Trilobites of the Hagastrand Member (Tøyen Formation, lowermost Arenig) from the Oslo Region, Norway. Part I: Asaphidae

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This is part one of a two-part description of the trilobite fauna of the Hagastrand Member of the Tøyen Formation. The Tøyen Formation (Lower Arenig) of the Oslo Region consists of poorly fossiliferous grey shales and black graptolitic shale. In the basal part of the Formation (i.e. Hagastrand Member) in the Eiker-Sandsvær, Modum and Oslo districts, limestone horizons contain trilobites of the *Megistaspis (Paramegistaspis) planilimbata* Zone. These beds were formerly assigned to the underlying Bjørkåsholmen Formation (former Ceratopyge Limestone). The studied trilobites and conodonts indicate a hiatus spanning the uppermost Tremadoc *Megistaspis (Ekeraspis) armata* Zone in the Eiker-Sandsvær area. The *M. (E.) armata* Zone is present in the deeper parts of the basin (in Oslo city), where some of the grey shales also contain graptolites. Limestones of the Hagastrand Member are considered to have been deposited on local highs, surrounded by more muddy substrates. They contain a trilobite fauna distinct from the underlying *Ceratopyge*-fauna. The present paper describes the 10 asaphids, including *Niobe (Proxiniobe) longicauda* n. subgen., n. sp. and *Gog* n. sp. The remaining 12 non-asaphid trilobite species found are described in the second part of this monograph (Hoel in press), where the localities studied are also described.

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Introduction

The Tøyen Formation (Erdtmann 1965; Owen et al. 1990) is predominantly a shale sequence 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 (formerly Ceratopyge Limestone), 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). It is also present in the Allochthons of the Scandinavian Caledonides to the northwest (Rasmussen & Bruton 1994). In Sweden it is known from very many Ordovician sections. The platform deposits in Sweden are dominated by a condensed limestone succession, while in the more distal deposits of the Oslo Region and Scania, which belong to the Oslo–Scania–Lysogor confacies belt (Erdtmann & Paalits 1994), the Tøyen Formation represents a facies change from limestones to graptolitic shale. In Norway, the Tøyen Formation is divided into two members: the grey, poorly fossiliferous, shaly Hagastrand Member at the base and the overlying black, fossiliferous graptolitic shale of the Galgeberg Member. In Eiker-Sandsvær, locally in the Modum area, and at Vekkerø in Oslo (see Fig. 1), the Hagastrand Member is developed as a condensed limestone succession (the 'Vestfossen Member' of Erdtmann 1965, p. 525), which contains a trilobite fauna similar to that described by Tjernvik (1956) from the *Megistaspis (Paramegistaspis) planilimbata* Zone in Sweden. These localities are described in detail in the second part of this monograph (Hoel, in press). Beneath the Hagastrand member, the topmost Tremadoc *Megistaspis (Ekeraspis) armata* Zone is missing. However, at Tøyen, Oslo, beds coeval with this zone have been identified from a study of the graptolites (Lindholm 1991, p. 11), and less abundant trilobites (herein). A specimen of *M. (E.) armata* occurs in the Hagastrand Member at Rortunet, Slemmestad, and is the only record of this species found in Norway. Higher in the Tøyen Formation a few thin, silty limestones contain trilobites, but the fauna is always sparse compared to equivalent horizons in Sweden.

In this first part I describe the asaphid species that occur in the Hagastrand Member, while the non-asaphid species are described in the second part of the monograph (Hoel in press). Most of the trilobites are recorded here for the first time from Norway, and previous collections from this interval are meagre. This is mainly because the beds are sparsely fossiliferous compared to the underlying Bjørkåsholmen Formation, to which these beds have earlier been assigned as the upper part. The fauna of the Bjørkåsholmen Formation is described by Ebbestad (in press) who also provide details of the localities containing the limestone facies of the Hagastrand Member (see also Fjelldal 1966).

In Norway, the limestones of the Bjørkåsholmen Formation and the succeeding Hagastrand Member of the Tøyen Formation (Owen et al. 1990) represent the latest Tremadoc–earliest Arenig regression (La1,5-La2) event (see Fig. 2). Trilobites from this interval have been described by Sars (1835), Boeck (1838), Angelin (1854),

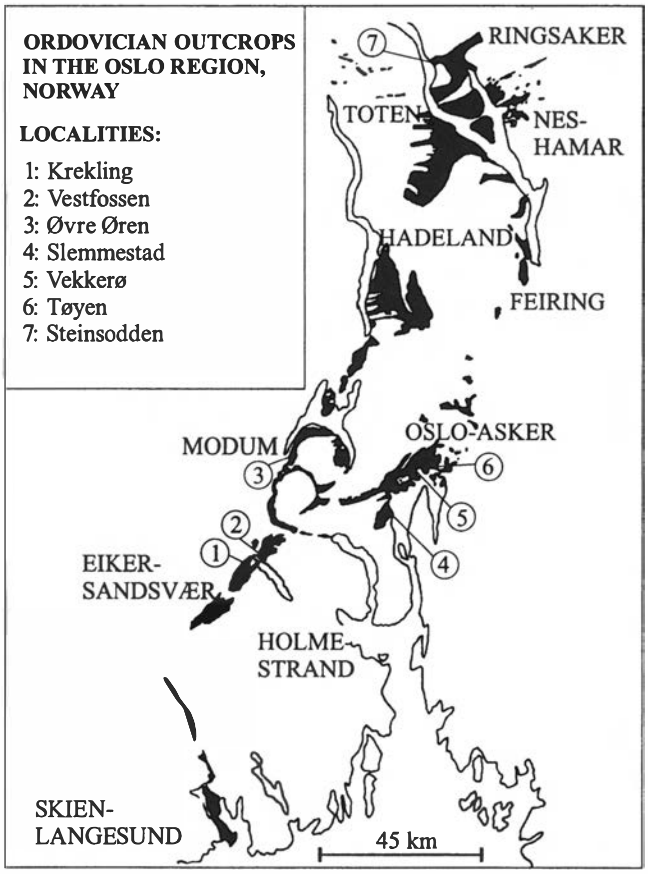


Fig. 1. Map of the Ordovician outcrops in the Oslo Region with location names. Descriptions of the localities are found in the second part of this monograph (Hoel in press).

