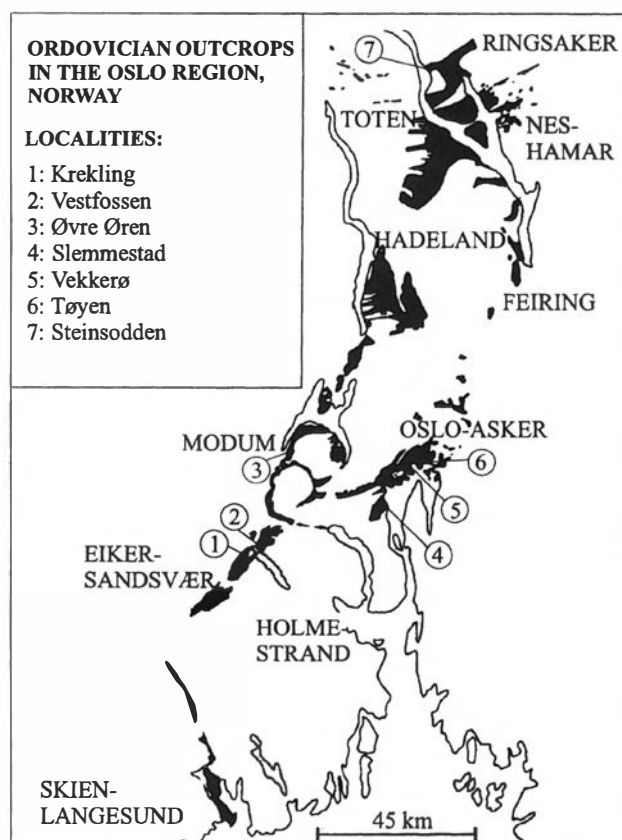


Fig. 1. Map of the Ordovician outcrops in the Oslo Region. Numbers correspond to the localities described herein.

part, the Hagastrand Member, consists of grey, poorly fossiliferous shales; the upper part, the Galgeberg Member, is a black, richly fossiliferous graptolitic shale. In Eiker-Sandsv  r, locally in the Modum area, and at Vekker   in Oslo, the Hagastrand Member is developed as a condensed limestone succession, which contains a trilobite fauna similar to the one found in the *Megistaspis* (*Paramegistaspis*) *planilimbata* Zone in Sweden.

For details on geological setting and stratigraphical data the reader is referred to Part I of this monograph (Hoel 1999).

The Tremadoc–Arenig boundary problem

Lapworth (1879, p. 14) defined the Ordovician System to include all rocks ‘between the base of the Lower Llandovery Formation and that of the Lower Arenig’. Following the work of Hicks (1875), Lapworth drew the lower boundary of the Ordovician at the base of the Upper Tremadoc (his ‘Lower Arenig’) and the upper boundary of the Cambrian at the top of the Lower Tremadoc. Lapworth thus originally included the Upper Tremadoc in the Arenig (Skevington 1966; Henningsmoen 1973). The later British use of the Arenig Series does not include this; The lower boundary is set above the ‘sub-Arenig’ unconformity. The large hiatus between the base of Sedgwick’s ‘Arenig Group’ and the top of the Tremadoc has since then limited the usefulness of the British successions in worldwide correlation at this level. This is also the reason behind the long-standing disagreement over the level at which the Cambrian–Ordovician boundary should be drawn.

Recently (Fortey & Owens 1978, 1987, 1991, 1992; Fortey et al. 1995), great effort has been made to attempt to show that the British succession is more complete than previously thought. This work has had considerable success, but although part of the ‘missing time’ has been filled in, the Welsh successions are still unsuitable to provide a solution to the Tremadoc–Arenig Boundary problem. This is mainly due to the scarcity of correlatable fossils in Wales, especially graptolites, which are mostly absent from the Welsh Basin.

No beds equivalent to the *Apatokephalus serratus* Zone are known in Great Britain (Lindholm 1991b), although an older species, *A. sarculum*, is found in the *Shumardia* (*Conophrys*) *salopiensis* Zone of Shropshire (Fortey & Owens 1991). Fortey & Owens (1992) reported the *Asaphellus* cf. *graffi* fauna from the Habberley Formation, Welsh Borderlands. This is the youngest Tremadoc found in Wales. They tentatively correlated this fauna with the Hunnebergian of Tjernvik (1956), but only because this interval lies between the Scandinavian equivalents of the British Tremadoc and Arenig. Their figure (Fortey & Owens 1992, fig. 2) shows that the sea level in the upper part of the Habberley Formation was falling. This indicates a possible correlation with the *Apatokephalus serratus* Zone of Scandinavia, in which the late Tremadoc sea level

fall (Ceratomyge Regressive Event of Erdtmann & Paalits 1995 reaches its lowest point, but this correlation is uncertain at best. None of the pandemic species present in the *Apatokephalus serratus* Zone of Scandinavia are found in Wales and this probably means that this time-interval is missing in Wales and Shropshire.

The subsequent transgression seen in the overlying Stiperstone Quartzite, which is taken as the local base of the Arenig, may correspond to the quartzites (‘Bl  kvarts’) of Arenig age found on Hardangervidda in Norway.

Trilobite faunas older than the Moridunian have been found in the Carmarthen district, south-west Wales (Fortey & Owens 1978), representing a level above the basal Arenig transgression. This area is dominated by olenids. Earliest Arenigian graptolites and acritarchs are found in the Skiddaw Group in England, which are thought to correlate with the *Tetragraptus approximatus* Zone (Molyneux & Rushton 1988). This age is confirmed by the occurrence of *Didymograptus rigoletto*, a short-ranging graptolite species characteristic of the Scandinavian *Tetragraptus phyllograptoides* Zone (Maletz et al. 1991). Although this is the area where the pre-Arenig hiatus is smallest in the British Isles, the earliest part of the Hunnebergian period (Lindholm 1991a) is not found in Great Britain.

The *Didymograptus deflexus* Zone is the lowest in the Arenig of North Wales (Williams et al. 1972). This corresponds to the upper part of the *Didymograptus balticus* Zone in Scandinavia (= Bendigonian 3 in Australia, Lindholm 1991a). The older graptolites of the Lake District, Northern England, range down to Middle Bendigonian (Be 1–2) age of the Australasian system, or the upper part of the *Tetragraptus phyllograptoides* Zone in Scandinavia (Lindholm 1991b). This leaves a considerable timespan (= La 1.5 to Be 3 of Australia) unrepresented by sediments in North Wales. Compared to the Scandinavian succession, the Tremadoc in North Wales ends approximately at the base of the *Apatokephalus serratus* Zone, and the base of the Arenig in the type area of North Wales (Moridunian 1) is contemporaneous with the base of the *Phyllograptus densus* Zone of Scandinavia (Cooper & Lindholm 1990). This level is found in the upper part of the Galgeberg Member of the T  yen Formation in Oslo (Erdtmann 1965), and correlates with the *Megalaspides* (*Megalaspides*) *dalecarlicus* Zone (Billingen substage) in Sweden (Tjernvik 1956).

The interval missing in North Wales thus corresponds to the time represented by the *Clonograptus tenellus* Zone to the *Didymograptus balticus* Zone. The duration of these zones has been estimated by Cooper & Lindholm (1990) to be approximately 10–15 Ma. Erdtmann (1988) and later Lindholm (1991a), proposed that the base of the Arenig should be drawn at the base of the *Araneograptus murrayi* Zone, or at the base of the *Oepikodus evae* conodont Zone. Alternatively, they suggested that the local Baltic Hunnebergian Substage should be elevated to Series rank; comprising the zones of *Hunnegraptus copiosus*, *Tetragraptus phyllograptoides* and *Didymograptus balticus*

TREMADOC		ARENIG		This paper	
HUNNEBERG SUBSTAGE		BILLINGEN SUBSTAGE			
TREMADOC	HUNNEBERG GROUP	BILLINGEN GROUP		Tjernvik 1956	
TREMADOC	HUNNEBERG SUBSTAGE	BILLINGEN SUBSTAGE		Tjernvik & Johansson 1980	
TREMADOC	HUNNEBERGIAN STAGE	BILLINGIAN STAGE		Cooper & Lindholm 1990	
TREMADOC	HUNNEBERGIAN SERIES EARLY	ARENIG (BILLINGIAN STAGE)		Lindholm 1991a	
TREMADOC	HUNNEBERGIAN STAGE EARLY	ARENIG (BILLINGIAN STAGE)		Erdmann letter 1994	
Graptolite zones		Trilobite zones		Conodont zones	
<i>P.densus</i>	<i>M.(P.) estonica</i>	<i>Oepikodus evae</i>		Be 4	
	<i>M.dale-carlicus</i>				
<i>D.balticus</i>	<i>M.(P.) aff. estonica</i>	<i>Prioniodus elegans</i>		Be 2	
<i>D.validus</i>					
<i>T.phyllo-graptoides</i>	<i>M.(P.) planilimbata</i>	<i>Paroistodus proteus</i>		upper-most La 3	
<i>H.copiosus</i>	<i>M.(E.) armata</i>			upper middle	
<i>A.murrayi</i>		lower middle La 2			
<i>K. supremus</i>	<i>A. serratus</i>	<i>Paltodus deltifer</i>		lower-most La 1,5	

Fig. 2. Historical review of the varying concept of the Hunnebergian interval.

and inserted between the Tremadoc and the Arenig (see Fig. 2).

The definition of the Tremadoc–Arenig Boundary has recently been debated by the International Subcommission on Ordovician Stratigraphy (ISOS). A proposal for a Global Stratotype Section and Point (GSSP) was made for a section at 'the Ledge', Cow Head Peninsula, Newfoundland, Canada (Williams et al. 1994). Several objections have been raised against this section, especially that the only clearly documented fossil below the first appearance of *Tetragraptus approximatus* is *Aorograptus victoriae*, which is long ranged. Williams et al. (1994) correlate the occurrence of *A. victoriae* with the *Hunnegraptus copiosus* Zone of Scandinavia, although the species ranges from the bottom of La2 to the top of La3 in Australasia (Cooper 1979). Another GSSP has been proposed at Diabasbrottet, Västergötland, Sweden by Maletz et al. (1995). Williams et al. (1994) noted that for a long time, the first occurrence of *T. approximatus* has been generally accepted as the lower boundary of the Arenig Series. Even in Great Britain the first occurrence of *T. approximatus* has been accepted

as the base of the Arenig, and beds of this age may be present at Trusmadoor, Lake District (Fortey et al. 1995). In Australasia this event signifies the start of the La3 substage.

If the correlation charts of Cooper & Lindholm (1990, fig. 1) are correct, the occurrence of *A. murrayi* in Scandinavia would correspond to the upper part of the Australasian of the *Aorograptus victoriae* Zone (La2). *Tetragraptus approximatus* is contemporary with *T. phyllograptoides* in Scandinavia (Monsen 1936; Cooper & Lindholm 1990), which means that the base of the *Tetragraptus phyllograptoides* Zone is the base of the Scandinavian Arenig. The result of internationally taking the first appearance of *Tetragraptus approximatus* as the base of the Arenig is that a Hunnebergian Series would include only the *Araneograptus murrayi* Zone and the *Hunnegraptus copiosus* Zone. This interval corresponds only to the middle and upper parts of the Lancefieldian 2 of Australasia. I therefore see no reason to retain the Hunnebergian as a Series. Further notes on the Stage boundaries of the Ordovician are found in Webby (1998).

Description of localities

Eiker-Sandsvør District

Krekling Farm, Øvre Eiker (Map coordinates UTM NM 433144). – This locality is located in the eastern roadside ditch near Krekling Farm some metres north of the junction with Åssideveien. Here the Hagastrand Member is readily accessible, above the (presently unexcavated) Bjørkåsholmen Formation. Fjellidal (1966, p. 21) records the lowest part of the Hagastrand Member as 50–60 cm of green, silty shale, fining upwards, and containing some inarticulate brachiopods in the upper part. The limestone facies of the Hagastrand Member, begins, however, with a thin, coarsely crystalline calcite layer, which gives way to more micritic limestone (mostly a marl) with horizontal and vertical intercalations of grey to black shale. All six main beds have a similar texture and, in hand specimens, the fossils occur randomly orientated in the rock. The lowest bed cleared in 1995 is overlain by 12 cm of unfossiliferous shale and then more limestone. This is not particularly fossiliferous, but specimens of *Shumardia nericiensis* were found 15 cm above the base, and *Promegaspides (Borogothus) stenorachis* and *M. (P.) planilimbata* 70 cm above the base. The Galgeberg Member lies directly above the last limestone bed, and contains *Tetraraptus pylograptoides*, *Didymograptus holmi*, *D. holthedahli* and *D. quadribrachiatus* near the base. These indicate the *Tetraraptus approximatus* Zone (upper part of 3b α , Monsen 1936).

Kårtveitbekken (Kårtveit rivulet), Krekling, Øvre Eiker (UTM NM436151). – Brøgger (1882, p. 18) noted that at Kårtveit, just north of Krekling Farm, the upper part of the Ceratopyge beds contained a different and much poorer fauna than that found in the main Ceratopyge Limestone. This younger fauna he believed could either belong to an upper division of the 'Ceratopyge Limestone', or a limestone facies of the overlying 'Lower Didymograptus Shale'. He did not state which of these two possibilities he favoured. Brøgger identified *Ceratopyge forficula*, *Megistaspis (Ekeraspis) heroides*, *Niobe (Niobella) bohlini* (his *Niobe laeviceps*), *Promegaspides (Borogothus) stenorachis* and *Orthis christianiae*.

In addition to these is a cranidium of a large *Megistaspis* (figured by Skjeseth 1952, pl. 1, fig. 4 as *M. (E.) heroides* Brøgger, 1882). This specimen, labelled 'Ceratopyge Limestone, Kårtveitbekken, Krekling' does not resemble any other species from this time interval and in my view it belongs to *Megistaspis (Megistaspis) polyphemus*, and comes from the uppermost part of the Tøyen Formation. I have not identified Brøgger's locality in Kårtveitbekken, and only a small outcrop of limestones of the Hagastrand Member is present about 50 m downstream from the road. The stream has cut through the shales of the overlying part of the Tøyen Formation, whilst the harder limestone is seen in the stream bottom. This limestone yielded an unusually high concentration of shells of *M. (P.) planilimbata*, *M.*

(P.) planilimbata subsp. A, *M. (P.)* sp., *Megaspides nericiensis*, *Niobe (Niobella) bohlini*, *N. (Proxiniobe) longicauda* Hoel, 1999 and *Promegaspides (Borogothus) stenorachis*.

Stavlum (Krekling), Øvre Eiker (UTM NM 445161). – Ebbestad (1993, appendix D–IV) presented a log based on a core section, drilled by Forsvarets Forskningsinstitutt in 1946, where the limestones of the Bjørkåsholmen Formation and the Hagastrand Member were found in the interval 19.04 m–20.67 m. One hundred metres north of Stavlum a 40 m long and 3 m high roadcut shows rocks from the Bjørkåsholmen Formation to the Huk Formation exposed in an anticline. I have identified *Megistaspis (Paramegistaspis) planilimbata* from the upper beds of the Hagastrand Member.

Vestfossen railway station, Øvre Eiker (UTM NM 487221). – This section is exposed in the western bank of the railway cutting where a small anticline contains tectonically altered and fractured rock from the Bjørkåsholmen Formation up to the Huk Formation (see Ebbestad 1997, fig. 2 and Ebbestad in press, fig. 8). The lowermost bed is poorly fossiliferous, containing trilobites together with lingulid and acrotretid brachiopods.

The three lower beds contain trilobites indicative of the lower part of the *Megistaspis (Paramegistaspis) planilimbata* Zone, including *Megistaspis (Ekeraspis) heroides*, *M. (Paramegistaspis) planilimbata* subsp. A, *Niobe (Niobella) bohlini*, *N. (Proxiniobe) longicauda* Hoel, 1999, *Gog n. sp.*, *Falanaspis aliena* and *Megaspides nericiensis*.

Numbers of specimens are higher in the upper beds, which have yielded *M. (P.) planilimbata*, *M. (P.)* spp., *Promegaspides (Borogothus) stenorachis*, *Varvia breviceps*, *Megaspides nericiensis* and *Hintzeia actinura*.

The disarticulated trilobite parts have no apparent preferred direction and appear to have been deposited in agitated water or disturbed by bioturbation. Some specimens are well preserved, but most seem to have been corroded and/or transported some distance before deposition.

Skarahaugen, Vestfossen, Øvre Eiker (UTM NM 472221). – This locality is where T. Klemm (Klemm 1982) made his collections in the early 1980's. It has since been improved through the construction of a new farm road, and provides a continuous exposure from the Upper Cambrian *Acerocare* Zone (Zone VI of Henningsmoen (1957)) to the Upper Arenig-Lower Llanvirn *Asaphus expansus* Zone (see Ebbestad 1993, appendix D–XIV). The lowermost bed of the Hagastrand Member is about 5 cm thick and has yielded inarticulate brachiopods and conodonts belonging to the upper middle Subzone of the *Paroistodus proteus* Zone (= lowermost part of the *Megistaspis (Paramegistaspis) planilimbata* Zone; Löfgren pers. comm. 1996). Trilobites from the lower three beds include *M. (E.) heroides*, *M. (P.) planilimbata* subsp.

