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

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This is Part II of a two-part description of the trilobite fauna of the Hagastrand Member (Tøyen Formation) in the Oslo, Eiker-Sandsvær, 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, Remopleurididae, Nileidae, Cyclopygidae, Raphiophoridae, Alsataspididae and Pliomeridae. One new species is described; Robergiella tjemviki n. sp.

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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-Sandsvær, 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.](image-url)
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-Sandsvær, locally in the Modum area, and at Vekkerø 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’ 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 Apatokeyphalus 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. graffii 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 Apatokeyphalus serratus Zone of Scandinavia, in which the late Tremadoc sea level fall (Ceratopyge 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 Apatokeyphalus 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 (‘Blåkvarts’) 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 Tetraraptus approximatus Zone (Molyneux & Rushton 1988. This age is confirmed by the occurrence of Didymograptus rigoletto, a short-ranging graptolite species characteristic of the Scandinavian Tetraraptus phyllograptoides Zone (Maetz et al. 1991). Although this is the area where the pre-Arenig hiatus is smallest in the British Isles, the earliest part of the Hunnegbergian 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 Tetraraptus 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 Apatokeyphalus 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 Tøyen 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 Hunnegbergian Substage should be elevated to Series rank; comprising the zones of Hunnegraptus copiosus, Tetraraptus phyllograptoides and Didymograptus balticus.

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Historical review of the varying concept of the Hunnebergian interval.

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 Hunnegbergian 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 Hunnegbergian as a Series. Further notes on the Stage boundaries of the Ordovician are found in Webby (1998).
Description of localities

Eiker-Sandsvær 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. Fjelldal (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 nericensis were found 15 cm above the base, and Promegalaspides (Borogothus) stenorachis and M. (P.) planilimbata 70 cm above the base. The Galgeberg Member lies directly above the last limestone bed, and contains Tetraraptus ptyllograptoides, Didymograptus holmi, D. holthedahli and D. quadribrachiatus near the base. These indicate the Tetraraptus approximatus Zone (upper part of 3bx, 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) herooides, Niobe (Niobella) bohlini (his Niobe laeviceps), Promegalaspides (Borogothus) stenorachis and Orthis christianiae.

In addition to these is a cranium of a large Megistaspis (figured by Skjeseth 1952, pl. 1, fig. 4 as M. (E.) herooides 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 subsp. A. M. (P.) sp., Megalaspides nericensis, Niobe (Niobella) bohlini, N. (Proxiniobe) longicauda Hoel, 1999 and Promegalaspides (Borogothus) stenorachis.

Stavulum (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 Stavulum 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) herooides, M. (Paramegistaspis) planilimbata subsp. A, Niobe (Niobella) bohlini, N. (Proxiniobe) longicauda Hoel, 1999, Gog n. sp., Falanaspis aliena and Megalaspides nericensis.

Numbers of specimens are higher in the upper beds, which have yielded M. (P.) planilimbata, M. (P.) spp., Promegalaspides (Borogothus) stenorachis, Varvia breviceps, Megalaspides nericensis 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.) herooides, M. (P.) planilimbata subsp.
A, Megalaspides nericiensis, Niobe (Niobella) bohlini, N. (Proxiobiobe) 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. (Proxiobiobe) 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 Tjornvik 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 (Proxiobiobe) longicauda Hoel, 1999, Gog n. sp., Robergiella sp. and Shumardia nericiensis.

Oslo–Asker district

Bjørkåsholmen, Slemmestad (UTM NM 843291). – This locality is close to Hagastad, the stratotype for the Tøyen Formation (Owen et al. 1990). Fjelldal (1966, p. 51) presented a log, and recorded Sympyurus 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 (Proxiobiobe) 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 ne stratotype for the Tøyen Formation at Hagastad, 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, Sympyurus angustatus, Megalaspides nericiensis, Niobe (Proxiobiobe) 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 (Tjornvik & 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 Finnmarksgrata (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 copiosis-fauna. Associated trilobites include Niobe (Niobe) sp., Promegalaspides (Borogothus) stenorachis, Geragnostus sp., Saltaspis
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

Genus Geragnostus (Geragnostella) Kobayashi, 1939

Type species. – Agnostus tullbergi Novák, 1883 (pl. 9, figs. 7,8,9,10) from the Sárka Formation (Llanvirn) 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.; Regnell, 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.
Non-asaphid trilobites, Oslo Region

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

Material. – Two pygidia and four cephalia.