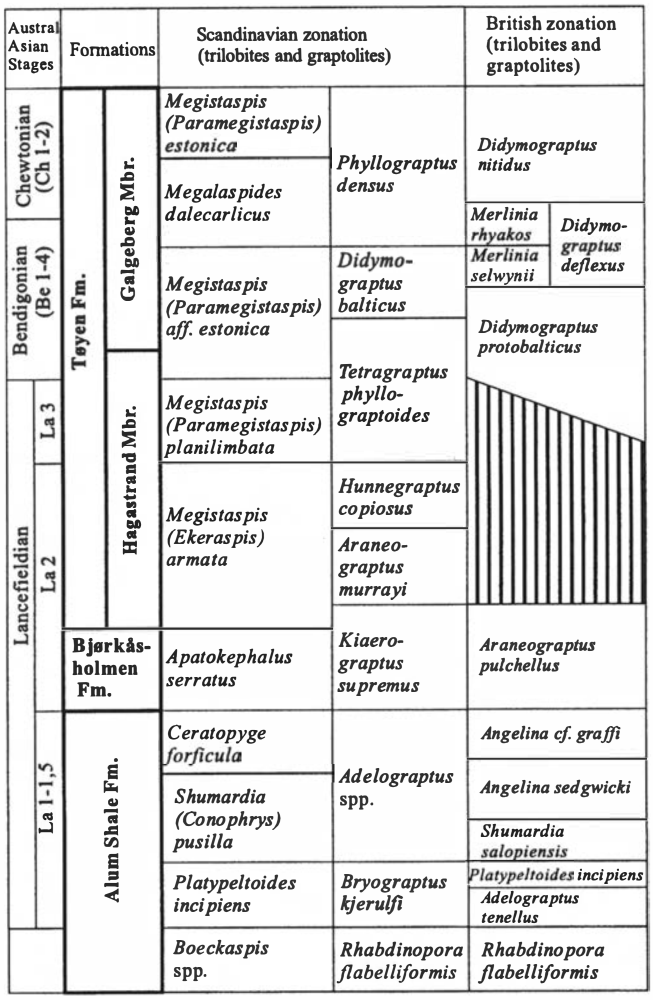


Fig. 2. Correlation chart comparing the British and Scandinavian biozonation with the standard chronostratigraphic zonation of Australasia.

Brøgger (1882, 1898), Størmer (1940), Tjernvik (1956), Henningsmoen (1959), and Ebbestad (in press). These authors concentrated on the '*Ceratopyge*-fauna' of the Bjørkåsholmen Formation, which almost everywhere is directly succeeded by the shales of the Tøyen Formation. Trilobites from the locally developed limestone facies in the Hagastrand Member have received little attention, but Brøgger (1882, p. 18) described *Megistaspis (Ekeraspis) heroides*, and noted that the stratigraphically higher fauna was different from that found in the highest part of the Ceratopyge Limestone (Bjørkåsholmen Formation). The trilobites of the Hagastrand Member are best studied at the Eiker-Sandsvær localities of Krekling and Vestfossen and in the Modum area. At Vekkerø (Brøgger 1882; Fjelldal 1966; Klemm 1982; Ebbestad 1993) corresponding limestones are developed, but are virtually unfossiliferous, and the location at Tøyen (Erdtmann 1965) is now inaccessible (see Fig. 3). In Eiker-Sandsvær, the boundary between the Bjørkåsholmen Formation and the Tøyen Formation is marked by one or more glauconitic horizons followed by muddy limestones (Ebbestad 1993). The latter contain trilobites of the *Megistaspis (Paramegistaspis) planilimbata* Zone recorded also from Modum, Tøyen and Vekkerø. Specimens in the collections of the Paleontologisk museum, Oslo, confirm the presence of this zone at Slemmestad and Engervik (Røyken). Higher in the Tøyen Formation trilobites are rare. Skjeseth (1952, p. 158) described a pygidium of *Megistaspis (Paramegistaspis) norvegica* (Tjernvik, 1956) from Ottestad (Hamar District), a species known from the *Megalaspides (Megalaspides) dalecarlicus* Zone in Sweden (Tjernvik 1956, p. 241). Trilobites possibly belonging to the *Megistaspis (Paramegistaspis) estonica* Zone have been recorded only at Nærsnes (Spjeldnæs 1986, fig. 1) and Slemmestad, Røyken (specimen RM 37918 from Naturhistoriska Riksmuseet, Stockholm). At Heramb, Ringsaker, Skjeseth (1952) also recorded trilobites thought to belong to the *Megalaspides (Megalaspides) dalecarlicus* Zone (= *Oepikodus evae* conodont Zone; *Phyllograptus densus* graptolite Zone), but Owen et al. (1990, p. 16) suggested that the unit (Herram Member of the Stein Formation) belongs to the *Megistaspis (Megistaspis) simon* Zone or *M. (M.) limbata* Zone. Later work on the graptolites by Lindholm (see Rasmussen & Bruton 1994, p. 204), and on conodonts, has suggested that the unit is slightly older and correlates with the *Megistaspis (Megistaspis) polyphemus* Zone (= *Baltoniodus navis* conodont Zone; *Didymograptus hirundo* graptolite Zone). From the uppermost part of the Tøyen Formation at the now inaccessible 'Graptolitt-