A. Megalaspides nericiensis, *Niobe* (*Niobella*) *bohlini*, *N. (Proxiniobe) longicauda* Hoel, 1999, *Promegalaspides (Borogothus) stenorachis*, Gog n. sp., *Falanaspis aliena* and *Geragnostus* aff. *wimani*, whilst those from the upper beds include *M. (P.) planilimbata*, *Megalaspides nericiensis*, *Niobe (Niobella) bohlini*, *N. (Proxiniobe) longicauda* Hoel, 1999, *Promegalaspides (Borogothus) stenorachis*, *Lapidaria rugosa*, *Shumardia nericiensis* and *Geragnostus wimani*. In the uppermost bed a specimen of *Niobe (Niobella)* sp. aff. *obsoleta* no. 2 (see Tjernvik 1956, p. 231) was found. This species occurs in the *M. (P.)* aff. *estonica* Zone in Sweden, and thus indicates its earliest Billingen age.

Modum district

Øvre Øren, Vikersund (UTM NM 555442). – This is a roadcut below Øren farm, 50 m long and 3 m high, exposing beds from the Bjørkåsholmen Formation to the Huk Formation (see Ebbestad 1993 appendix D–XVIII, 1997, fig. 2, and Ebbestad in press, fig. 9).

Above the Bjørkåsholmen Formation 20 cm of unfossiliferous shales occurs, possibly representing the *Megistaspis (Ekeraspis) armata* Zone. These shales are overlain by a 22-cm-thick limestone bed containing usually badly preserved trilobites belonging to the *Megistaspis (Paramegistaspis) planilimbata* Zone: *M. (P.) planilimbata*, *M. (P.)* sp., *Megalaspides nericiensis*, *Promegalaspides (Borogothus) stenorachis*, *Niobe (Proxiniobe) longicauda* Hoel, 1999, Gog n. sp., *Robergiella* sp. and *Shumardia nericiensis*.

Oslo–Asker district

Bjørkåsholmen, Slemmestad (UTM NM 843291). – This locality is close to Hagastrand, the stratotype for the Tøyen Formation (Owen et al. 1990). Fjellidal (1966, p. 51) presented a log, and recorded *Symphysurus angustatus* and *Megistaspis (Paramegistaspis) planilimbata*. See also Ebbestad (1993, appendix D–XLI).

Rortunet, Slemmestad (UTM NM 835278). – This section was measured and the lower part published by Owen et al. (1990, p. 7). It is the only locality in Norway from which *Megistaspis (Ekeraspis) armata* has been recorded. The specimen, a badly preserved complete carapace (PMO 158.239–240) comes from the 21.3 m level, or 3.5 m above the Bjørkåsholmen Formation. It occurs together with *Araneograptus murrayi*, the zonal fossil for the middle part of the *M. (E.) armata* Zone. *Tetragraptus phyllograptoides* is found at the 28 m level, indicating that the Hagastrand Member is at least 10.2 m thick here.

Vekkerø, Oslo (UTM NM 923428). – Here, 15 cm of shale separates the limestones of the Bjørkåsholmen Formation and the Hagastrand Member (Owen et al. 1990, p. 9; Ebbestad 1993, appendix D–XLVII, and Ebbestad 1997, fig. 2). The Galgeberg Member lies directly above the

limestones, but the shales are heavily distorted by tectonism and no graptolites have been found. Other fossils are rare in the Hagastrand Member and several blocks collected in 1995 produced only a few lingulid brachiopods and one badly preserved trilobite pygidium, probably belonging to *Niobe (Proxiniobe) longicauda* Hoel, 1999.

The scarcity of inarticulate brachiopods is very unusual, as they are very common elsewhere. The thickness of the Hagastrand Member at Vekkerø is about one metre. The sedimentary rate must have been very much lower here than at Tøyen (only 7 km to the east) where equivalent beds are at least 8 m thick. Erdtmann (1965, p. 525) proposed that the development at Vekkerø might represent a 'facies island'. Owen et al. (1990, p. 10) noted that Vekkerø and the localities in Eiker-Sandsvær represent areas of carbonate sedimentation on topographic highs above the larger area of mud accumulation to the north, east and southeast.

Tøyen, Oslo (UTM NM 992432). – In the Tøyen area several temporary sections have been available during construction work. In 1960–63 excavation for a new underground station revealed a section through 19.75 m of the Tøyen Formation (= 3b of Erdtmann 1965). This section is no longer available, and Owen et al. (1990) designated a neostratotype for the Tøyen Formation at Hagastrand, Asker. Erdtmann (1965, p. 495) notes the occurrence of *Megistaspis (Paramegistaspis) planilimbata* about 7 m above the base of the formation, but in collections made by him and G. Henningsmoen, the following trilobites of the *Megistaspis (Paramegistaspis) planilimbata* Zone have been identified from a limestone bed 6.5–6.8 m above the top of the Bjørkåsholmen Formation: *M. (P.) planilimbata*, *Symphysurus angustatus*, *Megalaspides nericiensis*, *Niobe (Proxiniobe) longicauda* Hoel, 1999, *Arthrorhachis* sp., *Robergiella* sp. and *Shumardia nericiensis*.

A sample collected 8.00–8.08 m above the Bjørkåsholmen Formation reveals *Pricyclopyge* sp. and *Niobe (Niobella) bohlini* on the same slab. The presence of the latter at such a high level is interesting and shows that the Latorp Stage is at least 8 m thick at Tøyen, and this is comparable to the thickness in the drill-core from the Bothnian Bay (Tjernvik & Johansson 1980).

Additional samples labelled '3 b' (= Tøyen Formation) have been collected lower in the section because they contain several of the index fossils of the underlying Bjørkåsholmen Formation (*Apatokephalus serratus* Zone). Trilobites from the *Megistaspis (Ekeraspis) armata* Zone have not been identified in samples from the section at Tøyen underground station. A section in Finnmarksgata (UTM NM 992435) contains a limestone layer about 3 m above the top of the Bjørkåsholmen Formation and Lindholm (1991a, fig. 3) marks this level as 'the good bed' containing the *Hunnegraptus copiosus*-fauna. Associated trilobites include *Niobe (Niobe)* sp., *Promegalaspides (Borogothus) stenorachis*, *Geragnostus* sp., *Saltaspis*

(?) sp. and *Symphysurus angustatus* (?), which suggests the presence of the *Megistaspis* (*Ekeraspis*) *armata* Zone.

In the spring of 1972, a trench dug in Finnmarksgata, (near the Munch Museum, and within 200 m of the Tøyen underground station), provided a second section which included part of the Alum Shale Formation up to the Tøyen Formation. Tove Bockelie sampled the section from her lowermost 'bed A' below the Bjørkåsholmen Formation to the uppermost 'bed P' in the lower Tøyen Formation and Gjessing (1976) shows a profile up to the lower boundary of the Bjørkåsholmen Formation. A sample from Gjessing's 'bed P' (not the same as Bockelie's) contains *Orometopus* aff. *elatifrons*, *Geragnostus crassus*, *Symphysurus* sp., *Euloma* sp. and *Apatokephalus* (?) sp., *Lingulella* sp., *Acrotreta* sp., *Nanorthis* (?) sp. and a cystoid plate, and is probably from the Bjørkåsholmen Formation.

Mjøsa district

Skjeseth (1952, pl. 1, fig. 10) described a specimen of *Megistaspis* (*Paramegistaspis*) *planilimbata*, from Ottestad, south of Hamar, which later became the holotype of *Megistaspis* (*Paramegistaspis*) *norvegica* (Tjernvik, 1956, p. 240, pl. 7, fig. 2). In Sweden this species occurs in the *Megalaspides dalecarlicus* Zone, confirming the equivalent zone in Norway.

Steinsodden, Ringsaker; (UTM NM 920535). – At Steinsodden (see Fjellidal 1966, p. 89; Ebbestad 1997, fig. 2), some 50–80 cm of grey shale separates the limestones of the Bjørkåsholmen Formation from a layer of limestone nodules (Strand 1929, p. 327). These nodules yielded *Lingulella lepis*, *Eoorthis christianiae*, *Ceratopyge forficula*, *Niobe insignis* and *Promegalaspides stenorachis*, the last-mentioned species being similar to material from the Hagastrand Member.

Re-examination of Strand's specimens and those later collected by Henningsmoen has led to the additional identification of *Leiocardinia difformis* (?), *Niobe* (*Niobella*) *obsoleta*, *Megistaspis* (*Paramegistaspis*) sp. and *Euloma* sp. aff. *ornatum* (similar to *Euloma* sp. 1 of Tjernvik 1956).

This fauna could be transitional between the Bjørkåsholmen Formation (*Apatokephalus serratus* Zone) and the lower part of the Tøyen Formation (*Megistaspis* (*Ekeraspis*) *armata* Zone). Steinsodden is now protected by law, and collecting can be arranged through the Palaeontological Museum, Oslo.

Systematic palaeontology

The following abbreviations denote institutions where particular specimens are housed:

PMO – Palaeontologisk Museum, University of Oslo, Norway

PMU – Palaeontologiska Museet, University of Uppsala, Sweden

RM – Naturhistoriska Riksmuseet, Stockholm, Sweden

In the occurrence of the species, the beds are numbered from 1 (lowest) to 6 (highest). Samples collected by T. Klemm from Skarahaugen were also marked with subdivisions as 1A, 1B, etc., and the letters *o*, *m* and *u* (*obere*: upper, *mittlere*: middle and *untere*: lower) to indicate subdivisions. Exactly which bed corresponds to Klemm's numbers is impossible to ascertain because he worked with a well-weathered outcrop later destroyed during the construction of the present tractor road. His field notes are not available. Beds 1–3, and 4–6 respectively, correspond to approximately the lower and upper 50 cm of the limestone beds. See also part I of this monograph (Hoel 1999).

Family *Metagnostidae* Jaekel, 1909

[= *Trinodidae* Howell, 1935; *Geragnostidae* Howell, 1935; *Arthrorhachidae* Raymond, 1913]

Genus *Geragnostus* (*Geragnostella*) Kobayashi, 1939

Type species. – *Agnostus tullbergi* Novák, 1883 (pl. 9, figs. 7, 8, 9, 10) from the Šárka Formation (Llanvirm) of Osek near Rokycany, Czech Republic.

Remarks. – Most recent authors have considered *Geragnostella* to be a junior synonym of *Geragnostus* Howell, 1935 (See Nielsen 1997 for a review). *Geragnostella* has been defined mainly on the effacement of the dorsal furrows around the posterior lobe of the pygidium, and the presence of a conspicuous node on the terminal end of the axis. Despite these seemingly dubious characters, Nielsen (1997, p. 484) has shown that they are useful, and intermediate forms between *Geragnostella* and *Geragnostus* have not been found. Following Nielsen, *Geragnostella* is treated as a subgenus of *Geragnostus*.

Geragnostus (*Geragnostella*) *wimani* Tjernvik, 1956

Figs. 3A–B.

1905b *Agnostus glabratus* A.; Wiman, pp. 12–13, pl. 1, figs. 27?–28.

1942 *Geragnostus* sp.; Regnéll, pp. 13–14, fig. 6a–b.

1956 *Geragnostus wimani* n.sp.; Tjernvik, pp. 192–193, text-fig. 27D, pl. 1, figs. 11–12.

1956 *Geragnostus* sp. aff. *crassus* n.sp.; Tjernvik, p. 191 [partim].

1956 *Geragnostus?* *explanatus* n.sp.; Tjernvik, p. 193 [partim], pl. 1, fig. 13 only.

1990 *Geragnostus wimani* Tjernvik; Ahlberg, p. 149, fig. 4.

1992 *Geragnostus wimani* Tjernvik; Ahlberg, pp. 549–552, figs. 9a–q.

1997 *Geragnostus* (*Geragnostella*) *wimani* Tjernvik; Nielsen, p. 483, fig. 22.

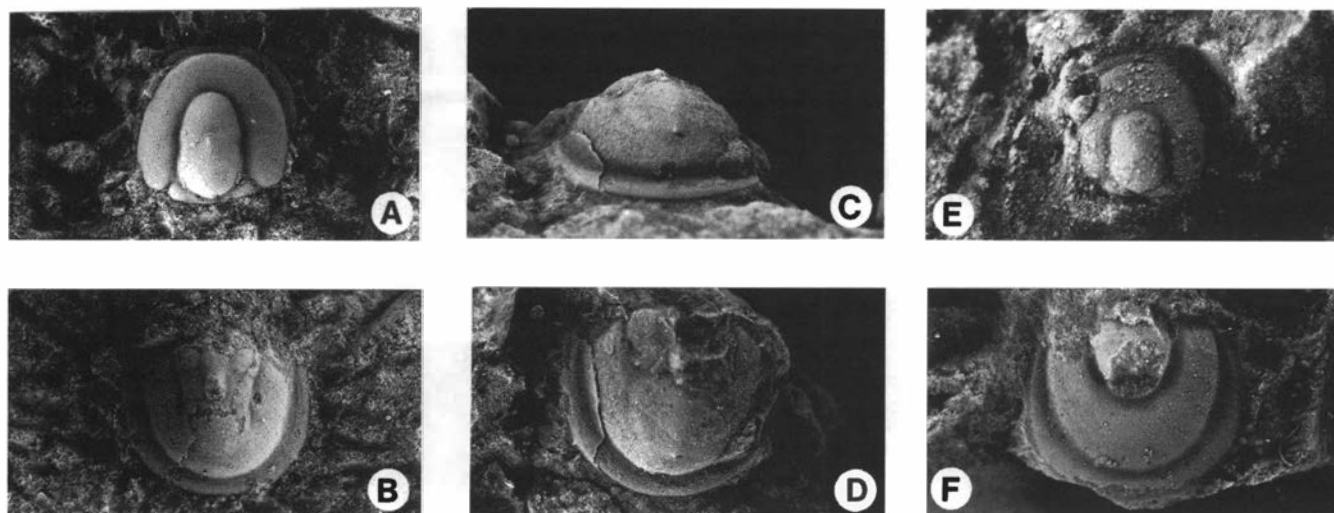


Fig. 3. (A–B) *Geragnostus wimani* Tjernvik, 1956: (A) Dorsal view of cephalon. $\times 15$, PMO 139.368/A. Bed 1B 'o', Skarahaugen, Vestfossen; (B) Dorsal view of pygidium. $\times 15$, PMO 139.326. Bed 6 'o', Skarahaugen, Vestfossen; (C–D) *Geragnostus explanatus* Tjernvik, 1956. Posterior and dorsal views of pygidium lacking the anterior part. $\times 15$, PMO 143.187. Bed 2, Vestfossen railway station; (E–F) *Arthrorhachis elliptifrons* (Tjernvik, 1956): (E) Dorsal view of cephalon. $\times 17$, PMO 143.351/A. Bed 1B 'u', Skarahaugen, Vestfossen; (F) Dorsal view of damaged pygidium. $\times 15.3$, PMO 143.193/A. Bed 3, Vestfossen railway station.

Holotype. – Pygidium (RM Ar 12291) from Stora Brottet, Lanna Närke, illustrated by Tjernvik (1956, pl. 1, fig. 12), refigured by Ahlberg (1992, fig. 9 h).

Material. – Two pygidia and four cephalae.

Remarks. – Ahlberg (1992, p. 551) provided a full description and noted considerable variation. In the present material, the anterior margin of the pygidium is straighter (tr.) and not backwardly curved as in the Swedish specimens. One specimen (Fig. 3B), shows weak pygidial spines.

Occurrence. – Bed 1B, 4A and 6o; Skarahaugen, Vestfossen and an unspecified level in the Hagastrand Member at Krekling.

***Geragnostus (Geragnostella) explanatus* Tjernvik, 1956**
Fig. 3D–E.

1956 *Geragnostus?* *explanatus* n. sp., Tjernvik, p. 193–194, pl. 1, fig. 14.

1992 *Geragnostus explanatus* Tjernvik; Ahlberg, p. 552, fig. 10g.

1997 *Geragnostus (Geragnostella) explanatus* Tjernvik; Nielsen, p. 483, fig. 22.

Holotype. – A pygidium (PMU no. N 290) from the upper part of the *Megistaspis (Paramegistaspis) planilimbata* zone at Stora Brottet, Lanna, Närke figured by Tjernvik (1956), and Ahlberg (1992).

Material. – One exfoliated pygidium.

Description of the Norwegian specimen. – Outline sagittally elongated, measured length/width ratio = 0.85 (in reality it is larger; the anterior part of the pygidium is

missing); anterior axial lobe (M1) probably not preserved, second lobe (M2) distinct, with an sagittally elongated tubercle-ridge which almost crosses the posterior furrow (F2); the posterior lobe (M3) nearly effaced and very faintly outlined, with a slight sagittal ridge reaching to the posterior end of the axis; posterior end of axis bears a small, but distinct tubercle (Fig. 1E); border is narrow (sag.), posteriorly occupying about 0.1 of total pygidial length, of similar width on all sides of the pygidium, no spines are seen.

Remarks. – Ahlberg (1992, p. 552) noted that Tjernvik's diagnosis applied for pygidia, but that the cranidium probably belonged to *G. wimani*. *G. lycaonicus* from the Seydisheir Formation, Southern Turkey (Dean 1971, pp. 6–7), is reminiscent of *G. explanatus* in the effacement of the posterior part of the axis and the indistinct dorsal furrows and Dean (1971, p. 7) noted that the Scandinavian species has a wider border. One specimen of *G. semipolitus* from the overlying Sobova Formation, Southern Turkey (Dean 1973, pl. 1, fig. 2) is even more similar to *G. explanatus*, having the same effacement of the posterior part of the axis, and also the proportionately very long pygidium. Other specimens figured by Dean (1973, pl. 1) are more semicircular in outline, and the long specimen may well belong to another species, probably related to *G. explanatus*.