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.

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 Seydisehir 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 Arthrhorachis Hawle & Corda, 1847

Type species. – Battus tardus Barrande, 1846 from the Kráľuv Dvur Formation (Ashgill) of Libomyšl near Zdice, Czechoslovakia; by monotypy.
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. l, 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, Kweichiwiella 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.
Shumardia (Conophrys) nericiensis Wiman, 1905

Figs. 4–5.


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


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 cephalon.

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 1/3 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.) ergensis Kobayashi, 1937 from the Lower Tremadoc of Bolivia and Argentina (Harrington & Leanza 1957), and also to S. (C.) pellizzarri Kobayashi, 1934 from Korea and south Mandsjurua (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 Sjurban, 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-
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 Remopleuridës aff. nanus from the lower Llanvirn of the Mjåsø 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 cranidium, PMO 143.180, from bed 4A, Skaraheugen, 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 (exsaq.) 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.) 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 (exsaq.) 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 tjernvikí 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 remopleurids.

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 Volkov Stage of Pavlisk, 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 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) rericeps 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. x 3.8, PMO 90418, Hagastrand Member, Tøyen under­ground station, Oslo; (C) Dorsal view of two pygidia. x 3.7, PMO 143.332, Bed 6, Stavum, 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. Barrande (1852) described Asaphus palpebrosus Dalman, 1827, from Husbyfjöl, Västergötland, Sweden.

Genus Symphysurus Goldfuss, 1843

Type species. – Symphysurus planilimbata Zone. 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 Mschr; p. 142.
1869 Symphysurus socialis n. sp., Linnarsson, p. 74, pl. 2, figs. 33–34.
1882 Symphysurus angustatus (Boeck); Børgger, 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.
1975 Symphysurus angustatus (Boeck); Courtessole & Pillet, pp. 263–266, pl. 26, figs. 1–16, 19, pl. 27, figs. 2–3.
1986 Symphysurus angustatus (Boeck); Fortey, p. 261.
1986 Symphysurus angustatus (Boeck); Berard, p. 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 Tjemvik 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. x 6, PMO 155.446, Bed 6, Vestfossen railway station; (C) Dorsal view of small, exfoliated pygidium. x 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
Type species. — Aegelina prisca Barrande, 1872, from the ‘d1’ zone of Barrande (Ordovician) of Czech Republic.

Remarks. — The occurrence of Pricyclopyge 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 glabellat furrows typical of Cyclopyge. The pygidium of Pricyclopyge? 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 Pricyclopyge. Until better material is available I follow Tjernvik & Johansson (1980) in assigning the present material to Pricyclopyge.

Pricyclopyge (?) 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 Pricyclopyge 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 Pricyclopyge 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 Billingestage (Tjernvik & Johansson 1980, p. 186), and in some levels of the Komstad Limestone, Cyclopyge (or Pricyclopyge?) 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

Genus Pytine Fortey, 1975

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


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.


Non-asaphid trilobites, Oslo Region

Fig. 12. *Pytine brevicauda* (Wiman, 1905): (A) Dorsal view of latex cast of incomplete cranidium. × 25, PMO 143.351/B, specimen of *Arthrorhachis ellipitifrons* (Fig. 3E) in background, Bed 1B 'a', 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. × 9, PMO 144.140, Bed 2, Vestfossen railway station; (C) Dorsal view of cranidium with unusually elongated glabella, × 15, PMU N 304, 47-50 cm above the alum shale, Stora Brottet, Lanna, Närke, Sweden; (D) Free cheek with mesh-like sculpture, × 14, PMU N 308, 47-50 cm above the alum shale, Stora Brottet, Lanna, Närke, Sweden; (E) Dorsal view of cranidium showing large bacculae. × 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, × 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. × 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. × 11, PMO 155.968/D, Stora Brottet, Lanna, Närke, Sweden; (I) Lectotype. Dorsal view of cranidium. × 16, RM Ar 12359. Original of Wiman 1905, pl. 1, fig. 19; (J) Dorsal view of exfoliated pygidium with strong segmentation. × 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 ellipitifrons* 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
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 at internal moulds.