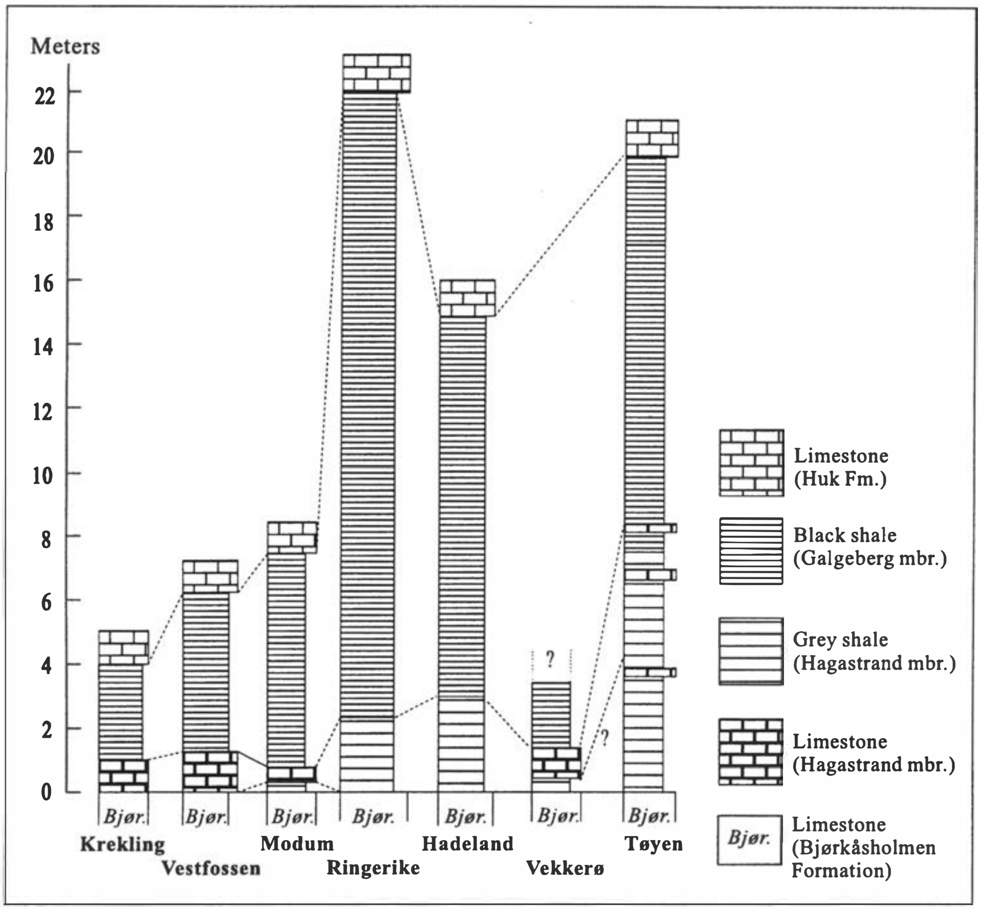


Fig. 3. Comparison of the thickness of the Tøyen Formation between the districts of the Oslo Region. For locations, see Fig. 1. *'Bjør.'* is the underlying Bjørkåsholmen Formation, formerly the 'Ceratopyge Limestone' (Data mostly from Owen et al. 1990).

dalen', Slemmestad, D. Bruton (pers. comm. – 1980) collected a complete specimen of *Megistaspis (Megistaspis) polyphemus* (Brøgger, 1882), thereby confirming the stratigraphical inference of Brøgger (1882, p. 75) that the type specimen was from around the base of the Huk Formation. Skjeseth (1952, pl. 1, fig. 4) figured a cranidium of this species (identified as *Megistaspis (Ekeraspis) heroides*) probably from the Tøyen Formation at Krekling, and Nielsen (1995, p. 143, fig. 109A) records it from the lowermost centimetres of the Huk Formation.

Geological setting

In the Tremadoc–Arenig reconstructions of Scotese & McKerrow (1991) and Torsvik et al. (1990), the continent of Baltica is shown to be situated at about 50°–60° south with a drift north towards Laurentia at a rate of about 6–8 cm/year. A similar result, and a counterclockwise rotation of Baltica of about 20°/10 my was presented by Perroud et al. (1992), based on data from Norway and Sweden. An influence of terrigenous material in the western part of the platform is attributed to the converging movements between Baltica and Laurentia causing the early uplift of the Caledonides (Rasmussen 1989).

Lindström (1984) regarded the virtual absence of structures related to waves or strong currents as an indication that the Lower Ordovician rocks of the Baltic area were probably deposited in rather deep water. Against this view one can argue that some disturbance of the sediment during deposition is indicated by skeletal fragments that are often found in vertical positions and locally concentrated in what otherwise are generally unfossiliferous beds (Bohlin 1955, p. 119). Both Jaanusson (1982) and Nielsen (1995) have argued for deposition in shallower water within the photic zone. The only positive evidence of shallow depth from the Bjørkåsholmen Formation, a report of green-algae by Wöltje (1989), seems to have been erroneous (J. O. R. Ebbestad pers. com. – 1998).

In Ringerike, Hadeland and Oslo–Asker districts, where the succession is most complete, the Hagastrand Member is developed as a greenish shale up to 10 m thick, while in the southern part of the Eiker- Sandsvær and Modum districts and at Vekkerø, Oslo, it consists of about 1 m of marly limestone with individual beds about 10–15 cm thick, intercalated with thin layers of shale. With the exception of the Modum area, the Hagastrand Member is also everywhere underlain by a thin glauconitic layer, indicating that this was an area of very slow sedimentation (see Fig. 3). Conodonts from the lowermost limestone bed of the Hagastrand Member at Skarahaugen, Vestfossen (kindly identified by Dr Anita Löfgren of Lund University, Sweden), indicate that in this area the earliest part of the Tøyen Formation belongs to the *Paracordylodus gracilis* Subzone of the *Paroistodus proteus* conodont Zone;