Occurrence. – Bed 2, Hagastrand Member, Vestfossen railway station. According to Ahlberg (1992), this Norwegian record is the first outside Sweden.

Genus *Arthrorhachis* Hawle & Corda, 1847

Type species. – *Battus tardus* Barrande, 1846 from the Králův Dvůr Formation (Ashgill) of Libomyšl near Zdice, Czechoslovakia; by monotypy.

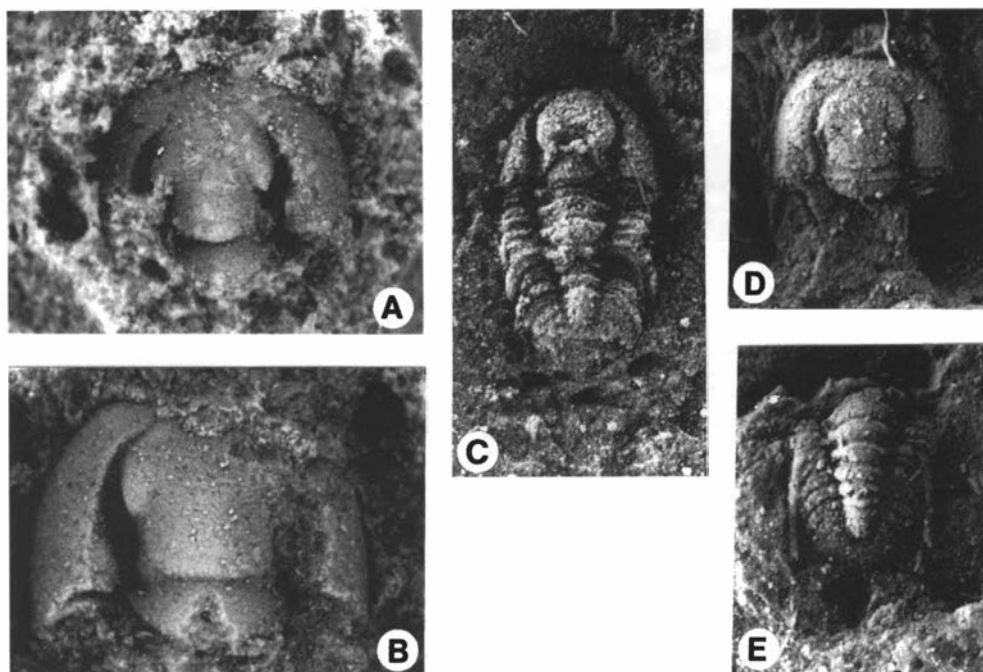


Fig. 4. *Shumardia (Conophrys) nericiensis* Wiman, 1905: (A) Dorsal view of cephalon showing anterior margin. $\times 40$, PMO 139.339, Bed 6 'o', Skarahaugen, Vestfossen; (B) Dorsal view of large cephalon showing posterolateral corner. $\times 40$, PMO 139.346, Bed 6 'o', Skarahaugen, Vestfossen; (C) Dorsal view of entire specimen. $\times 14.5$, RM Ar 11860. 'Shumardia Shale' (*M. (P.) planilimbata* Zone), Lanna, Närke, Sweden. Original of Wiman 1905, pl. 1, fig. 13; (D) Dorsal view of cephalon. $\times 16$, RM Ar 11862. Horizon as for C. Original of Wiman 1905, pl. 1, fig. 15; (E) Dorsal view of pygidium and five thoracic segments, showing macropleural 4th segment. $\times 15$, RM Ar 11861. Horizon as for C. Original of Wiman 1905, Pl. 1, fig. 14.

***Arthrorhachis elliptifrons* (Tjernvik, 1956)**
Figs. 3E–F.

1905b *Agnostus lentiformis* A.; Wiman, pp. 13–14, pl. 1, figs. 21–22.

1956 *Trinodus elliptifrons* n. sp.; Tjernvik, p. 196, ll. 1, figs. 16, 17.

1992 *Arthrorhachis elliptifrons* (Tjernvik); Ahlberg, pp. 561–564, fig. 16 j–t.

Holotype. – An internal mould of an enrolled specimen (RM Ar 12331a) figured by Tjernvik (1956, pl. 1, figs. 16–17) and Ahlberg (1992, figs. 16 j–k).

Material. – One cephalon and two pygidia.

Remarks. – This species is easily recognized by its short and smooth glabella and pygidial axis. The present cephalon (Fig. 3E) is slightly longer than those from Sweden. Ahlberg (1992, p. 563) notes intraspecific variation, especially in the shape of the pygidial axis; and cites Capera et al. (1978), who believe that *A. elliptifrons* may be a junior synonym of *A. chinianensis* (Howell, 1935) from the Montagne Noire, France, and that this species together with *A. corpulentus* (Howell, 1935) and *A. abruptus* (Howell, 1935) may be synonyms. In my view, there is little or no similarity between *A. elliptifrons* and Howell's species; the cranidium of *A. chinianensis* (Howell 1935, pl. 23, fig. 12) has a longer glabella and narrower (trans.) genae, while the pygidium (Howell 1935, pl. 23, fig. 13) has a square outline and an axis which does not taper as much as *A. elliptifrons*. The glabella of *A. abruptus* (Howell 1935, pl. 23, fig. 15) is squared off anteriorly. The pygidium of *A. corpulentus* (Howell 1935,

pl. 23, fig. 14) is too small to be directly compared, but the axis seems to be proportionately longer.

Occurrence. – Bed 1Bu, Skarahaugen; Bed 3, Vestfossen railway station, and an unidentified level within the Tøyen Formation at Tøyen underground station, Oslo.

Family Shumardiidae Lake, 1907

Genus *Shumardia* Billings, 1862

Type species. – By original designation; *Shumardia granulosa* Billings, 1862, pp. 92–93, fig. 83, from the *Shumardia* Limestone (Lower Llanvirn), Lévis, Quebec, Canada.

Subgenus *Shumardia (Conophrys)* Callaway, 1877

Type species. – By original designation; *Conophrys salopiensis* Callaway, 1877, p. 677, pl. 24, fig. 7, from the Shineton Shales (Tremadoc), South Shropshire, Great Britain.

Remarks. – Fortey & Owens (1987, pp. 119–120) discuss the great morphological range shown by *Shumardia* Billings, 1862, *Conophrys* Callaway, 1877, *Kweichiwia* Chang, 1964 and *Shumardia (Shumardella)* Pribyl & Vanek, 1980, and regard each as subgenera of *Shumardia*. *Shumardia (Conophrys)* is distinguished by the small anterolateral glabellar lobes, macropleural segment present and axis reaching the posterior border, but as in the other subgenera, species of *Shumardia (Conophrys)* show inconsistencies in their characters. *Shumardia (Conophrys) nericiensis* Wiman, 1905 thus has a short axis, or rather, it has a wide (sag.) postaxial field.

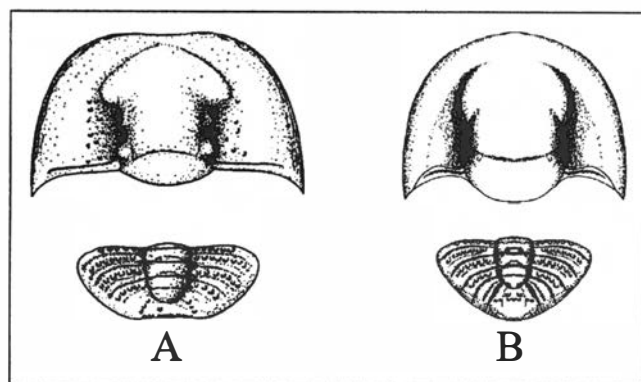


Fig. 5. Comparison between (A) *Shumardia (Conophrys) pusilla* (Sars, 1835) from the Bjørkåsholmen Formation and (B) *S. (C.) nericiensis* Wiman, 1905 from the Tøyen Formation (A drawn by J. O. Ebbestad).

Shumardia (Conophrys) nericiensis Wiman, 1905

Figs. 4–5.

1905b *Shumardia nericiensis* n. sp.; Wiman, pp. 14–15, pl. 1, figs. 13–15.

1956 *Shumardia* sp.; Tjernvik (listed), pp. 124, 126, 166, 176 (as *Shumardia* sp.); pp. 131, 135, 179 (as *Shumardia nericiensis*)

1980 *Shumardia nericiensis* Wiman; Tjernvik & Johansson (listed), p. 184.

Diagnosis. – Glabella narrow, widening forwards with very small anterolateral lobes; occipital furrow deep and wide; dorsal furrow deep posteriorly, fading out at the anterior end of the glabella. Pygidium semicircular to triangular, axis short, pleural furrows shallow, posterior margin evenly rounded.

Norwegian material. – Eighteen cephalae.

Description. – Cephalon up to about 1 mm in length, 2 mm in width; semicircular in outline. Glabella slightly pear-shaped, relatively narrow, widening forwards; rising well above fixed cheeks and being separated from them with deep dorsal furrow. Dorsal furrow is deep posteriorly, shallows forwards and vanishes at the front end of the glabella, thereby blending the glabella into the frontal area. Anterolateral glabellar lobes bent slightly backwards, being small to non-existent, widening the glabella only slightly. No glabellar furrows are visible behind the one pair demarcating the anterolateral lobes. Occipital ring of equal width as the glabella; the length (sag.) being about 1/4 of the length of the glabella. A mesial tubercle has not been observed on this material. Posterior margin of the fixigenae mostly at right angles to the axis, not sloping backwards as in many other *Shumardia*-species. Posterior border furrow present. Genal angles slightly pointed on internal moulds, with a thin, moderately long genal spine present when the outer test is preserved (not as wide as shown by Wiman 1905b, pl. 1, fig. 13). Thorax and pygidium known from Swedish specimens only: Thorax with 7 segments, the width of the axis rapidly increases forwards, the pleurae of the fifth

segment elongated into long, backward-pointing spines. Pygidium subrectangular in outline, length/width ratio 0.65; axis wide, occupying at frontal margin about 1/3 of total width, tapering rapidly backwards, its length about 2/3 of total pygidial length, bearing three or four transverse furrows; pleural fields rather smooth, or segmented.

Discussion. – *Shumardia (Conophrys) nericiensis* differs from *S. (C.) pusilla* (Sars, 1835) in having a wide pygidial border, without a border furrow, as present in many other species. On the cephalon, the anterolateral glabellar lobes are very small, backwardly curved, and usually only weakly separated from the glabella (Fig. 5). Judging from the meraspis specimens figured by Fortey & Owens (1991, fig. 13), this lack of a preglabellar furrow is a juvenile trait. The glabella of *S. (C.) nericiensis* is almost pear-shaped compared to the T-, or arrow-shaped glabella of *S. (C.) pusilla*, which also possesses a prominent preglabellar furrow. In its glabellar shape *S. (C.) nericiensis* resembles *S. (C.) bottnica* Wiman, 1905a from the Lower Tremadoc of Sweden. *S. (C.) bottnica* is rather similar to *S. (C.) erquensis* Kobayashi, 1937 from the Lower Tremadoc of Bolivia and Argentina (Harrington & Leanza 1957), and also to *S. (C.) pellizzarii* Kobayashi, 1934 from Korea and south Mandsjuria (Kobayashi 1934), although the latter has two pairs of short posterior glabellar furrows. The square pygidium of *S. (C.) nericiensis* resembles that of *S. (C.) oelandica* Moberg, 1900, from the Middle Tremadoc of Sweden.

Occurrence. – Specimens of *S. (C.) nericiensis* occur in the uppermost limestone bed of the Hagastrand Member at Skarahaugen and Øvre Øren, while at Krekling the species occurs only a few centimetres above the base of the lowermost limestone bed. In Oslo (Finnmarksgata), the specimens collected by T. Bockelie are from an unknown level in the Hagastrand Member. In Sweden a specimen (PMU D 446) was collected by Tjernvik (1956, p. 166) 30 cm above the base of the *Megistaspis (Ekeraspis) armata* zone at Sjurberg, Dalarna. Fortey & Rushton (1980) noted that *Shumardia* and the related *Acanthopleurella* were probably shallow, infaunal deposit feeders living in soft, muddy sediments. This fits with the Swedish specimens collected in the thin, green shale partings between limestones, while in Norway, *Shumardia* occur in argillaceous limestones.

Family Remopleurididae Hawle & Corda, 1847

Subfamily Remopleurididae Hawle & Corda, 1847

Genus *Robergiella* Whittington, 1959

Type species. – By original designation; *Robergiella sagittalis* Whittington, 1959 from the lower part of the Edinburgh Limestone, east of Lacey Spring post office, Rockingham County, Virginia, USA.

Remarks. – Material described here (Fig. 6) differs from the type species, but resembles that assigned to *Rober-*

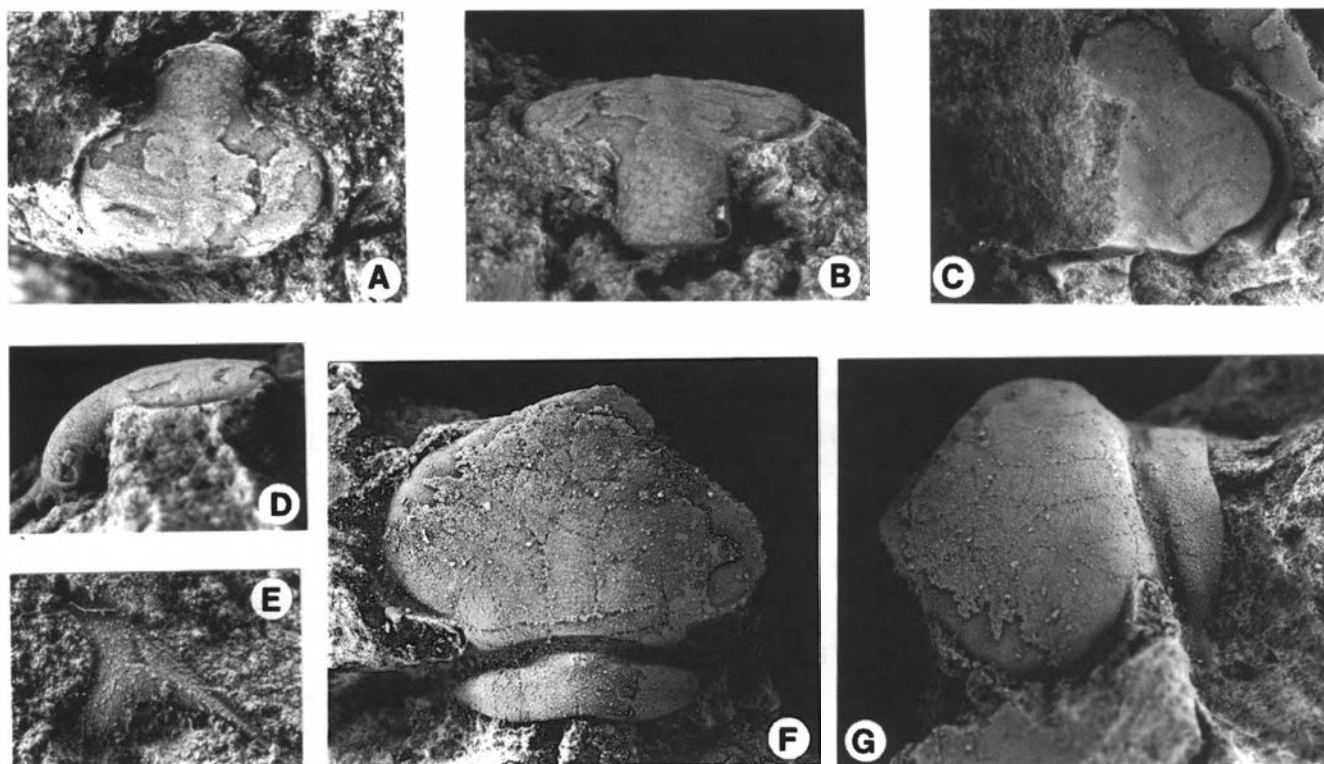


Fig. 6. *Robergiella tjernviki* n. sp.: (A–B, D) Dorsal, anterior and lateral views of incomplete cranium, showing first pair of glabellar furrows and glabellar tongue. $\times 5.5$, PMO 121.655, ~ 40 cm above the base of the Hagastrand Member, Øvre Øren, Vikersund; (C) Dorsal view of incomplete cranium, showing palpebral rim and furrow, all three pairs of glabellar furrows and glabellar tongue. $\times 6.5$, PMO 143.193/B, Bed 3, Vestfossen railway station; (E) Dorsal view of incomplete free cheek cautiously referred to this species. $\times 5$, PMO 143.577, Bed 1B 'o', Skarahaugen, Vestfossen; (F) Dorsal view of incomplete cranium, showing the occipital ring with tubercle. $\times 6.5$, PMO 143.180, Bed 4A, Skarahaugen, Vestfossen; (G) Dorsally lateral view of the specimen in F, showing the tiny posterior fixed cheek projecting ventrally.

giella by Fortey (1980, p. 44), and the specimen figured as *Robergiella?* sp. by Nikolaisen (1982, p. 287, pl. 13, figs. 18–19). Nikolaisen (1982, p. 266), remarked that species of *Sculptella* resemble earlier Scandinavian species previously assigned to *Remopleuridiella* and probably represent a new genus. Tjernvik (1956, pp. 203–204) described *Remopleuridiella* sp. no. 1 from the *Megistaspis* (*Paramegistaspis*) *planilimbata* Zone and *Remopleuridiella* sp. no. 2 from the *Megistaspis* (*Paramegistaspis*) *estonica* zone. The pygidium of the latter was figured by Nikolaisen (1982, p. 267, text-fig. 3d) and shows only three pairs of pleural spines while there are five in the type species (*Remopleuridiella caudalimbata* Ross, 1951). Skjeseth (1952, pp. 157–158) described *Remopleurides* aff. *nanus* from the lower Llanvirn of the Mjøsa area which may be closely related to *Remopleuridiella* sp. no. 2, and *R. groenwalli* Poulsen, 1965. Cranidia of *R. obtusa* Flower, 1968 and *R. angularis* Young, 1973, are very different from the Scandinavian specimens, and probably belong to *Opipeuter* Fortey, 1974.