A specimen (Fig. 12E) collected by Tjernvik at Lanna, Närke, Sweden, has large baculæ. 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 baculæ (Berard 1986, pl. 12, fig. 10, 18). Such large baculæ are also found in Carinocranium cariniferum Dean (1989, pl. 14, fig. 10, 18). A specimen figured as Ampyx (?) sp. by Dean (1971, pl. 1, fig. 4) resembles Pytine brevicauda, but it seems to lack baculæ. 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 baculæ 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 Tjemvik, 1956: (A) Dorsal view of small cranidium. x 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. x 5.8, PMO 155.438, unknown level in the Haganrand Member, Krekling; (C) Dorsal view of cranidium showing faint muscle scars on the glabella. x 8.2, PMO 136.087, Bed 3A '0', Skarahaugen, Vestfossen.

Occurrence. - Norway: Bed 1 Bu, Skarahaugen; Bed 2, Vestfossen railway station. Sweden: Stora Brottet, Lanna, Narke (47–50 cm above the Alum Shale in the profile of Tjemvik 1956, pp. 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 Tjemvik, 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 (Tjemvik 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 Tjemvik, 1956

Type species. - (By original designation) Falanaspis aliena Tjemvik, 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. Tjemvik (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.

Fig. 15. Revised reconstruction of fused free cheeks and cranidium of Falanaspis aliena Tjemvik, 1956. Cranidium after Tjemvik (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 celsaroa* Ross, 1951; originally designated by Harrington (1957, p. 811 as *Protopliomerops aemula* Hintze, 1952 (=P. celsaroa (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. celsaroa* (Ross, 1951), but it is not easy to find any difference between *Hintzeia* and *Pliomeros* Raymond, 1905, a point made by Regnell (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 *Kanoschia* Harrington, 1957. This is very unlikely, as the type species of *Kanoschia, 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. celsaroa* 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 *Calyrnene actinura* (Dalman); Dalman, p. 38.

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

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

1913 *Protopliomerops celsaroa* Ross, 1951;

1824 *Pliomera mathesi* Angelin n. sp.; Angelin, p. 35; pl. 22, figs. 1, la–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. × 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. × 7, PMO 143.179, Bed 5, Vestfossen railway station; (D) Dorsal view of complete exoskeleton. × 3, PMO 155.968/A, from a loose boulder at Stora Brottet, Lanna, Närke, Sweden; (E) Dorsal view of thorax and incomplete pygidium. × 3.6, PMO 157.571, from a loose boulder at Stora Brottet, Lanna, Närke, Sweden; (F) Dorsal view of incomplete cranidium. × 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); Regnell, 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.

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

Material. – One damaged exoskeleton, one incomplete cranidium and one hypostoma. In addition, several complete specimens from Lanna, Närke, Sweden.
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 \((\text{trans.})\), 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 \((\text{sag.})\) and shallow; both occipital furrow and occipital ring bent forward mesially; occipital ring of equal width \((\text{sag.})\); eyes rather small, located immediately behind the anterior most \((\text{outermost})\) 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 \((\text{sag.})\), 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 \((\text{trans.})\); anterior lobe is three times as long \((\text{sag.})\) 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 \((\text{Figs. 16A, C. Thorax constituting about half of total length of animal;}\) with 14 segments; axis narrow, occupying about 1/4 of the total width of thorax, tapering slightly backwards; rings narrow \((\text{sag.})\), 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 \((\text{trans.})\), 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* \((\text{Dalman, 1824});\) Tjernvik \((1956, p. 266)\) assigned material from the *Megistaspis (Paramegistaspis) planimibata* 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 \((\text{Figs. 16D–E};\) 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 \((\text{five in two specimens};\) 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 craniid from a limestone unit in the Solheim Slate \((\text{Örnberget Fm., Lower Allochthon})\) at Groslii Seter, Valdres, to *Parapilekia* sp., but Ebbestad \((\text{in press})\) believes this specimen belongs to *Pliomeroides primigenus* \((\text{Angelin, 1854).}\)

Occurrence. – Bed 5, Vestfossen railway station. Unknown levels in the *M. (P.) planimibata* Zone in Närke and on Öland, Sweden. Bendigonian \((\text{Bel = Didymograp tus balticus} \text{Zone})\) in the Canning Basin, western Australia.

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