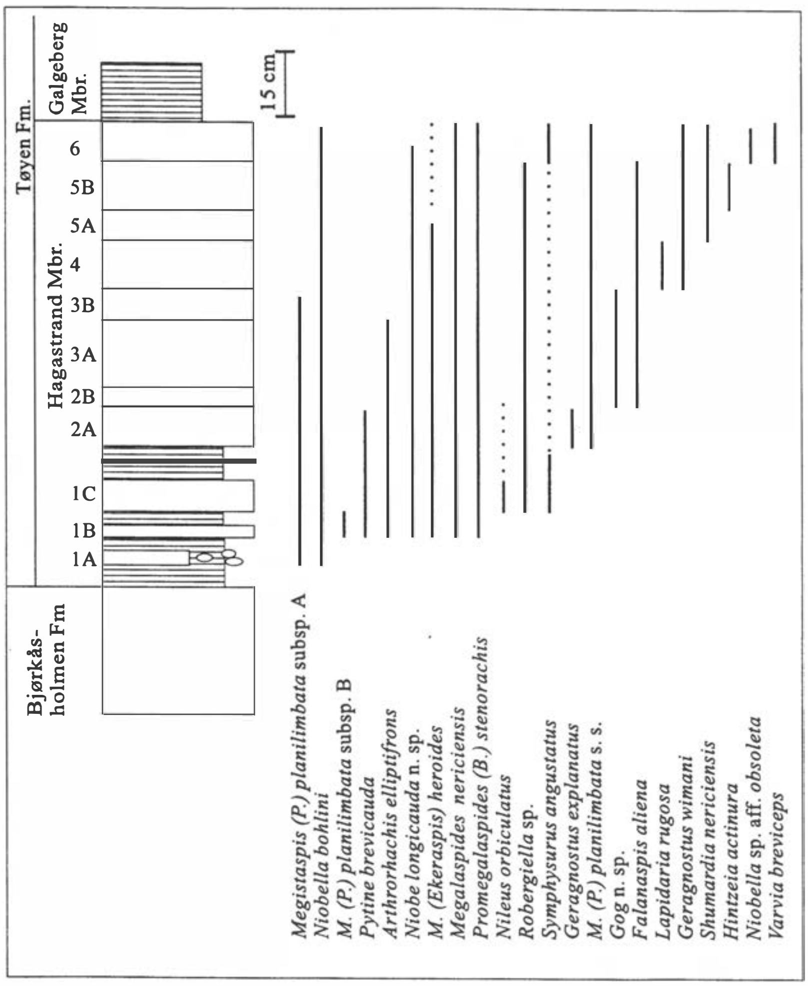


Fig. 4. Stratigraphic ranges of the trilobites of the Hagastrand Member. The numbers refer to the probable extent of Klemm's bed numbering. The development of the limestones is similar at most localities, except at Øvre Øren, where there are only two thin limestone beds, probably corresponding to the lower part of the limestone succession elsewhere.

correlated with the lower part of the *Megistaspis (Paramegistaspis) planilimbata* Zone. The hiatus between the Bjørkåsholmen Formation and the Hagastrand Member here is thus equal to at least the whole *Megistaspis (Ekeraspis) armata* Zone (*Araneograptus murrayi* and *Hunnegraptus copiosus* graptolite Zones).

The impure limestones are clay-rich, and large crystals of pyrite occur in the matrix. Sedimentologically, these beds are very similar to the calcarenitic upper part of the Bjørkåsholmen Formation. In the Slemmestad area, the Hagastrand Member consists of more shale, but with thin calcareous sandstone beds. Everywhere the Hagastrand Member limestones contain mainly trilobites, but brachiopods, both articulate and inarticulate are present. The fossils appear to have been transported, but any damage seems to have been caused by diagenesis, resulting in either partial dissolution or recrystallization.

Biostratigraphic summary

The trilobite fauna of the Hagastrand Member appears to be slightly more diverse near the base (see Fig. 4), but the number of specimens increases upwards, culminating 20–30 cm below the base of the overlying graptolite shale of the Galgeberg Member. In the uppermost part, specimens become rare and often very difficult to identify because of poor preservation. Some species have restricted ranges (Fig. 3), but this may be a result of their extreme rarity. Of the more common species, *Megistaspis (Paramegistaspis) planilimbata* sensu stricto is absent from the lowermost part of the unit, while *Megistaspis (Paramegistaspis) planilimbata* n. subsp. A is found only in the lower three beds, at least in Eiker–Sandsvær. *Megistaspis (Ekeraspis) heroides* is not found in the upper part of the unit, but its range slightly overlaps that of *M. (P.) planilimbata.* Of the trilobites described in part II of this monograph, *Arthrorhachis elliptifrons* and *Pytine brevicauda* have only been found in the lower half, while *Geragnostus wimani, Shumardia nericiensis* and *Hintzeia actinura* are typical of the upper part of the unit.

Systematic palaeontology

The following abbreviations denote institutions where particular specimens are housed:

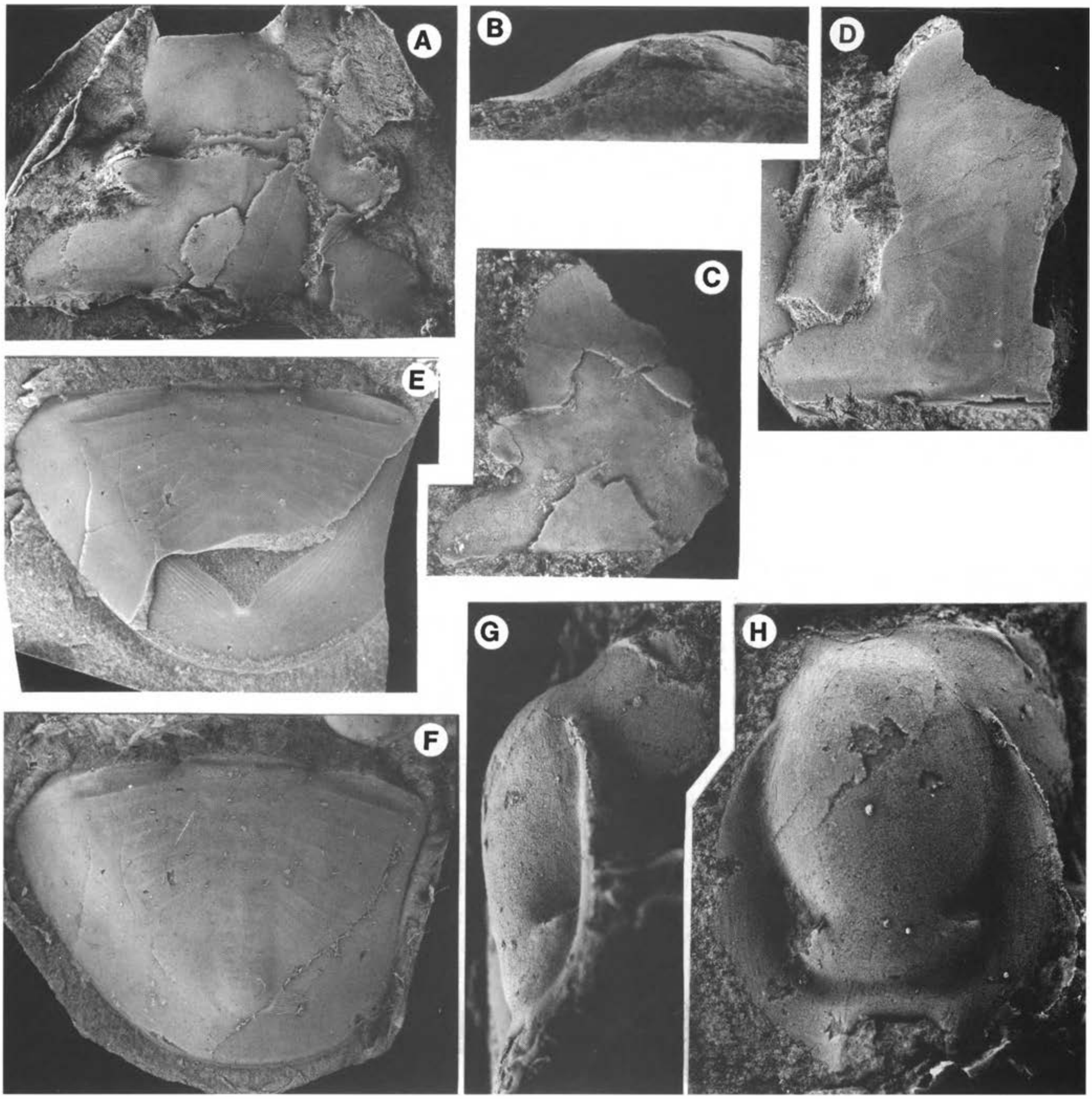


Fig. 5. Megalaspides (Lannacus) nericiensis Wiman, 1905, (A) Dorsal view of latex cast of incomplete cranidium. × 1.9, PMO 139.383, Bed 2B *'o'*, Skarahaugen, Vestfossen; (B–C) Lateral and dorsal view of incomplete cranidium. ×2, PMO 121.634, ~40 cm above base of Hagastrand Member, Øvre Øren, Vikersund; (D) Dorsal view of incomplete cranidium showing muscle scars. ×1.7, PMO 142.070, Bed 1C *'u'*, Skarahaugen, Vestfossen; (E) Dorsal view of well-preserved pygidium, showing the shape of the doublure. ×1.8, PMO 144.118/2, Bed 6(?), Kårtveitbekken, Krekling; (F) Dorsal view of latex cast of well-preserved pygidium (counterpart of 5e). ×1.8, PMO 144.119/2; (G–H) Lateral and dorsal view of latex cast of hypostome. ×3.4, PMO 121.651, ~40 cm above base of Hagastrand Member, Øvre Øren, Vikersund.

PMO – Paleontologisk Museum, University of Oslo, Norway

PMU – Paleontologiska 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

Family Asaphidae Burmeister, 1843
Subfamily Isotelinae Angelin, 1854
Genus *Megalaspides* Brøgger, 1886

Type species. – *Megalaspis dalecarlicus* Holm, 1882 from the *Megalaspides dalecarlicus* Zone (Tøyen Formation) (Lower Arenig) at Skattungbyn, Dalarna, Sweden.

Remarks. – Tjernvik (1956) erected *Lannacus* as a subgenus of *Megalaspides* with *M. (L.) nericiensis* as type species. Fortey (1975, p. 18) described the upper Arenig *Megalaspides striatellus* from Spitsbergen, and remarked that he was unable to distinguish between *Megalaspides (Megalaspides)* and *Megalaspides (Lannacus)*, with which I concur. Tjernvik (1956) noted that *Megalaspides (Lannacus)* is derived from *Asaphellus*-like forms. This is probably correct; *M. nericiensis* is indeed very similar to *Asaphellus catamarcensis* Kobayashi, 1935 from Argentina as figured by Harrington & Leanza (1957), especially the specimens from the Upper Tremadoc (*Notopeltis orthometopa* Zone). Specimens of this species from the Lower Tremadoc (*Kainella meridionalis* Zone) look different; pygidia seem to be more semicircular and more convex than the younger specimens, with narrower axis and border. The two variants seem to constitute two well differentiated groups. The differences do not appear to be caused by distortion, as stated by Harrington & Leanza (1957, p. 151). The pygidium (Harrington & Leanza 1957, fig. 65–2) is very different from the other pygidia figured (and very like *M. nericiensis*) in having a wide border and rather distinct segmentation. The Upper Tremadoc *Asaphellus homfrayi* Salter, 1866 from Wales (see Fortey & Owens 1991, pp. 444–449) is also very similar to *M. nericiensis* except for a slightly wider axis, more diverging frontal part of the facial suture and a more elevated pygidial axis. The hypostoma of *A. homfrayi* is also very similar, but has shorter posterior wings (Fortey & Owens 1991, fig. 7f). Balashova (1966, p. 13) described *M. (L.) popovkiensis* from $B_{II\alpha}$ (Middle Arenig) of Popovka, Lava and Volkhov (Estonia). The pygidium has a very low convexity, its pleural fields are even more effaced than in *M. nericiensis*, but the dorsal furrows are slightly more prominent. This makes it rather similar to *M. striatellus*. Owing to the poor quality of Balashova's illustration, it is difficult to make any further comparison. A possible phylogeny of *Megalaspides* derived from *Asaphellus*, could be *M. nericiensis*, *M. dalecarlicus*, *M. paliformis*, *M. popovkiensis* and *M. striatellus*.