Robergiella tjernviki n. sp.

Fig. 6, 7.

1956 *Remopleuridiella* sp. no. 1; Tjernvik, p. 203, pl. 2, figs. 5–6, text-fig. 31.

Holotype. – Incomplete cranium, PMO 143.180, from bed 4A, Skarahaugen, Vestfossen.

Other material. – Seven incomplete cranidia and one free cheek.

Diagnosis. – A species of *Robergiella* with narrower glabellar tongue and less impressed glabellar furrows than in the type species, and a free cheek with a small genal notch and rather transverse genal spines.

Description. – Glabellar tongue long (sag.), comprising about 1/3 of the glabellar length, and narrow (trans.), comprising about 1/4 of total cranidial width, sloping steeply down anteriorly; glabella transversely elliptical in outline, flat dorsally, having three pairs of long, transverse glabellar furrows, which are bowed backwards adaxially; only the posteriormost pair (S 1) is developed as an impressed furrow, wide (exsag.) and shallow, the two anterior pairs (S 2 and S 3) are visible only as dark muscle scars on specimens retaining the exoskeleton; median area narrow (trans.) with ornamentation of extremely fine lines only around a median tubercle located directly behind the occipital furrow; palpebral furrows broad and deep, of about equal depth throughout its length; Occipital furrow broad and deep, bowed slightly forward medially; width (trans.) of occipital ring 0.62 of glabella, length (sag.) less than 0.17 of total cranidial length; posterior margin of occipital ring bent forward medially; occipital tubercle strong and prominent; posterior fixigena narrow (trans.), not wider than the level of the palpebral lobes, wide

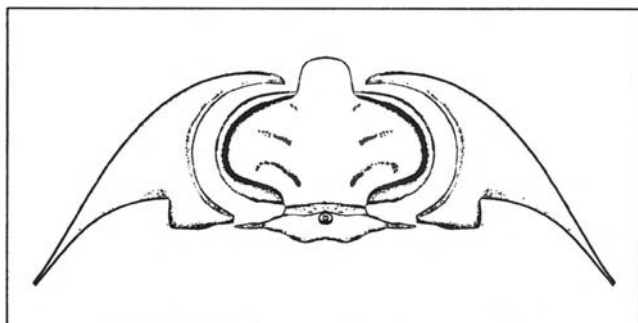


Fig. 7. Reconstruction of the cephalon of ?*Robergiella tjernviki* n. sp. based on the Norwegian material.

(exsag.) adaxially, narrowing rapidly abaxially, making the outline of the posterior fixigena almost triangular. A free cheek (see Fig. 6E), found in the lowermost bed of the *Megistaspis* (*Paramegistaspis*) *planilimbata* Zone (slightly lower than the cranidia), is very different from the one described by Tjernvik (1956, pl. 2, fig. 6). It has a much wider area between eye socle and border, and only a slight genal notch. The spine arises level with the middle of the eye as it does in the free cheek of *Remopleurella burmeisteri* (Bancroft, 1949) figured by Nikolaisen (1982, text-fig. 3h and pl. 14, fig. 17), and *Robergiella brevilingua* Fortey (1980, pl. 5, figs. 7,8). The spine seems to have had a slightly more transverse position than in most other remopleuridids.

Remarks. – I have not been able to identify the anterior glabellar tubercle mentioned by Tjernvik (1956, p. 203), but a tubercle is present just behind the occipital furrow. The cranidium is remarkably similar to that of *Robergiella* sp. (Nikolaisen 1982, pl. 13, figs. 18–19), and also to *Robergiella lundehukensis* Fortey (1980, pl. 5, figs. 9, 12–14, 16), except for the smooth exoskeleton. This may indicate close relationship between the Scandinavian early Arenigian forms and the younger ones from Spitsbergen. Another closely related species may be the specimen of *Remopleurides nanus* Leuchtenberg, 1843 (see Schmidt 1894, pl. 6, fig. 35b) from the lower Volkhov Stage of Pavlosk, Estland. This specimen has a narrower glabellar tongue and occipital ring than the other specimens figured under the same name by Schmidt (1894, pl. 6, figs. 34–35).

Family Nileidae Angelin, 1854

Genus *Nileus* Dalman, 1827

Type species. – *Asaphus* (*Nileus*) *armadillo* Dalman, 1827 (subsequently designated by Hawle & Corda 1847), from the lower Llanvirn of Östergötland, Sweden.

Discussion. – Fortey (1975, p. 40) provided a new diagnosis of the genus, listed 22 species and described a new species and two subspecies from Spitsbergen. Schrank (1972) described 11 species (among them five new) of Tremadoc to Caradoc age found in erratics from the Baltic and listed (p. 354) more than 30 species and subspecies

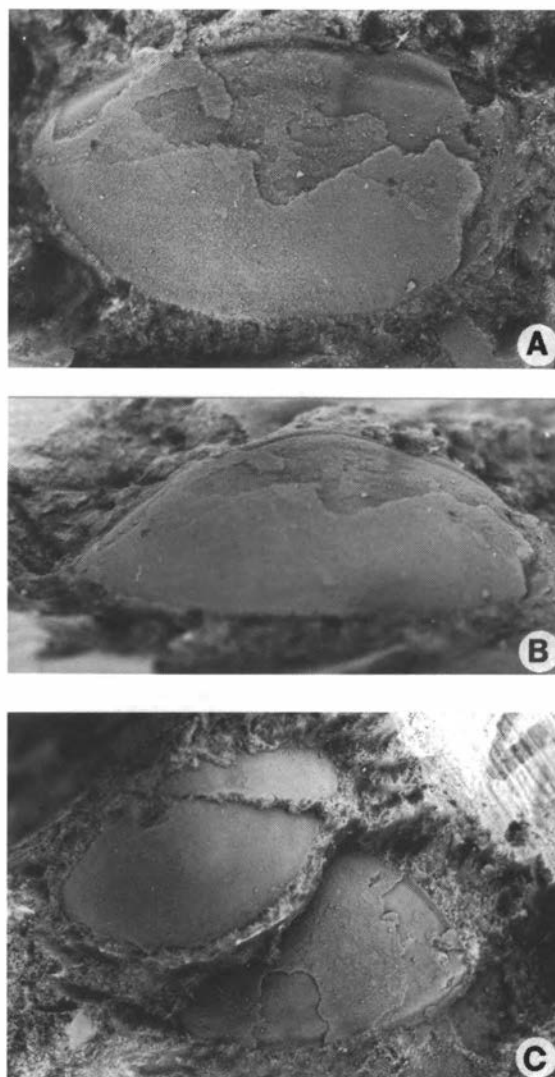


Fig. 8. *Nileus orbiculatus* Tjernvik, 1956: (A–B) Lateral and posterior views of pygidium showing the distinctive lack of a border. $\times 6.5$, PMO 139.353, Bed 1C 'u', Skarahaugen, Vestfossen; (C) Dorsal view of two pygidia retaining most of the test. $\times 4$, PMO 138.182/1–2, Bed 1C 'u', Skarahaugen, Vestfossen.

across the northern hemisphere. According to Nielsen (1995, p. 66), the morphological variation included can be linked to the environment, especially depth and substrate hardness, and that some of the species and subspecies are ecophenotypes rather than separate species. Nielsen (1995, p. 199) added 22 other non-Scandinavian species of *Nileus* (some doubtful) to Fortey's list, bringing the total number of species to 58 and provided a chart showing the stratigraphical distribution of the Scandinavian species of *Nileus* up to the *Asaphus* (*Asaphus*) «*raniceps*» Zone (Lower Llanvirn).

Nileus orbiculatus Tjernvik, 1956

Fig. 8.

1956 *Nileus orbiculatus* n.sp.; Tjernvik; p. 210, pl. 2, figs. 22–23, text-fig. 33 C.

1972 *Nileus orbiculatus* Tjernvik; Schrank; p. 357, pl. 1, figs. 5–8.

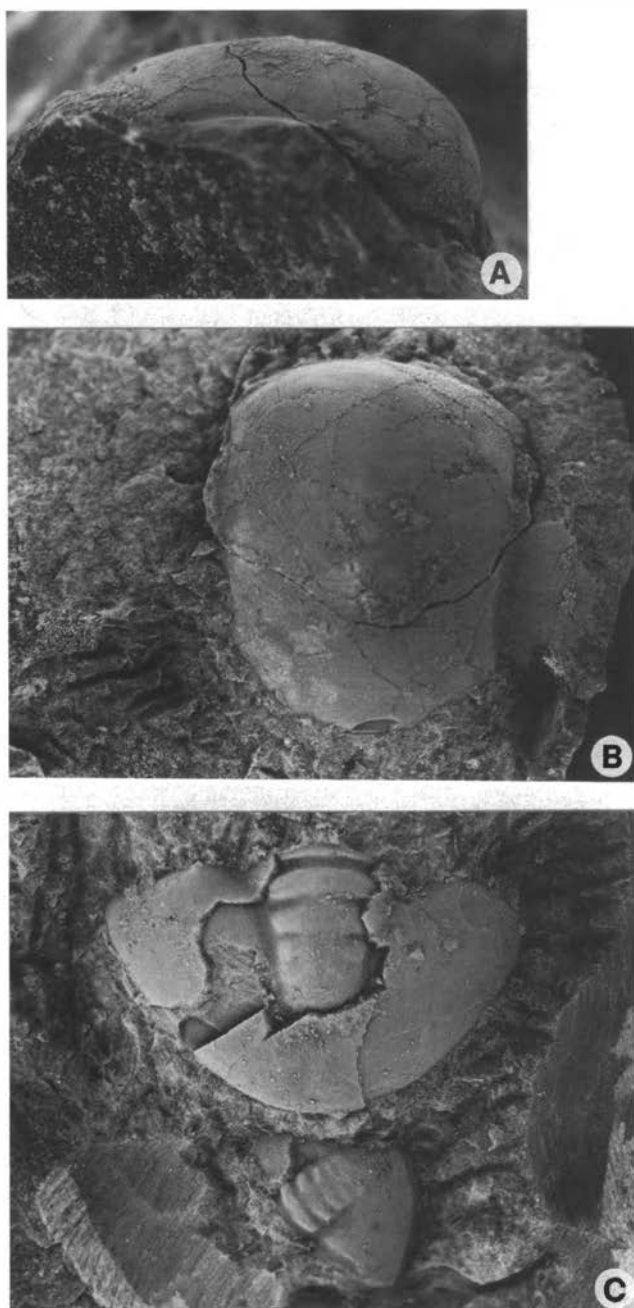


Fig. 9. *Symphysurus angustatus* (Boeck, 1838): (A–B) Lateral and dorsal views of incomplete cranidium. $\times 3.8$, PMO 90418, Hagestrand Member, Tøyen underground station, Oslo; (C) Dorsal view of two pygidia. $\times 3.7$, PMO 143.332, Bed 6, Stavlum, Krekling.

Holotype. By original designation: Internal mould of cranidium, PMU N 796, from the *Megistaspis* (*Paramegistaspis*) aff. *estonica* Zone at Gymninge, Närke, Sweden.

Material. – Five pygidia.

Remarks. – The Norwegian specimens are quite similar to those from Sweden figured by Tjernvik (1956). He (Tjernvik 1956, p. 211) records this species from the *M. (P.)* aff. *estonica* Zone (see Tjernvik & Johansson 1980) at Gymninge, Närke. In Norway the species occurs only in the lower part of the Hagestrand Member (*M. (P.)*

planilimbata Zone). This stratigraphical discrepancy is likely to be caused by the species' ecological requirements. The limestone of the *M. (P.)* aff. *estonica* Zone at Gymninge overlies a hiatus, as does the limestones of the Hagestrand Member at Vestfossen. This indicates that *Nileus orbiculatus* inhabited shallow water.

Genus *Symphysurus* Goldfuss, 1843

Type species. – Subsequently designated by Barrande (1852); *Asaphus palpebrosus* Dalman, 1827, from Husbyfjöl, Västergötland, Sweden.

Discussion. – The type species was redescribed by Fortey (1986). He listed the eight species so far described from the Tremadoc and Arenig of Scandinavia, Spitsbergen, Bohemia, Turkey and China.

He also noted that these species comprise a morphologically coherent group, the only specific characters being minor differences in proportions, sculpture and glabella shape. The genus was exceptionally widespread at a time when provinciality was at its most extreme, and Fortey (1986) connected this to its occurrence in deep water, argillaceous biofacies at the peripheral edges of the continents.

Symphysurus angustatus (Boeck, 1838)

Fig. 9.

1838 *Trilobites angustatus* n. sp., Sars & Boeck Mscr; p. 142.

1869 *Symphysurus socialis* n. sp., Linnarsson, p. 74, pl. 2, figs. 33–34.

1882 *Symphysurus angustatus* (Boeck); Brøgger, p. 60, pl. 3, figs. 9–11.

1902 *Symphysurus angustatus* (Boeck); Pompeckj, pp. 3–4, fig. 1.

1906 *Symphysurus angustatus* (Boeck); Moberg & Segerberg, pp. 90–91, pl. 5, figs. 15–16, 21.

1940 *Symphysurus angustatus* (Boeck); Størmer, p. 143.

1956 *Symphysurus* (*Symphysurus*) *angustatus* (Boeck); Tjernvik, pp. 211, 212, pl. 2, figs. 24–25.

?1973 *Symphysurus angustatus* (Boeck); Modlinski; pp. 51–52, pl. 3, figs. 5–6.

1973 *Symphysurus angustatus* (Boeck); Dean, p. 328.

Non 1975 *Symphysurus angustatus* (Boeck); Courtesole & Pillet, pp. 263–266, pl. 26, figs. 1–16, 19, pl. 27, figs. 2–3.

1986 *Symphysurus angustatus* (Boeck); Fortey, p. 261.

Non 1986 *Symphysurus angustatus* (Boeck); Berard, pl. 9, figs. 4, 6, 10.

In press *Symphysurus angustatus* (Boeck); Ebbestad, figs. 66–68.

Lectotype. – A cranidium (PMO 56215a) selected by Størmer (1940, p. 143) from the Bjørkåsholmen Formation (*Apatokephalus serratus* Zone), probably at Trefoldighetskirken, Oslo.

Material. – Four cranidia and four pygidia.

Remarks. – The species is thoroughly described by Ebbestad (in press.) and the few and badly preserved specimens from the Hagastrand Member do not diverge from the older specimens, except to note that the cranidium that is certainly from the *M. (P.) planilimbata* Zone (Figs. 9A–B) has a very steep anterior portion of the glabella, even bent down and backwards, similar to the condition in *Varvia* and steeper than illustrated by Ebbestad (in press). The other cranidia seem to be similar to those figured by Ebbestad (in press.), but may come from the Bjørkåsholmen Formation. The pygidia of the three nileid species present in the Hagastrand Member, *Nileus orbiculatus*, *Symphysurus angustatus* and *Varvia breviceps* are rather similar, but *S. angustatus* can be distinguished from *N. orbiculatus* by having a longer, more convex axis with more distinct dorsal and transverse furrows, deeper first pair of pleural furrows and convex border (see Tjernvik 1956, pl. 2, figs. 23 and 25). The species is most common in the upper part of the Bjørkåsholmen Formation, and is also mostly found in the upper part of the Hagastrand Member, although very infrequently. This indicates a similar environment, probably a change from solid to soft bottom conditions.

Subfamily uncertain

Genus *Varvia* Tjernvik, 1956

Type species. – *Symphysurus breviceps* Angelin, 1854 from the *Megistaspis (Paramegistaspis) planilimbata* Zone at Oltorp, Västergötland, Sweden.

Discussion. – *Varvia* was originally placed in the family Asaphidae (Tjernvik, 1956, p. 212) and in the Symphysurinae, a subfamily of Nileidae in Harrington et al. (1959, p. O354). According to Fortey & Chatterton (1988, p. 200) the Symphysurinae includes only *Symphysurina* Walcott, 1924, and other genera assigned here, including *Varvia*, were regarded as conventional asaphids, and thus placed in the Asaphidae. Presently, R. Fortey (pers. com. 1998) considers *Varvia* to be a primitive nileid retaining a median suture.

Varvia breviceps Tjernvik, 1956

Fig. 10.

1854 *Symphysurus breviceps* n. sp., Angelin, p. 61, pl. 33, fig. 13.

1905b *Symphysurus breviceps* Angelin; Wiman, p. 11, pl. 1, figs. 1–6.

1956 *Varvia breviceps* (Angelin); Tjernvik, pp. 213–214, pl. 3, figs. 1–6, text-fig. 34c.

Lectotype. – A cranidium (RM no. Ar. 14651) from Oltorp, Västergötland, Sweden, selected by Tjernvik (1956, p. 213).

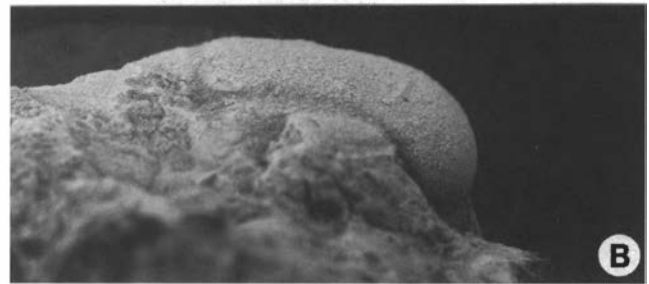
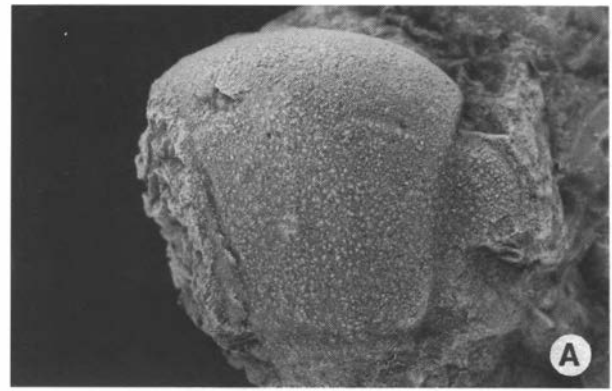


Fig. 10. *Varvia breviceps* (Angelin, 1854): (A–B) Dorsal and lateral views of small, exfoliated cranidium showing prominent muscle scars on the anterior part of the glabella. $\times 6$, PMO 155.446, Bed 6, Vestfossen railway station; (C) Dorsal view of small, exfoliated pygidium. $\times 7$, PMO 139.972, Bed 6, Vestfossen railway station.

Material. – Three cranidia and one pygidium.

Remarks. – A detailed description was given by Wiman (1905b) and Tjernvik (1956), and the Norwegian material fits this description. It can be noted that the glabellar tubercle seems to be placed slightly more posteriorly on the smallest Norwegian specimen than it is on the Swedish specimens. This is a rare species in Norway, but Tjernvik (1956, p. 214) says it is 'very common in the lower beds' of the *Megistaspis (Paramegistaspis) planilimbata* Zone in Sweden.

Occurrence. – Bed 6 at Vestfossen Railway Station.

Family Cyclopygidae Raymond, 1925

Subfamily Pricyclopyginae Fortey & Owens, 1987

Genus *Pricyclopyge* Richter & Richter, 1954



Fig. 11. *Priscyclopyge* sp.: Ventrolateral view of fragmentary free cheek showing part of the visual surface and doublure. $\times 8$, PMO 142.074, 8 m above base of the Tøyen Formation, Tøyen underground station, Oslo.

Type species. – *Aegolina prisca* Barrande, 1872, from the 'd₁' zone of Barrande (Ordovician) of Czech Republic.

Remarks. – The occurrence of *Priscyclopyge* in the Lower Ordovician of Scandinavia (see Tjernvik & Johansson 1980), is somewhat uncertain in that cranidia lack the characteristic two centrally located pits near the glabellar tubercle. They also fail to show the straight, converging sides of the glabella and the single pair of glabellar furrows typical of *Cyclopyge*. The pygidium of *Priscyclopyge?* *gallica* (Tjernvik, 1956) is very much shorter than that of *Cyclopyge*, and although it has transverse axial furrows, the outline is more rounded than the triangular pygidium seen in the type species of *Priscyclopyge*. Until better material is available I follow Tjernvik & Johansson (1980) in assigning the present material to *Priscyclopyge*.

***Priscyclopyge* (?) sp.**

Fig. 11.

Material. – One eye with lens pattern and a fragment of the anterior doublure. Collected 8.00–8.08 m above the base of the Tøyen Formation at Tøyen underground station, Oslo. Associated with *Niobe* (*Niobella*) *bohlini*.

Description. – Only the lower portion of the visual surface seems to be preserved, showing the honeycomb structure of the small, six-sided lenses. The lenses seem to be very slightly smaller at the lower margin of the eye, and their packing arrangement seems to be a logarithmical spiral, as described by Clarkson (1975, p. 20) for the Bohemian species *Priscyclopyge binodosa* (Salter). The lens files bend downwards and backwards. It does not seem to show two different generative areas as in *P. binodosa*, but this may be a result of the incomplete state of the Norwegian specimen. The preserved lenses seem to have had a visual field about 45° below the horizontal. The facial suture follows the front of the eye and has its anteriormost part at the anterior margin of the animal. A very thin remnant of the free cheek lies below the eye, and the doublure is upwardly bent but narrow, becoming increasingly narrower posteriorly. Anteriorly, the doublure widens, and

becomes rather similar to a rostral plate. The free cheeks are fused anteriorly. The Norwegian specimen is very similar to the free cheek on the drawing of the type species of *Priscyclopyge* in Harrington et al. (1959, p. O362).

Remarks. – The presence of a cyclopygid is in accordance with sedimentological data, which indicate a somewhat deeper-water (more muddy) environment at Tøyen than at Vekkerø and in Eiker-Sandsvær. Nielsen (1995, p. 71) noted that cyclopygids are typical of transgressive phases. In the 'transition Beds' at the base of the Billingen Stage (Tjernvik & Johansson 1980, p. 186), and in some levels of the Komstad Limestone, *Cyclopyge* (or *Priscyclopyge*?) is very abundant. Nielsen (1995, p. 71) suggested that *Cyclopyge* lived in the outer shelf environments later destroyed in continental collisions.

Family Raphiophoridae Angelin, 1854

Subfamily Endymioniinae Raymond, 1920

Remarks. – According to Fortey (1975, p. 64) the Endymioniinae contains four genera; *Endymionia* Billings, 1865, *Salteria* W. Thomson, 1864, *Anisonotella* Whittington, 1965 and *Pytine* Fortey, 1975. A later addition is *Carinocranium* Dean, 1989

Genus *Pytine* Fortey, 1975

Type species. – By original designation *Pytine graia* Fortey, 1975, from the Upper Arenig (*Isograptus gibberulus* Zone) Olenidsletta Member of the Valhallfonna Formation, north Ny Friesland, Spitsbergen.

Remarks. – According to Fortey (1975, p. 91), *Pytine* does not closely resemble other raphiophorid trilobites. He compared it with *Anisonotella* Whittington, 1952, having a similar glabella. The deeply impressed transverse branch of the dorsal furrow in *Anisonotella* seems to delimit a remnant of an ocular ridge. Small cranidia of *Endymionia* resemble *Pytine* and may indicate a close relationship, and *Carinocranium cariniferum* Dean, 1989 from Zone J of Midcontinent USA (equivalent to the *Phyllograptus densus* Zone of Scandinavia) is very similar to *Pytine*, except in the more prominent eye ridges.

***Pytine brevicauda* (?) Wiman, 1905**

Figs. 12–13.

1905b *Ampyx brevicauda* n. sp.; Wiman; p. 12, pl. 1, figs. 19–20.

?1905 *Orometopus* sp.; Wiman; p. 15, pl. 1, figs. 16–17(?), non pl. 1, fig. 18.

1980 *Pytine* n. sp.; Tjernvik & Johansson; p. 184 (listed).

1996b *Nambeetella fitzroyensis* Legg, 1976; Laurie & Shergold; p. 125, pl. 14, figs. 14–16, 25, 27–31.

?1998 Raphiophorinae gen. et sp. indet.; Zhou et al.; p. 279, pl. 2, fig. 14.

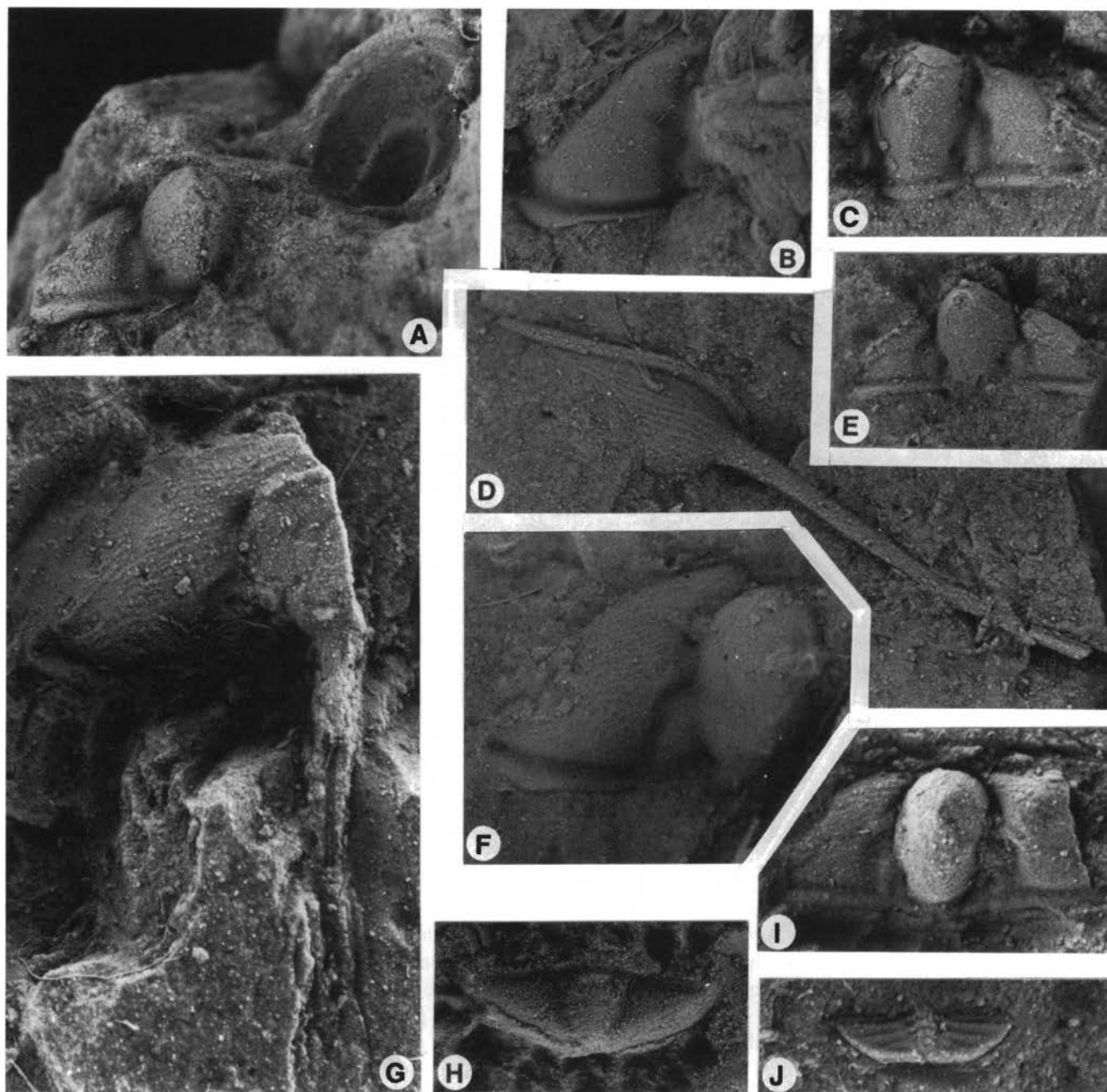


Fig. 12. *Pytine brevicauda* (Wiman, 1905): (A) Dorsal view of latex cast of incomplete cranidium. $\times 25$, PMO 143.351/B, specimen of *Arthrorhachis elliptifrons* (Fig. 3E) in background, Bed 1B 'u', Skarahaugen, Vestfossen; (B) Dorsal view, latex cast of the left half of a cranidium lacking the glabella showing the divergent branch of the dorsal furrow and mesh-like sculpture on the anterior part of the fixed cheek. $\times 9$, PMO 144.140, Bed 2, Vestfossen railway station; (C) Dorsal view of cranidium with unusually elongated glabella, $\times 15$, PMU N 304, 47–50 cm above the alum shale, Stora Brottet, Lanna, Närke, Sweden; (D) Free cheek with mesh-like sculpture, $\times 14$, PMU N 308, 47–50 cm above the alum shale, Stora Brottet, Lanna, Närke, Sweden; (E) Dorsal view of cranidium showing large bacculae. $\times 16$, PMU N 305, 47–50 cm above the alum shale, Stora Brottet, Lanna, Närke, Sweden; (F) Dorsal view, latex cast of large cranidium with mesh-like sculpture and glabellar tubercle, $\times 15$, PMU N 306, 47–50 cm above the alum shale, Stora Brottet, Lanna, Närke, Sweden; (G) Dorsal view of cranidium with large glabellar spine. $\times 16$, RM Ar 12349, 'Shumardia Shale' (*M. (P.) planilimbata* Zone), Lanna, Närke, Sweden. Original of Wiman 1905, pl. 1, fig. 17; (H) Dorsal view of exfoliated pygidium. $\times 11$, PMO 155.968/D, Stora Brottet, Lanna, Närke, Sweden; (I) Lectotype. Dorsal view of cranidium. $\times 16$, RM Ar 12359, Original of Wiman 1905, pl. 1, fig. 19; (J) Dorsal view of exfoliated pygidium with strong segmentation. $\times 16$, RM Ar 12360, horizon and locality as for G. Original of Wiman 1905, pl. 1, fig. 20.

Lectotype (here selected). – An internal mould of a cranidium (RM Ar 12359) from the 'Shumardia Shale' (*Megistaspis* (*Paramegistaspis*) *planilimbata* Zone) at Lanna, Närke (Sweden) figured by Wiman (1905b, pl. 1, fig. 19.), herein Fig. 12I.

Norwegian material. – One fragmentary internal mould of

a cranidium from Skarahaugen (bed 1Bu), associated with *Arthrorhachis elliptifrons* and one fragmentary internal mould of a cranidium from Vestfossen railway station (bed 2).

Swedish material. – Four cranidia and a free cheek, collected from the 'Shumardia Shale' at Lanna (Tjernvik

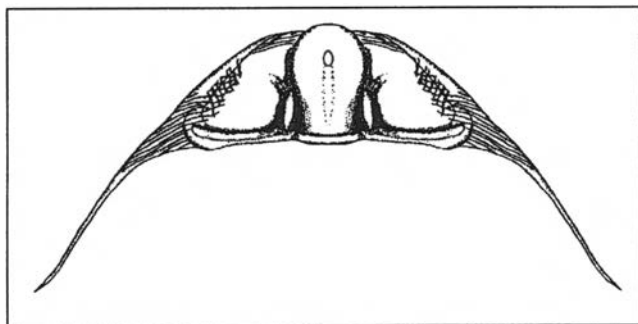


Fig. 13. Reconstruction of cephalon of *Pytine brevicauda* (Wiman, 1905).

1956, p. 269) and one exfoliated pygidium collected by M. Høyberget from the *Megistaspis* (*Paramegistaspis*) *planilimbata* zone at Lanna, Närke, associated with *Ampyx* cf. *pater* and *Hintzeia actinura*. In addition the specimens figured by Wiman (1905b, figs. 16, 20) have been studied.

Diagnosis. – Glabella higher and more bulbous than in the type species, glabella almost defaced apart from the first pair of glabellar furrows (1P); not very distinctly marked transverse branch of dorsal furrows; bacculae larger than in the type species; glabellar tubercle elongated to spine.

Description. – The cranidium has a triangular outline. The glabella is longer than wide and with semi-elliptical outline, widest at 1/3 glabellar length (sag.) measured from the anterior end; rather high (about 1/4 the cranidial width), the highest point coinciding with the widest part of the glabella; the anterior part of the glabella does not protrude forward of the anterior margin. Swedish specimens show that the anterior end of the glabella must be rather steep. In anterior view, the top of the glabella is slightly pointed. Most specimens have the glabellar tubercle on the highest point of the glabella, but this is the base of a prominent, glabellar spine (Fig. 12G), directed upwards and backward at about 30–45°. First pair of glabellar furrows (1P) indicated as a pair of minute lateral pits, connected to the dorsal furrows. Dorsal furrows very broad and deep posteriorly, widening and deepening even more just lateral to the widest point of the glabella. At this point a lateral branch of the furrow is curving outwards, making a wide and deep pit; the anterior part of the dorsal furrow is narrow and shallow in front of the glabella. Bacculae very wide and long, being much larger than in the type species. Posterior border furrows almost straight, wide and deep; bending forwards at the posterolateral corners, which are downflexed. Posterior border very narrow (exsag.), widening at posterolateral corners. The fixed cheeks have a surface sculpture of minute, intercrossing, mesh-like ridges.

Free cheek (Fig. 12D) narrow (trans.), with deep border furrow and a rope-like border; surface sculpture of prominent ridges sub-parallel to the border. Lateral spine long, pointing out- and backwards, and is ventrally bent in the outer 1/3.