***Megalaspides nericiensis* Wiman, 1905**
Fig. 5

1886 *Asaphus (Megalaspides?)* sp.; Brøgger, pp. 26–27, pl. 1, figs. 1, 20. (Hypostoma)
1905 *Megalaspides nericiensis* n. sp.; Wiman, p. 8, pl. 2, figs. 1–4.
1908 *Megalaspides* sp. (partim); Wiman, p. 92, pl. 5, figs. 8, 10.
1956 *Megalaspides (Lannacus) nericiensis* Wiman; Tjernvik, pp. 251–252, pl. 9, figs. 1–5, text-fig. 40.
1959 *Lannacus nericiensis* Wiman; Harrington et al., p. O341, fig. 252,2.

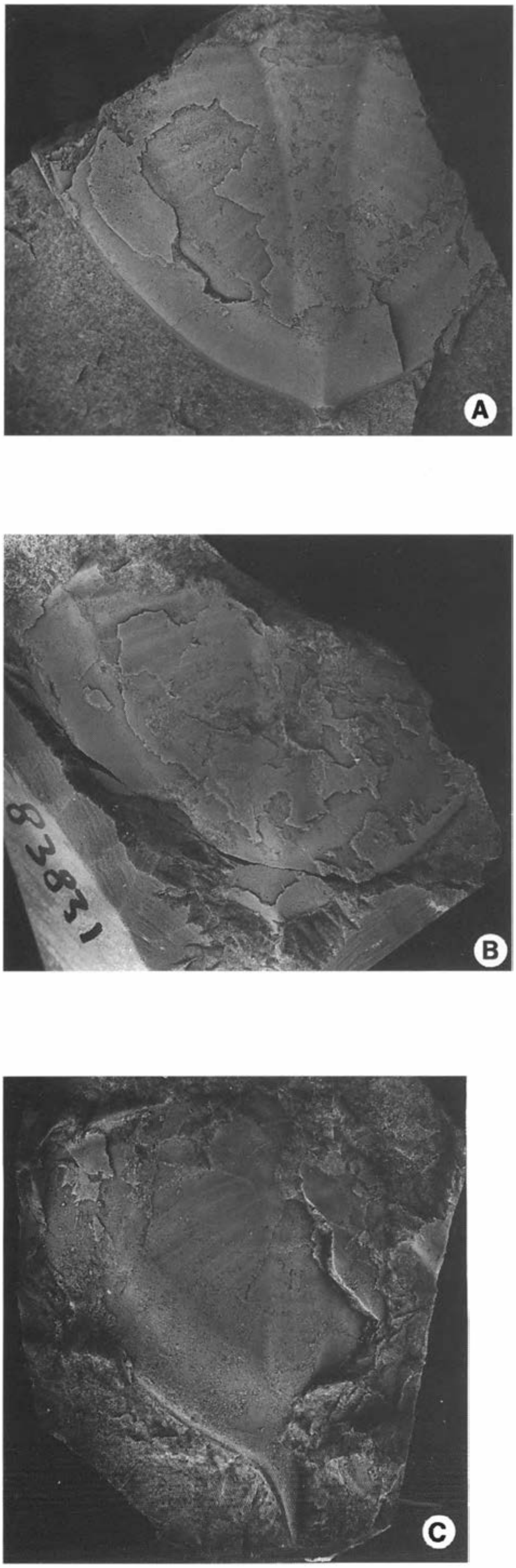
Lectotype. – Selected by Tjernvik (1956): A cranidium RM AR 12820. Original of Wiman 1905, pl. 2, fig. 3).

Material. – Nine cranidia, 5 free cheeks, 3 hypostomata, 23 pygidia.

Remarks. – Tjernvik (1956) described the species in detail, but the following remarks are noteworthy: One cranidium (Fig. 3D herein) shows faint muscle scars on the glabella; the three anteriormost pairs (S_2–S_4) are oval in outline, the two anteriormost (S_3–S_4) set at an angle of about 35° inwards and forwards to the sagittal line, S_2 slants backwards at an angle of about 15°, while S_1 is crecent-shaped, the anterior portion of which is bent outwards, the posterior part lying parallel to the sagittal line. The glabella of this specimen also shows a median keel, from the occipital furrow to the level of S_4. Norwegian specimens have the rounded form of the anterior branches of the facial suture; the posterior limbs are slightly more rounded distally, not as abruptly cut off as described by Tjernvik; pygidial L/W = 0.66, axis relatively wide, occupying at anterior end 0.27 of total pygidial width. In contrast to the flattened cephalon, the hypostoma is very deep (height/sag. length = 0.37), and must have protruded significantly below the lower edge of the doublure.

The cranidium of *M. nericiensis* can sometimes be mistaken for a flattened *Megistaspis (Ekeraspis) heroides* because of the similar course of the anterior part of the suture and the hindmost part of the glabella. The best characteristic for correct identification is the fixed cheeks which are separated from the glabella by a deeper dorsal furrow in the *M. (Ekeraspis)* species. In *M. nericiensis*, the posterior furrow is also placed further back, the posterior limbs are wider (exsag.), and the posterior part of the suture is perpendicular to the posterior margin of the cranidium. Pygidia are easily recognized because of the flattened form and the very faint pleural ribs.