Pygidium very short, about three times as wide as long; the axis occupies about 0.22 of total pygidial width at anterior end and tapers gently backwards, the dorsal furrows enclosing an angle of about 25°; pygidium has three or four transverse axial furrows, all of which seem to reach the dorsal furrows. The axis reaches onto the posterior border; pleural fields are very short (exsag.) and exhibits almost no trace of segmentation, except a deep and wide furrow delimiting the anterior half ring; posterior border is rather wide, being prominent on the dorsal surface; posterior margin high, not seen to be arched up at mid-line; no surface sculpture seen. The smaller pygidium figured by Wiman (1905b, pl 1, fig. 20) has more prominent pleural furrows than the larger one, which is the normal condition in Raphiophorids and allied groups.

Remarks. – This species resembles *Pytine graia* Fortey, 1975 in the overall shape of the cranidium but has the highest point of the glabella more anteriorly, and the fixed cheeks are lower. Tjernvik & Johansson (1980, p. 184) listed *Pytine* n. sp. from the *Megistaspis* (*Paramegistaspis*) *planilimbata* Zone, which is probably *P. brevicauda*. Only one specimen (Fig. 12G) shows the long glabellar spine preserved, this is usually seen only as a node on internal moulds.

A specimen (Fig. 12E) collected by Tjernvik at Lanna, Närke, Sweden, has large bacculae. It is thus similar to *Raymondella elegans* (Cooper, 1953) (see Whittington 1959, p. 488, pl. 36). Specimens figured as *Ampyxinella* (*Eoampyxinella*) *villebruni* by Berard (1986, pl. 12, figs. 12–16, 18, pl. 13, figs. 2–5) are remarkably like *P. brevicauda*, especially in that some small individuals have a backwardly pointed glabella with spine (Berard 1986, pl. 12, fig. 16; pl. 13, fig. 3), while the larger specimens have a more rounded glabella and large bacculae (Berard 1986, pl. 12, fig. 10, 18). Such large bacculae are also found in *Carinocranium cariniferum* Dean (1989, p. 17). A specimen figured as *Ampyx* (?) sp. by Dean (1971, pl. 1, fig. 4) resembles *Pytine brevicauda*, but it seems to lack bacculae. The specimens assigned to *Nambeetella* by Laurie & Shergold (1996b, pl. 14, figs. 14–16, 25, 27–31) from a slightly younger horizon in the Canning Basin, Australia are remarkably similar to *P. brevicauda* and are reassigned to that species herein. Specimens figured as *Ampyx* sp. undet. 2 by Laurie & Shergold (1996b; pl. 14, figs. 5–6, figs. 7–13) lack bacculae and these probably belong to *Nambeetella fitzroyensis* of Legg 1976, pl. 6, figs. 14, 18. The pygidium figured by Laurie & Shergold (1996b, pl. 14, fig. 26) resembles *Orometopus* sp. (see Wiman 1905, pl. 1, fig. 18). The pygidium figured by Zhou et al. (1998) as Raphiophorine gen. et sp. indet. is also quite similar and of exactly the same age as *P. brevicauda*. While *P. brevicauda* has only a slight mesh-like surface sculpture, the sculpture of *Carinocranium cariniferum* has developed into rather coarse, criss-crossing ridges, but the prominent eye-ridges of *C. cariniferum* preclude a direct relationship between these two species.

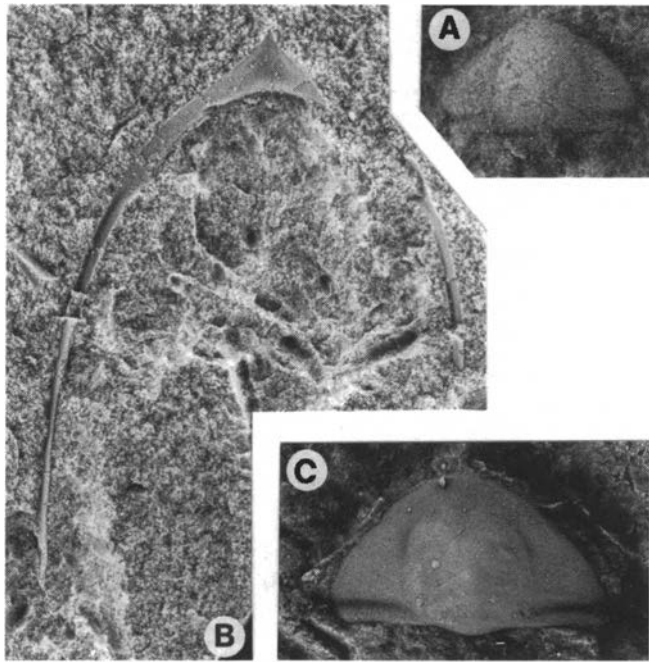


Fig. 14. *Falanaspis aliena* Tjernvik, 1956: (A) Dorsal view of small cranidium. $\times 7.5$, PMO 143.576, Bed 1–2, Vestfossen railway station; (B) Dorsal view of free cheeks showing the thin frontal spine originating on the doublure. $\times 5.8$, PMO 155.438, unknown level in the Hagastrand Member, Krekling; (C) Dorsal view of cranidium showing faint muscle scars on the glabella. $\times 8.2$, PMO 136.087, Bed 3A 'o', Skarahaugen, Vestfossen.

Occurrence. – Norway: Bed 1 Bu, Skarahaugen; Bed 2, Vestfossen railway station. Sweden: Stora Brottet, Lanna, Närke (47–50 cm above the Alum Shale in the profile of Tjernvik 1956, p. 136 and 35–42 cm above the Alum Shale in the profile of Wiman 1905b, p. 4). Australia: Emmanuel Formation (*Priceaspis oepiki*–*P. rochei* Trilobite Zone; Be 2), Canning Basin. Possibly northwest China: Upper Qiulitag group (*Paroistodus proteus* conodont zone), western Tarim, Xinjiang. If it proves correct, this wide distribution is very suggestive of a planctonic life style for this species.

Family Alsataspididae Turner, 1940

Remarks. – Fortey (1975, p. 92) believes *Falanaspis* Tjernvik, 1956 and *Seleneceme* Clark, 1924 to be closely related to both the raphiophorids (lack of eye and marginal facial sutures) and the hapalopleurids. In *Hapalopleura longicornis* Harrington & Leanza, 1957, the frontal spine probably arises from the cephalic doublure, as in *Falanaspis* (Tjernvik 1956, p. 273) and *Seleneceme* (Whittard 1958, p. 119). Fortey & Shergold (1984, p. 352) considered the presence of a frontal spine originating from the cephalic doublure as a shared, derived character unusual enough to indicate monophyletic origin. They subsequently included the following genera in the Alsataspididae: *Seleneceme*, *Falanaspis*, *Nambeetella* Legg, 1976 and '*Hapalopleura*' *longicornis* Harrington & Leanza, 1957. The Australian form described by Laurie & Shergold (1996b) as *Endymionia* sp. und. also seems to belong here,

as it resembles *Falanaspis extensa* Fortey, 1975. The large number of thoracic segments seen in *Seleneceme* (at least 28 in *S. acuticaudata*; see Whittard 1958, p. 119) seems to be an adaptation to life in oxygen-poor environments, and thus of little or no taxonomic significance.

Genus *Falanaspis* Tjernvik, 1956

Type species. – (By original designation) *Falanaspis aliena* Tjernvik, 1956, pp. 272–274, from the uppermost Tremadoc *Megistaspis* (*Ekeraspis*) *armata* Zone, Stenbrottet, Västergötland, Sweden.

Remarks. – Fortey (1975, p. 93) was not certain that *Falanaspis* and *Seleneceme* can be distinguished from each other. The type species of *Seleneceme* (*S. propinqua* Clark, 1924, p. 108, pl. 9, fig. 10), has a more elongated cranidium than does *Falanaspis aliena*, while in *S. acuticaudata* (Hicks, 1875) it is more heart-shaped, where the suture bends backwards behind the frontal spine, creating a median notch in the anterior margin. Tjernvik (1956, p. 273) states that *Falanaspis* differs from *Seleneceme* in lacking a median glabellar furrow and the frontal spine arising from the cephalic doublure. However, the median glabellar furrow of *Seleneceme* is an artefact caused by flattening, and the frontal spine does arise from the cephalic doublure. It is likely that *Falanaspis* is a junior synonym to *Seleneceme*, but better material is needed.

Falanaspis aliena Tjernvik, 1956

Figs. 14–15.

1956 *Falanaspis aliena* n. sp.; Tjernvik, pp. 272–274, pl. 11, figs. 19–21, text-fig. 44.

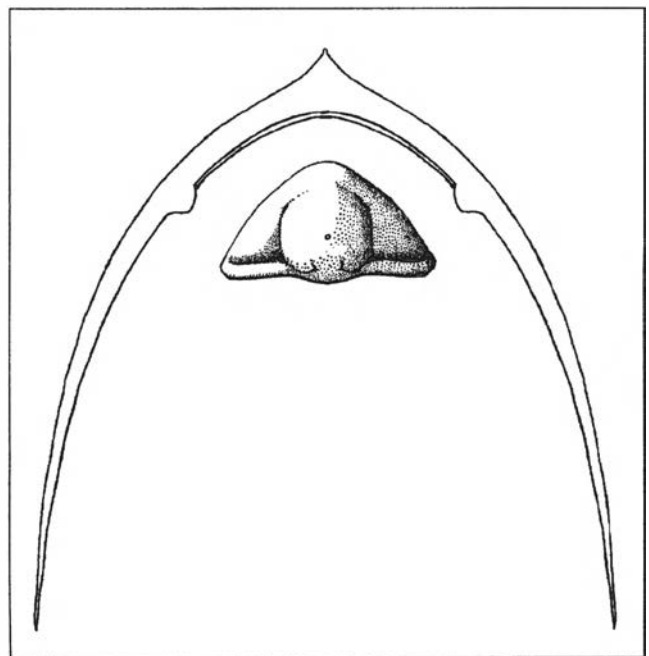


Fig. 15. Revised reconstruction of fused free cheeks and cranidium of *Falanaspis aliena* Tjernvik, 1956. Cranidium after Tjernvik (1956, p. 273).

1959 *Falanaspis aliena* Tjernvik; Harrington et al., p. O428.

1959 *Falanaspis aliena* Tjernvik; Henningsmoen, p. 171, pl. 1, fig. 8.

1984 *Falanaspis aliena* Tjernvik; Fortey & Shergold, p. 352.

In press: *Falanaspis aliena* Tjernvik; Ebbestad, fig. 75.

Holotype. – A cranidium (PMU Vg 389) figured by Tjernvik (1956, pl. 11, fig. 20) from the *Megistaspis* (*Ekeraspis*) *armata* Zone (Uppermost Tremadoc) of Västergötland, Sweden.

Norwegian material. – Three cranidia and one cephalic doublure with frontal and genal spines.

Description. – Glabella circular to quadratic in outline, with a glabellar tubercle situated halfway between anterior and posterior end of glabella; no glabellar furrows visible, but pairs of faint muscle scars occur in front of the glabellar tubercle (circular) and one behind it (transversely elongated); the glabella of Norwegian specimens from the Tøyen Fm. seems to be more square than on the Swedish specimens. In the small cranidium (Fig. 14A), the glabella is proportionately longer (sag.). A very faint occipital furrow is discernible, shallow at the median line, slightly deeper on both sides and disappearing before connecting with the posterior border furrow; dorsal furrows extremely shallow, deepening slightly at anterolateral corners of glabella, preglabellar furrow visible only as a change in the angle of the slope of the preglabellar area; preglabellar area short (sag.), continuous with fixed cheeks, occupying about 20% of total cranidial length; fixed cheeks triangular, evenly sloping and featureless; posterior border furrow deep and wide (exsag.), angling somewhat backwards adaxially. The free cheeks (Fig. 14B), do not seem to be 'connected by triangular dorsal and ventral plates' as stated by Tjernvik (1956, p. 274), but rather are continuous across the median line; they constitute a very thin border around the anterior part of the cranidium of almost even width, widening slightly at posterolateral corners where a panderian organ may be present, widening somewhat more at the median line, making the base of the frontal spine a small triangular area; frontal spine extremely thin and of unknown length, possibly swung somewhat upwards; outline of the lateral spines follow the parabolic course of the suture; the spines are proportionately very long, their length from the posterolateral corners of cranidium at least about three times the length of the cranidium.

Dimensions. – Largest cranidium 3 mm long and 5 mm wide, smallest 1.5 mm long and 3 mm wide. The free cheeks are 11.4 mm wide and 14.2 mm long from the tip of the anterior spine (the spines are broken both anteriorly and posteriorly), having enclosed a cranidium about 2.4 mm long, genal spines about 0.2 mm thick.

Occurrence. – Norway: Upper part of the Bjørkåsholmen Fm. (*Apatokephalus serratus* Zone) at Modum, Ringerike

and Oslo; Beds 2B–5B of the lowermost Tøyen Fm. (*Megistaspis planilimbata* Zone) at Modum, Vestfossen and Krekling. Sweden: *Megistaspis armata* Zone (latest Tremadoc) of Västergötland, Öland and Jämtland.

Family Pliomeridae Raymond, 1913

Remarks. – Whittington (1961) did not follow the classification of Harrington et al. (1959), but excluded the *Pilekia* group and the Diaphanometopinids, and included *Ectenonotus* Raymond, 1920 (see Whittington 1961) and *Colobinion* Whittington, 1961 in the family. He also suggested that the Pliomeridae should not be divided at the subfamilial level, and this view is followed here.

Genus *Hintzeia* Harrington, 1957

Type species. – *Protopliomerops celsaroe* Ross, 1951; originally designated by Harrington (1957, p. 811 as *Protopliomerops aemula* Hintze, 1952 (= *P. celsaroe* (Ross, 1951)); see Laurie & Shergold 1996a, p. 90) from the Arenig of Utah, USA.

Remarks. – The genus was erected by Harrington (1957) to encompass three species from Utah, namely *H. aemula* (Hintze, 1952), *H. firmimarginis* (Hintze, 1952) and *H. celsaroe* (Ross, 1951), but it is not easy to find any difference between *Hintzeia* and *Pliomerops* Raymond, 1905, a point made by Regnéll (1940) who compared the two species. The Argentinian Tremadocian species *Protopliomerops rossi* (Harrington & Leanza 1957, p. 217, fig. 119: 3a–f) is also very similar to *Hintzeia* and is assigned to this genus. Laurie & Shergold (1996a, p. 90) described material of *Hintzeia* from the Canning Basin, Australia, and considered *Hintzeia* to be a senior synonym of *Kanoshia* Harrington, 1957. This is very unlikely, as the type species of *Kanoshia*, *K. kanoshensis* (Hintze, 1952) has a medial glabellar furrow, the anterior pair of glabellar furrows (3p) placed behind or at the anterolateral angles of glabella, a hypostome with a bifurcate posterior margin and granulose surface ornamentation, while the type species of *Hintzeia*, *H. celsaroe* has no medial furrow, the anterior pair of glabellar furrows (3p) are placed well in front of the anterolateral angles of glabella and the hypostome has a pointed posterior margin. This means that the stratigraphic range for *Hintzeia* is not as extended as stated by Laurie and Shergold (1996a). *Hintzeia* thus has only a lower Ordovician distribution in the interior United States, Argentina, Scandinavia and Australia.

Hintzeia actinura (Dalman, 1824).

Fig. 16.

1824 *Entomostracites actinurus* Dalman; Dalman, p. 368; pl. 4, figs. 1A–C.

1827 *Calymene actinura* (Dalman); Dalman, p. 38.

?1854 *Pliomera mathesii* Angelin n. sp.; Angelin, p. 35; pl. 22, figs. 1, 1a–c.

1854 *Pliomera actinura* (Dalman); Angelin, p. 35; pl. 22, fig. 2.