This is the most common trilobite in the Hagastrand Member, occurring at all levels and localities studied. It constitutes over 10% (at least 59 specimens) of the collected fauna. It is especially abundant at Kårtveitbekken, Krekling, where pygidia are sometimes stacked coquina-like. In the Mjøsa area, the species seems to be absent, and is replaced by *Niobe (Niobella) bohlini*. The hypostoma figured by Tjernvik (1956, pl. 6, fig. 13) as *Megistaspis (Paramegistaspis) estonica* from the *M. (P.) estonica* Zone, does not belong to this species. This was acknowledged by Tjernvik & Johansson 1980 (p. 186), but they failed to recognize how similar the hypostoma is to that of *M. nericiensis*. The only obvious difference is that the posterior notch is more rounded, and the posterior wings are shorter in the specimen from the *Megistaspis (Paramegistaspis) estonica* Zone. This hypostoma may belong to *Megalaspides paliformis*, as this species is found in the upper part of the *M. dalecarlicus* Zone and possibly also in the *M. (P.) estonica* Zone.



Dimensions. – The largest pygidium collected at Kårtveitbekken, Krekling, is 7 cm wide and 4.5 cm long, indicating a whole-specimen length of more than 14 cm.

Genus *Megistaspis* Jaanusson, 1956

(pro *Megalaspis* Angelin, 1851; non-*Megalaspis* Bleeker, 1851)

Type species. – Designated by Jaanusson (1956): *Trilobites limbatus* Boeck, 1838, from the *Megistaspis (Megistaspis) limbata* Zone (Huk Formation), Upper Arenig, Oslo area. The type specimen (Størmer 1940, p. 141), is an almost complete specimen (PMO 1631) from Akersbakken, Oslo, the pygidium of which was figured by Brøgger (1882, pl. 9, fig. 2). The entire carapace was figured by Jaanusson (1956, pl. 1, figs. 1–3)

Remarks. – An exhaustive treatment of the history of the genus *Megistaspis* was carried out by Nielsen (1995, p. 102), and his classification of *Megistaspis* and corresponding subgenera is followed here. I will only emphasize that *Megistaspis (Varvaspis)* Tjernvik & Johansson, 1980 is an objective junior synonym of *Megistaspis (Paramegistaspis)* Balashova, 1976.

Subgenus *Megistaspis (Ekeraspis)* Tjernvik, 1956

Type species. – *Megistaspis (Ekeraspis) armata* Tjernvik, 1956, from the *Megistaspis (Ekeraspis) armata* Zone (Latorp Limestone) at Stenbrottet, Västergötland.

Remarks. – Although the subgenus is short lived, known only from uppermost Tremadoc–lower Arenig rocks, it seems to have been widespread. If correctly identified, *M.(Ekeraspis)* has been recorded outside Baltoscandia from Montagne Noir, France (*Didymograptus extensus* Zone, Dean (1966)), Tasmania (Lancefieldian 2–3, Jell & Stait (1985)) and Nevada (Trilobite Zone G, Ross (1970)).

Megistaspis (Ekeraspis) armata Tjernvik, 1956

1956 *Plesiomegalaspis (Ekeraspis) armata* n. sp.; Tjernvik, p. 242, pl. 7, figs. 7–13.

1959 *Megistaspis (Ekeraspis) armata* Tjernvik; Harrington et al., p. O349, fig. 259, 1a–c.

Material. – A poorly preserved exoskeleton (PMO 158.239–240) showing the pointed pygidial spine, from the 21.30 m level in the Rortunet section of Owen et al. (1990, p. 7).

Remarks. – This is the only record of this species in Norway. The terminal pygidial spine seems to be proportionately slightly longer on the Norwegian specimen

Fig. 6. Megistaspis (Ekeraspis) heroides (Brøgger, 1882), (A) Dorsal view of large pygidium with small posterior spine. ×1.7, PMO 89675, 6 m below base of the Huk Fm, Kårtveit–Stavlum, roadcut on the eastern side; (B) Dorsal view of large pygidium with very thin posterior spine. ×1.7, PMO 83831, bed 3, Skaralrysset; (C) Dorsal view of latex cast of pygidium with large, complete posterior spine. ×1.8, PMO 20085, Krekling.

than in the Swedish ones, though preservation is poor. The specimen was found 3.5 m above the glauconite layer at the top of the Bjørkåsholmen Formation and 40 cm below beds with *Clonograptus norvegicus* and *Araneograptus murrayi* (?). This means that the *M. (E.) armata* Zone can be recognized in sections where the Hagastrand Member is developed as a thick unit of grey shales (Tøyen, Slemmestad), but not in sections containing limestone (Eiker–Sandsvær and Vekkerø).

***Megistaspis (Ekeraspis) heroides* (Brøgger, 1882)**
Fig. 6

1882 *Megalaspis heroides* n. sp.; Brøgger, p. 82, pl. 4, figs. 3, 4.
1908 *Megalaspis heroides* Brøgger; Wiman, p. 91 (report on find of pygidia).
1952 *Megalaspis heroides* Brøgger (partim); Skjeseth, p. 164, pl. I, fig. 8.
1956 *Plesiomegalaspis (Ekeraspis) heroides* (Brøgger); Tjernvik, pp. 244–245, pl. VIII, figs. 1–4.

Lectotype. – Selected by Skjeseth (1952): pygidium showing the posterior end: PMO H2698 (Original of Brøgger 1882, pl. 4, fig. 4), and syntype: PMO H2643 (Original of Brøgger 1882, pl. 4, fig. 3). Syntype PMO H1538 of Skjeseth, a cranidium, belongs to *M. (Megistaspis) polyphemus* (Brøgger 1882).

Material. – One cranidium, nine pygidia.

Emended description of pygidium, based on the Norwegian material. – Length of pygidium excluding the spine somewhat more than 3/5 the width, which is slightly longer than the Swedish specimens described by Tjernvik (1956); anterior margin almost straight; border concave and moderately wide; basal part of spine much narrower than in the type species, but slightly wider than in the Swedish specimen (cf. Tjernvik 1956, pl. 8, figs 3, 4); axis narrow, occupying at anterior end less than 1/6 the pygidial width, narrowing backwards for about 3/5 of the axial length, behind this subequal in width, widening slightly again at posterior end, showing about 12 slightly undulating transverse furrows; on outer surface the axis posesses an extremely low and narrow median keel, which continues as a low, but wider keel from the end of the axis to the spine; posterior end of axis pointed in dorsal view; pleural fields well distinguished from the border, with 8–9 rather weakly defined pleural furrows, defining 8–9 straight pleural lobes with wide and shallow interpleural furrows; width of doublure equal to that of the border.