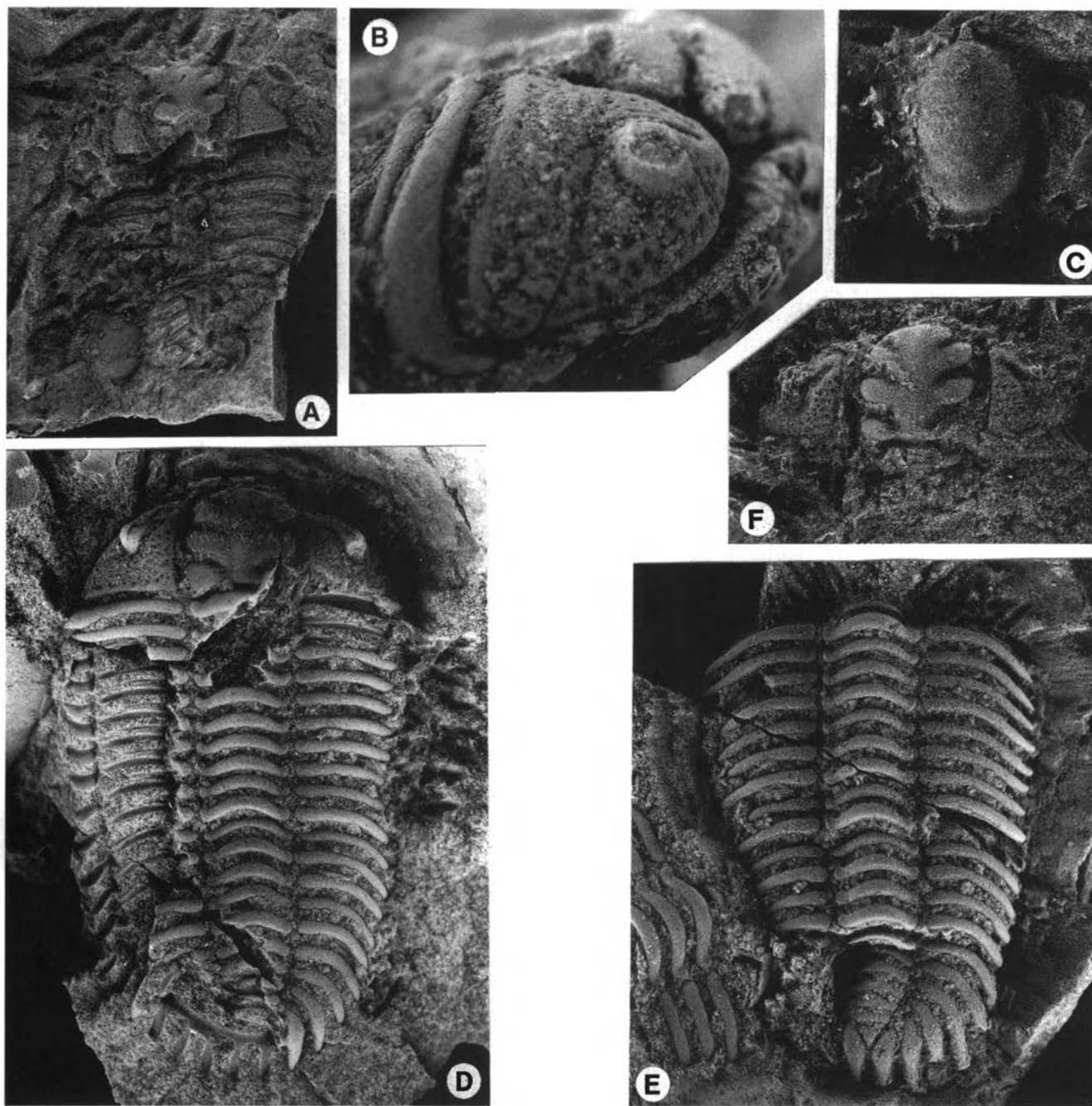


Fig. 16. *Hintzeia actinura* (Dalman, 1824): (A) Dorsal view of incomplete exoskeleton with rotated pygidium. $\times 3.6$, PMO 143.178, Bed 5, Vestfossen railway station; (B) Lateral view of incomplete cephalon showing the facial suture and eye. PMO 157.572, from a loose boulder at Stora Brottet, Lanna, Närke, Sweden; (C) Dorsal view of incomplete hypostome. $\times 7$, PMO 143.179, Bed 5, Vestfossen railway station; (D) Dorsal view of complete exoskeleton. $\times 3$, PMO 155.968/A, from a loose boulder at Stora Brottet, Lanna, Närke, Sweden; (E) Dorsal view of thorax and incomplete pygidium. $\times 3.6$, PMO 157.571, from a loose boulder at Stora Brottet, Lanna, Närke, Sweden; (F) Dorsal view of incomplete cranidium. $\times 3.8$, PMO 143.195, Bed 5, Bed 5, Vestfossen railway station.

1908 *Pliomera actinura* (Dalman); Wiman, pp. 87–89; pl. 7, figs. 9–12.

1940 *Pliomera actinura* (Dalman); Regnéll, pp. 7–10; pl. 1, fig. 7.

1956 *Pliomerops actinurus* (Dalman); Tjernvik, p. 266.

1996a *Hintzeia* sp. undet.; Laurie & Shergold; p. 90, pl. 6, figs. 1–11.

Material. – One damaged exoskeleton, one incomplete cranidium and one hypostoma. In addition, several complete specimens from Lanna, Närke, Sweden.

Description. – Dorsal exoskeleton elliptical in outline, about half as wide as long (at greatest width); cephalon subsemicircular in outline; length about $2/5$ the width; occupying about 0.22 of total length of animal; moderately convex, the ventral anterior margin bent upwards, the resulting notch being as wide as the glabella. Anterior border narrow (sag.) and raised, of about the same width (sag.) as the cranial posterior border; anterior border furrow narrow and rather shallow in front of glabella, widening slightly and conspicuously deepening in front of fixed cheeks; anterior margin almost straight; glabella

rising above level of fixed cheeks; rectangular posteriorly, slightly rounded in front, its outline even-sided to very slightly tapering forwards, longer than wide ($L/W = 7/6$), well defined by narrow (trans.), rather shallow dorsal furrows; 3 pairs of lateral glabellar furrows directed obliquely adaxially backwards; most conspicuous on internal moulds; innermost part of posterior (1p) furrows reaching almost back to occipital furrow; anterior (3p) furrows located in front of anterolateral angles of glabella; occipital furrow wide (sag.) and shallow; both occipital furrow and occipital ring bent forward mesially; occipital ring of equal width (sag.); eyes rather small, located immediately behind the anteriormost (outermost) part of the median (2p) glabellar furrow, halfway on a hypothetical straight line between the anterior margin of the cephalon and the genal angles; a slightly curved palpebral ridge runs along this line from the eye to the anterolateral angle of the glabella, although without crossing the dorsal furrow; fixed cheeks almost L-shaped, posterior border of equal width (sag.), well defined by deep and wide border furrow; posterior margin sloping obliquely backward near to the glabella, bending slightly obliquely forwards when approaching the genal angles; genal angles rounded. Free cheeks small, its outline approximately similar to 25% sector of a circle. Surface of glabella and cephalic borders finely granulose, surface of fixed cheeks and free cheeks coarsely pitted. Hypostoma of typical pliomerid form; anterior border is seemingly rather wide; anterior wings seem to be wide (trans.); anterior lobe is three times as long (sag.) as the posterior lobe, median furrow between these two areas is very faint along the median line, but is continuous across the width of the median body; maculae bulbous, faintly delimited by the median furrow from the anterior lobe, clearly delimited from the lateral border by a wide, shallow border furrow; the shape of the outer border is not preserved in the Norwegian specimens (Figs. 16A, C. Thorax constituting about half of total length of animal; with 14 segments; axis narrow, occupying about 1/4 of the total width of thorax, tapering slightly backwards; rings narrow (sag.), curved forward, with a knob just inside of the axial furrows; pleurae with proximal part straight and normal to axis, outer part curving backward-downward, outermost part curving forward; internal casts showing mid-pleural furrow, normal to the axis, dividing the pleura into a wider frontal part and a narrower posterior part; extremities may be produced into spines, particularly in the hind part of the thorax, in the frontal part the extremities seem to be flatter, more paddle-shaped. Pygidium semicircular in outline, its width twice the length; axis narrow (trans.), occupying at anterior margin 0.35 of total width, rapidly tapering backward, with five rings and short, triangular terminal segment; pleural fields with five pleurae ending in pointed spines, pointing almost directly downward-backward; last pair of pleurae totally embracing the terminal segment, being almost fused at the midline just behind the terminal segment, but separated posteriorly as the spines curve downwards.

Discussion. – This species has not been redescribed since Wiman (1908, p. 87), who regarded *Pliomera mathesii* Angelin, 1854 as being a junior synonym of *Hintzeia actinura* (Dalman, 1824). Tjernvik (1956, p. 266) assigned material from the *Megistaspis* (*Paramegistaspis*) *planilimbata* Zone and another very similar form from the *M. (Ekeraspis) armata* Zone to the genus *Pliomerops* because of the absence of the median furrow and denticulation of the anterior border of the cephalon. Wiman (1908, p. 88) stated that some of the specimens exhibited a median furrow, but this must have been an artefact as none of the material that I have studied shows this. The species is common in Närke and on Öland, where well-preserved, articulated specimens are known (Figs. 16D–E; see also Regnéll 1940). The specimens figured as *Hintzeia* sp. by Laurie & Shergold (1996a) are rather badly preserved, but have a similar glabella and facial suture. The difference is that the Australian specimens have a wider occipital ring and six segments in the pygidium (five in two specimens; pl. 6, figs. 10, 11), while the Scandinavian ones have only five. They are probably conspecific. Bruton et al. (1989, fig. 4; 2) assigned a similar cranidium from a limestone unit in the Solheim Slate (Ørnberget Fm., Lower Allochthon) at Groslii Sæter, Valdres, to *Parapilekia* sp., but Ebbestad (in press) believes this specimen belongs to *Pliomeroides primigenus* (Angelin, 1854).

Occurrence. – Bed 5, Vestfossen railway station. Unknown levels in the *M. (P.) planilimbata* Zone in Närke and on Öland, Sweden. Bendigonian (Be1 = *Didymograptus balticus* Zone) in the Canning Basin, western Australia.

Acknowledgements. – During the preparation of this monograph invaluable help, both scientifically and morally, has been provided by my adviser Professor D. L. Bruton and much was learned from unpublished profiles made by the late Professor G. Henningsmoen. Technical problems of all kinds were solved by Dr H. A. Nakrem, Dr J. H. Hurum and Cand.Scient. A. K. Norborg. Photographic help was provided by P. Aas. Type material was generously made available to me by the Curators at Uppsala, S. Stuanes, and at Riksmuseet, Stockholm, C. Franzén. Conodonts were kindly identified by A. Løfgren, Lund. I also thank J. O. Ebbestad, Uppsala and my friends B. Funke and M. Høyberget for many stimulating discussions and field trips.

Manuscript received May 1999

References

- Ahlberg, P. 1990: Agnostid trilobites from the Ordovician of the Siljan district, Sweden. *Geologiska Föreningens i Stockholm Förhandlingar* 112, 145–156.
- Ahlberg, P. 1992: Agnostid trilobites from the Lower Ordovician of southern Sweden. *Transactions of the Royal Society of Edinburgh: Earth Sciences* 83, 539–570.
- Angelin, N. P. 1851: *Palæontologia Suecia. Part I. Reprinted in Palæontologia Scandinavica.*, 96 pp.
- Angelin, N. P. 1854: *Palæontologia Scandinavica. Crustacea Formationis Transitionis.* 96 pp. P. A. Nordstedt & Söner, Stockholm, pls. I–XLII. Reissued and edited in 1878.
- Angelin, N. P. 1878: *Palæontologia Scandinavica. Crustacea Formationis Transitionis. Holmiæ 1878.* 96 pp. Edited by G. Lindström. Apud Samson & Wallin. P. A. Nordstedt & Söner, Stockholm, pls. I–XLII.
- Barrande, J. 1846: *Notice préliminaire sur le Système silurien et les Trilobites de Bohême.* 97 pp., Leipzig.
- Barrande, J. 1852: *Système Silurien du center de la Bohême: 1^{re} Partie.* Vol. I. Trilobites, Crustacés divers et Poissons. 935 pp. [publisher?], Prague, Paris.
- Barrande, J. 1872: *Système Silurien du center de la Bohême: 1^{re} Partie.* Supplément au Vol. I. Trilobites, Crustacés divers et Poissons. 647 pp. Prague, Paris.
- Berard, P. 1986: Trilobites de l'Ordovicien Inferieur des Monts de Cabrieres (Montagne Noire-France). *Université des Sciences et Techniques du Langue-*

- doc (Montpellier II): *Mémoires du Centre d'Etudes et de Recherches Géologiques et Hydrologiques* no. 24, 220.
- Billings, E. 1861–65: *Palaeozoic fossils, vol. 1*. Geological Survey of Canada (Montreal), 426 pp.
- Boeck, C. 1838: Übersicht der bisher in Norwegen gefunden Formen der Trilobiten familie. In Keilhau, B. M. (ed.): *Gaea Norvegica I*, 138–145. [publisher?], Christiania.
- Bruton, D. L., Harper, D. A. T. & Repetski, J. E. 1989: Stratigraphy and faunas of the Parautochthon and Lower Allochthon of Southern Norway. In Gayer, R. A. (ed.): *The Caledonide Geology of Scandinavia*, 231–241. Graham & Trotman, London.
- Brøgger, W. C. 1882 *Die Silurischen Etagen 2 und 3 im Kristianiagebiet und auf Eker*. 1–376. Kgl. Fredriks univ. Christiania (Oslo). Universitetsprogram 2. Semester 1882.
- Callaway, C. 1877: On a new area of Upper Cambrian rocks in South Shropshire, with a description of a new fauna. *Quarterly Journal of the Geological Society of London* 33, 652–672.
- Capera, J. C., Courtessole, R. & Pillet, J. 1978: Contribution à l'étude de l'Ordovicien inférieur de la Montagne Noire, biostratigraphie et révision des Agnostida. *Annales des Sociétés géologiques du Nord* 98, 67–88.
- Chang, Went'ang, 1964: See Chang, Went'ang et al. 1964.
- Chang, Went'ang, et al. 1964: In *Atlas of Palaeozoic fossils from North Guizhou. Nanjing* (In Chinese), pls. 5–10 (no text).
- Clark, T. H. 1924: The paleontology of the Beekmantown Series at Levis, Quebec. *Bulletins of American Paleontology*. 10, No. 41, 119.
- Clarkson, E. N. K. 1975: The evolution of the eye in trilobites. *Fossils and Strata* 4, 7–31.
- Cooper, B. N. 1953: Trilobites from the Lower Champlainian formations of the Appalachian Valley. *Geological Society of Amerika. Memoir* 55, 1–69.
- Cooper, R. A. 1979: Sequence and correlation of Tremadoc graptolite assemblages. *Alcheringa* 3, 7–19.
- Cooper, R. A. & Lindholm, K. 1990: A precise worldwide correlation of early Ordovician graptolite sequences. *Geological Magazine* 127, 497–525.
- Courtessole, R. & Pillet, J. 1975: Contribution à l'étude des faunes trilobitiques de l'Ordovicien inférieur de la Montagne Noire. Les Eulominae et les Nileidae. *Annales de la Société Géologique du Nord* 95, 251–272.
- Dalman, J. W. 1824: Några petrificater, fundne i Östergötlands Öfvergångskalk, aftecknade och beskrifne. *Kungliga Svenska Vetenskaps-Akademiens Handlingar* 1824, 368–377. pl. 4.
- Dalman, J. W. 1827: Om Palæaderna eller de så kallade Trilobiterna. *Kungliga Svenska Vetenskaps-Akademiens Handlingar* 1827 (separat Stockholm 1828), 78 pp.
- Dean, W. T. 1971: The lower Palaeozoic Stratigraphy and Faunas of the Taurus Mountains near Beysehir, Turkey. II. The Trilobites of the Seydisehir Formation (Ordovician). *Bulletin of the British Museum (Natural History), Geology series* 20, 1–24.
- Dean, W. T. 1973: The lower Palaeozoic Stratigraphy and Faunas of the Taurus Mountains near Beysehir, Turkey. III. The Trilobites of the Sobova Formation (Lower Ordovician). *Bulletin of the British Museum (Natural History), Geology series* 24, 281–348.
- Dean, W. T. 1989: Trilobites from the Survey Peak, Outram and Skoki Formations (Upper Cambrian–Lower Ordovician) at Wilcox Pass, Jasper National Park, Alberta. *Geological Survey of Canada, Bulletin* 389, 141 pp.
- Ebbestad, J. O. R. 1993: Trilobites of the Bjørkåsholmen Formation (Tremadoc) in the Oslo Region, Norway. Unpublished thesis, 2 vols. University of Oslo, 131 pp., 22 pls., appendix 110 pp.
- Ebbestad, J. O. R. 1997: Bjørkåsholmen Formation (upper Tremadoc) in Norway: regional correlation and trilobite distribution. In Stouge, S. (ed.): WOGOGOB-94 Symposium, Working Group on Ordovician Geology of Baltoscandia. *Danmarks og Grønlands Geologiske Undersøkelse Rapport* 1996/98, 27–34.
- Ebbestad, J. O. R. [In press]: Trilobites of the Tremadoc Bjørkåsholmen Formation in the Oslo Region, Norway. *Fossils & Strata* 47.
- Erdtmann, B.-D. 1965: Outline stratigraphy of graptolite-bearing 3b (Lower Ordovician) strata in the Oslo Region, Norway. *Norsk Geologisk Tidsskrift* 45, 481–547.
- Erdtmann, B.-D. 1988: The Baltic Hunneberg Series: Missing link between Tremadoc and Arenig? In Williams, S. H. & Barnes, C. R. (eds.): *Fifth International Symposium on the Ordovician System; Program and Abstracts*, St. John's, Canada, 29 pp.
- Erdtmann, B.-D. & Paalits, I. 1995: The Early Ordovician 'Ceratopyge Regressive Event' (CRE): its correlation and biotic dynamics across the East European Platform. *Lithuanian Geol. Soc. 'Geologija'* 117, 36–57.
- Fjellidal, Ø. 1966: The Ceratopyge Limestone (3a) and limestone facies in the Lower Didymograptus Shale (3b) in the Oslo Region and adjacent districts. Unpublished thesis, University of Oslo, 129 pp.
- Flower, R. H. 1968: Fossils from the Smith Basin Limestone of the Fort Ann Region, New York. *Memoirs of the Institute of Mineralogy and Technology, New Mexico* 22, 23–27.
- Fortey, R. A. 1974: A new pelagic trilobite from Ordovician of Spitsbergen, Ireland, and Utah. *Palaeontology* 17, 111–124.
- Fortey, R. A. 1975: The Ordovician trilobites of Spitsbergen. II. Asaphidae, Nileidae, Raphiophoridae and Telephinae of the Valhallfonna Formation. *Norsk Polarinstitutt, Skrifter*, No. 162, 207 pp.
- Fortey, R. A. 1980: The Ordovician trilobites of Spitsbergen. III. Remaining trilobites of the Valhallfonna Formation. *Norsk Polarinstitutt, Skrifter*, No. 171, 163 pp.
- Fortey, R. A. 1986: The type species of the Ordovician trilobite *Symphysurus*: Systematics, functional morphology and terrace ridges. *Paläontologische Zeitschrift* 60, 255–275.
- Fortey, R. A. & Chatterton, B. D. E. 1988: Classification of the suborder Asaphina. *Palaeontology* 31, 165–222.
- Fortey, R. A., Harper, D. A. T., Ingham, J. K., Owen, A. W. & Rushton, A. W. A. 1995: A revision of Ordovician series and stages from the historical type area. *Geological Magazine* 132, 15–30.
- Fortey, R. A. & Owens, R. M. 1978: Early Ordovician (Arenig) stratigraphy and faunas of the Carmarthen district, south-west Wales. *Bulletin of the British Museum (Natural History), Geology Series* 30, 225–294.
- Fortey, R. A. & Owens, R. M. 1987: The Arenig Series in South Wales: Stratigraphy and Palaeontology. I. The Arenig Series in South Wales. *Bulletin of the British Museum (Natural History), Geology Series* 41, 69–307.
- Fortey, R. A. & Owens, R. M. 1991: A trilobite fauna from the highest Shineton Shales in Shropshire, and the correlation of the latest Tremadoc. *Geological Magazine* 128, 437–464.
- Fortey, R. A. & Owens, R. M. 1992: The Habberley Formation: Youngest Tremadoc in the Welsh Borderlands. *Geological Magazine* 129, 553–566.
- Fortey, R. A. & Rushton, A. W. A. 1980: *Acanthopleurella* Groom 1902: origin and life-habits of a miniature trilobite. *Bulletin of the British Museum (Natural History), Geology Series* 33, 79–89.
- Fortey, R. A. & Shergold, J. H. 1984: Early Ordovician trilobites, Nora Formation, Central Australia. *Palaeontology* 27, 315–366.
- Gjessing, J. 1976: Tremadocian stratigraphy and fauna in the Oslo Region, Norway. Unpublished thesis, University of Oslo, 136 pp., 14 plates.
- Harrington, H. J. 1957: Notes on new genera of Plimeridae (Trilobita). *Journal of Palaeontology* 31, 811–812.
- Harrington, H. J. & Leanza, A. F. 1957: *Ordovician trilobites of Argentina. Department of Geology, University of Kansas Special Publication* No. 1. University of Kansas Press, Lawrence, Kansas, 276 pp.
- Harrington, H. J., et al. 1959: *Treatise on Invertebrate Paleontology. Part O: Arthropoda* 1. 560 pp. University of Kansas Press.
- Hawle, I. & Corda, A. J. C. 1847: *Prodrom einer Monographie der Böhmischen Trilobiten*. 176 pp. J. G. Calve'sche Buchhandlung, Prague.
- Henningsmoen, G. 1957: The trilobite Family Olenidae. *Norsk Vitenskaps-Akademi Skrifter, Matematisk-naturvitenskapelig klasse I*, 304 pp.
- Henningsmoen, G. 1959: Rare Tremadocian trilobites from Norway. *Norsk Geologisk Tidsskrift* 39, 153–173.
- Henningsmoen, G. 1973: The Cambro-Ordovician boundary. *Lethaia* 6, 423–439.
- Hicks, H. 1875: On the succession of the ancient rocks in the vicinity of St. David's, South Wales, and their fossil contents. *Quarterly Journal of the Geological Society of London* 31, 167–195.
- Hintze, L. F. 1952: Lower Ordovician trilobites from western Utah and eastern Nevada. *Utah Geological and Mineralogical Survey. Bulletin* 48, 249 pp.
- Hoel, O. A. 1999: Trilobites of the Hagastrand Member (Tøyen Formation, lowermost Arenig) from the Oslo Region, Norway. Part I: Asaphidae. *Norsk Geologisk Tidsskrift* 79, 259–280.
- Howell, B. F. 1935: Cambrian and Ordovician trilobites from Hérault, southern France. *Journal of Paleontology* 9, 222–238.
- Jaekel, O. 1909: Über die Agnostiden. *Zeitschrift der Deutsche Geologischen Gesellschaft* 61, 380–401.
- Klemm, T. 1982: The Ordovician succession at Vestfossen and Krekling. In Bruton, D. L. & Williams, S. H. (eds): *Fourth International Symposium on the Ordovician System, Field Excursion Guide*, 139–143. Paleontological Contributions from the University of Oslo, No. 279.
- Kobayashi, T. 1934: The Cambro-Ordovician formations and faunas of South Chosen. Palaeontology. Part II. Lower Ordovician faunas. *Journal of the Faculty of Science, Imperial University of Tokyo. Section II, Geology, Mineralogy, Geography, Seismology* 3, 521–585.
- Kobayashi, T. 1937: The Cambro-Ordovician shelly faunas of South America. *Journal of the Faculty of Science, Imperial University of Tokyo. Section II, Geology, Mineralogy, Geography, Seismology* 4, 369–522.
- Kobayashi, T. 1939: On the Agnostids (Part I). *Journal of the Faculty of Science, Imperial University of Tokyo. Section II, Geology, Mineralogy, Geography, Seismology* 5, 69–198.

- Lake, P. 1906–46: *A Monograph of the British Cambrian Trilobites*. Parts I–XIV. 350 pp., pl. I–XLVII., London.
- Lapworth, C. 1879: On the tripartite classification of the Lower Palaeozoic rocks. *Geological Magazine, New Series* 2, 1–15.
- Laurie, J. R. & Shergold, J. H. 1996a: Early Ordovician trilobite taxonomy and biostratigraphy of the Emanuel Formation, Canning Basin, Western Australia. Part 1. *Palaeontographica A* 240, 65–103.
- Laurie, J. R. & Shergold, J. H. 1996b: Early Ordovician trilobite taxonomy and biostratigraphy of the Emanuel Formation, Canning Basin, Western Australia. Part 2. *Palaeontographica A* 240, 105–144.
- Legg, D. P. 1976: Ordovician trilobites and graptolites from the Canning Basin, Western Australia. *Geologica et Palaeontologica* 10, 1–58.
- Leuchtenberg von, H. 1843: *Thierreste von die Urwelt am Zarskoje selo*.
- Lindholm, K. 1991a: Hunnebergian graptolites and biostratigraphy in southern Scandinavia. *Lund Publications in Geology No. 95*, 36 pp.
- Lindholm, K. 1991b: Ordovician graptolites from the Early Hunneberg of southern Scandinavia. *Palaeontology* 34, 283–327.
- Linnarsson, J. G. O. 1869: Om Vestergötlands Cambriska och Siluriska aflägringar. *Kongliga Svenska Vetenskaps-Akademiens Handlingar* 8, No. 2, 89 pp., 2 pls.
- Maletz, J., Rushton, A. W. A. & Lindholm, K. 1991: A new early Ordovician Didymograptid, and its bearing on the correlation of the Skiddaw Group of England with the Tøyen Shale of Scandinavia. *Geological Magazine* 128, 335–343.
- Maletz, J., Löfgren, A. & Bergström, S. 1995: The Diabasbrottet section at Mt. Hunneberg, Province of Västergötland, Sweden: a proposed candidate for a Global Stratotype Section and Point (GSSP) for the base of the Second Series of the Ordovician System. In Cooper, J. D., Droser, M. L. & Finney, S. C. (eds): *Ordovician Odyssey: Short papers for the Seventh International Symposium on the Ordovician System. The Pacific Section Society for Sedimentary Geology (SEPM); Book 77*, 139–143.
- Moberg, J. C. 1900: Nya bidrag till utredning af frågan om gränsen mellan Undersilur och Kambrium. *Geologiska Föreningens i Stockholm Förhandlingar* 22, 523–540, pl. 14.
- Moberg, J. C. & Segerberg, C. O. 1906: Bidrag till kännedomen om Ceratopygerregionen med särskild hänsyn till dess utveckling i Fogelsångstrakten. *Meddelande från Lunds Geologiska Fältkлубb. Serie B, No. 2*, 116 pp., 8 pls.
- Modlinski, Z. 1973: Stratigraphy and development of the Ordovician in north-eastern Poland. *Instytut Geologiczny Prace LXXII (Warszawa)*, 74 pp.
- Molyneux, S. G. & Rushton, A. W. A. 1988: The age of the Watch Hill Grits (Ordovician), English Lake District: Structural and palaeogeographical implications. *Transactions of the Royal Society of Edinburgh: Earth Sciences*, 79, 43–69.
- Monsen, A. 1936: Die graptolithenfauna im Unteren Didymograptusschiefer (Phyllograptusschiefer) Norwegens. *Norsk Geologisk Tidsskrift* 16, 57–266.
- Nielsen, A. T. 1995: Trilobite systematics, biostratigraphy and palaeoecology of the Lower Ordovician Komstad Limestone and Huk Formations, southern Scandinavia. *Fossils and Strata* 38, 374 pp.
- Nielsen, A. T. 1997: A review of Ordovician agnostid genera (Trilobita). *Transactions of the Royal Society of Edinburgh: Earth Sciences* 87, 463–501.
- Nikolaisen, F. 1982: The Middle Ordovician of the Oslo region, Norway-32. Trilobites of the family Remopleuridae. *Norsk Geologisk Tidsskrift* 62, 231–329.
- Novák, O. 1883: Zur kenntnis der böhmischen Trilobiten. In *Beiträge zur Paläontologie Österreich-Ungarns und des Orients; herausgegeben von E. Mojsvics und M. Neymayr* 3:1/2, 22–63, pls. (1)–5(12), Vienna.
- Owen, A. W., Bruton, D. L., Bockelie, J. F. & Bockelie, T. G. 1990: The Ordovician successions of the Oslo Region, Norway. *Norges Geologiske Undersøkelse, Special Publication No. 4*, 54 pp.
- Pompeckj, J. F. 1902: Aus dem Tremadoc der Montagne Noire (Süd-Frankreich). *Neues Jahrbuch für Mineralogie, Geologie und Palaeontologie* 1, 1–8.
- Poulsen, V. 1965: An Early Ordovician Trilobite Fauna from Bornholm. *Meddelelser fra Dansk Geologisk Forening* 16, 49–115.
- Pribyl, A. & Vanek, J. 1980: Ordovician trilobites of Bolivia. *Rozprawy Československé Akademie věd* 90(2), 3–90.
- Rasmussen, J. A. & Bruton, D. L. 1994: Stratigraphy of Ordovician limestones, Lower Allochthon, Scandinavian Caledonides. *Norsk Geologisk Tidsskrift* 74, 199–212.
- Raymond, P. E. 1905: Trilobites of the Chazy Limestone. *Annales of the Carnegie Museum* 3, 328–386.
- Raymond, P. E. 1913: Some changes in the names of genera of trilobites. *Ottawa Naturalist* 26, 137–142.
- Raymond, P. E. 1920: Some new Ordovician trilobites. *Bulletin of the Museum of Comparative Zoology, Harvard University* 64, 273–296.
- Raymond, P. E. 1925: Some trilobites of the lower Middle Ordovician of eastern North America. *Bulletin of the Museum of Comparative Zoology, Harvard University* 67, 3–180.
- Regnéll, G. 1940: Om faunan i Planilimbatakalkstenen vid Köping på Öland. *Kungliga Fysiografiska Sällskapets i Lund Förhandlingar* 10, No. 1, 15 pp.
- Regnéll, G. 1942: Stratigraphical and paleontological remarks on the Lower Ordovician of central and northern Öland with special reference to Köpings Klint. *Meddelelser från Lunds Geologiska och Mineralogiska Institutionen* 99, 1–17.
- Richter, R. & Richter, E. 1954: Die trilobiten der Ebbe-Sattels und zu vergleichende Arten (Ordovizium, Gotlandium/Devon). *Senckenberg Naturforschungsgesellschaft, Abhandlungen* 488, 1–76.
- Ross, R. J. 1951: Stratigraphy of the Garden City Formation in Northeastern Utah, and its Trilobite faunas. *Peabody Museum of Natural History, Bulletin* 6, 1–161.
- Salter, J. W. 1864–83: A monograph of the British trilobites. *Palaeontographical Society (London) Monographs*, 244 pp.
- Sars, M. 1835: Über einige neue oder unvollständig bekannte Trilobiten. *Isis (Oder Encyclopedische Zeitung)*, Oken 1835, 333–343.
- Schmidt, F. 1894: Revision der Ostbaltische Trilobiten. Abtheilung IV: Calymmeniden, Proetiden, Bronteiden, Harpeiden, Trinucleiden, Remopleuriden und Agnostiden. *Mémoires de l'Académie Impériale des Sciences de St.-Petersbourg, VII^e Série: XLII, No. 5*, 93 pp., 6 pls.
- Schrank, E. 1972: Nileus-Arten (Trilobita) aus Geschieben des Tremadoc bis tieferen Caradoc. *Berichten der Deutsche Gesellschaft für geologische Wissenschaft A. Geologie und Paläontologie* 17, 351–375.
- Skevington, D. 1966: The lower boundary of the Ordovician System. *Norsk Geologisk Tidsskrift* 46, 111–119.
- Skjeseth, S. 1952: On the Lower Didymograptus Zone (3B) at Ringsaker, and contemporaneous deposits in Scandinavia. *Norsk Geologisk Tidsskrift* 30, 138–182.
- Strand, T. 1929: The Cambrian beds of the Mjøsen district in Norway. *Norsk Geologisk Tidsskrift* 10, 308–365.
- Størmer, L. 1940: Early descriptions of Norwegian trilobites. *Norsk Geologisk Tidsskrift* 20, 113–151.
- Tjernvik, T. E. 1956: On the Early Ordovician of Sweden, stratigraphy and fauna. *Bulletin of the Geological Institutions of the University of Uppsala* 36, 107–284.
- Tjernvik, T. E. & Johansson, J. V. 1980: Description of the upper portion of the drillcore from Finngrundet in the South Bothnian Bay. *Bulletin of the Geological Institutions of the University of Uppsala, New series* 8, 173–204.
- Turner, F. E. 1940: *Alsataspis bakeri*, a new lower Ordovician trilobite. *Journal of Paleontology* 14, 516–518.
- Walcott, C. D. 1924: Cambrian geology and paleontology V, No. 2, Cambrian and lower Ozarkian trilobites. *Smithsonian Miscellaneous Collections* 75, 51–60.
- Webby, B. D. 1998: Steps toward a global standard for Ordovician stratigraphy. *Newsletters in Stratigraphy* 36, 1–33.
- Whittard, W. F. 1955–66: The Ordovician Trilobite fauna of the Shelve Inlier, West Shropshire. *Palaeontographical Society (Monograph)*, 196 pp., 25 pls.
- Whittington, H. B. 1952: The trilobite family Dionidiidae. *Journal of Paleontology* 26, 1–11.
- Whittington, H. B. 1959: Silicified Middle Ordovician Trilobites: 8: Remopleuridae, Trinucleidae, Raphiophoridae, Endymioniidae. *Bulletin of the Museum of Comparative Zoology, Harvard University* 121, 371–496.
- Whittington, H. B. 1961: Middle Ordovician Plimeridae (Trilobita) from Nevada, New York, Quebec, Newfoundland. *Journal of Paleontology* 35, 911–922.
- Whittington, H. B. 1965: Trilobites of the Ordovician Table Head Formation, Western Newfoundland. *Bulletin of the Museum of Comparative Zoology, Harvard University* 132, 277–441.
- Williams, A., Strachan, I., Bassett, D. A., Dean, W. T., Ingham, J. K., Wright, A. D. & Whittington, H. B. 1972: A correlation of Ordovician rocks in the British Isles. *Geological Society of London Special Report*, No. 3.
- Williams, S. H., Barnes, C. R., O'Brien, F. H. C. & Boyce, W. D. 1994: A proposed global stratotype for the second series of the Ordovician System: Cow Head Peninsula, western Newfoundland. *Bulletin of Canadian Petroleum Geology* 42, 219–231.
- Wiman, C. 1905a: Studien über das Nordbaltische Silurgebiet. I: Olenellussandstein, Obolussandstein und Ceratopygeschiefer. *Bulletin of the Geological Institution of the University of Uppsala* 6, 12–76.
- Wiman, C. 1905b: Ein Shumardiaschiefer bei Lanna in Nerike. *Arkiv för Zoologi* 2, No. 11, 20 pp., 2 pls.
- Wiman, C. 1908: Studien über das Nordbaltische Silurgebiet. II. *Bulletin of the Geological Institution of the University of Uppsala* 8, 73–168.
- Young, G. E. 1973: An Ordovician (Arenigian) trilobite faunule of great diversity from the Ibex Area, western Utah. *Geological Studies of the Brigham Young University* 20, 91–115.
- Zhou, Zhi-yi, Zhou, Tian-rong & Yuan, Wen-wei 1998: Ordovician trilobites from the upper Qiulitag Group, western Tarim, Xinjiang, Northwest China. *Acta Palaeontologica Sinica* 37, 269–282, pls. 1–2.