Remarks. – The Norwegian specimens have a narrower axis than the Swedish specimens, and the transverse axial furrows are undulating, not straight as described by Tjernvik (1956). The cranidium figured by Skjeseth (1952, pl. 1, fig. 4), probably belongs to *Megistaspis (Megistaspis) polyphemus* (Brøgger 1882), from the early part of the *Didymograptus hirundo* Zone. Brøgger (1882, p. 18) correctly described *M. (E.) heroides* as occurring in the lowermost part of the Lower Didymograptus Shale (Tøyen Formation), but later (Brøgger 1886, p. 41) considered these beds to belong to the upper part of the Tøyen Formation.

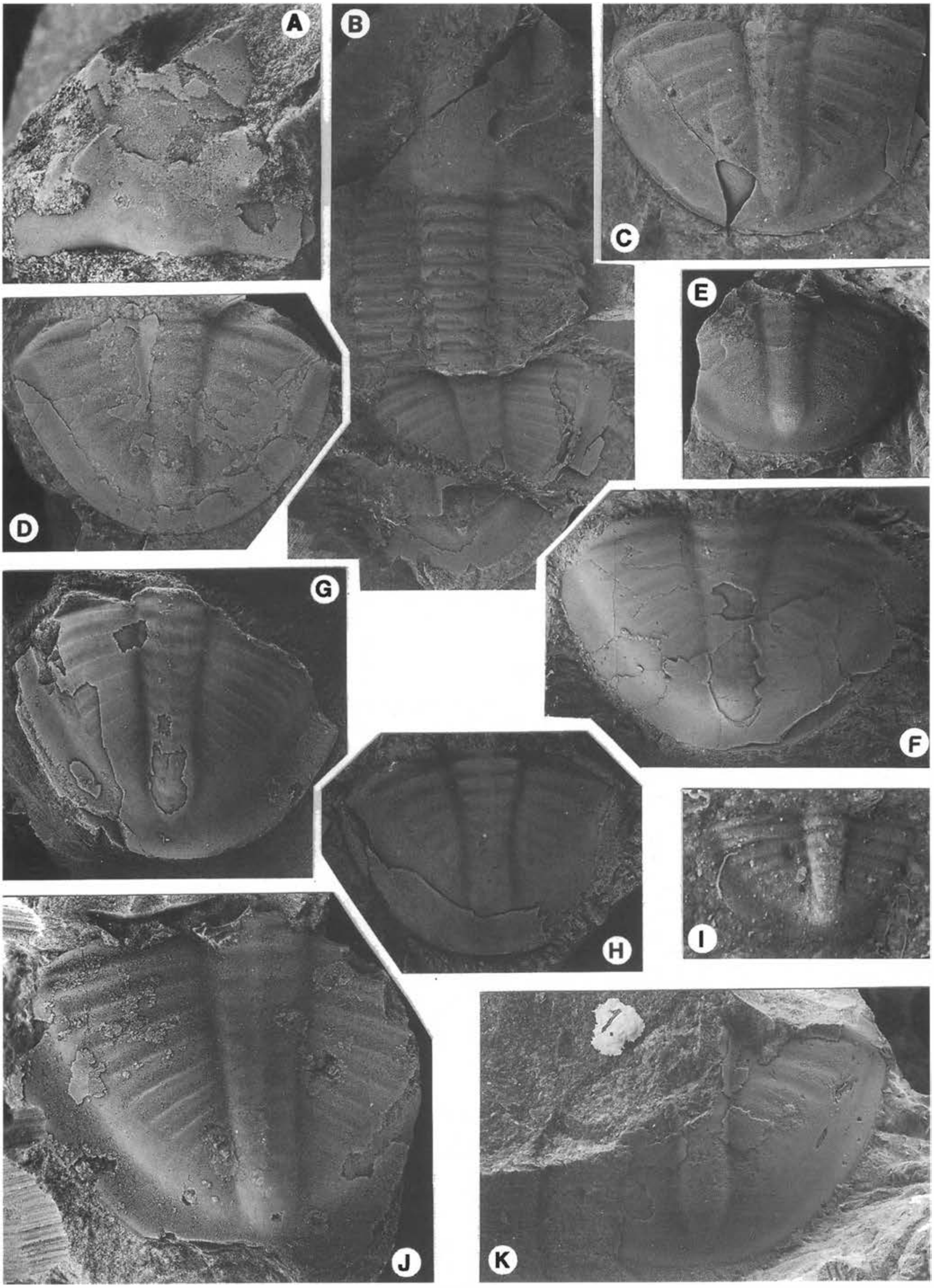
Affinities. – This species can be compared with specimens of *Megistaspis saltaensis* (Kayser 1898) figured by Harrington & Leanza (1957, p. 161, figs. 73; 2, 3, 6, 8; non-figs. 73; 4, 5). The unflattened specimen (Harrington & Leanza 1957, fig. 73, 3), has about the same number of axial furrows (9–10) and pleural furrows (9) as *M. (E.) heroides* (9 axial and 8 pleural furrows). The axis has a similar shape and the caudal spine is about the same size and shape (only slightly wider at the base and slightly longer). It differs in the interpleural furrows which are very narrow and oblique to the pleural lobes in *M. saltaensis*, while in *M. (E.) heroides* they are almost as wide and deep as the pleural furrows and follow the direction of the pleural lobe. *M. (E.) nevadensis* and *M. (E.) floweri* from the Arenig of Nevada (Ross 1970), are rather like *M. (E.) heroides*, especially *M. (E.) floweri*, which has a similar outline, the same slender axis and thin median spine. The pleural fields are similar in segmentation, the difference being the number of axial rings and pleura (12 and 9 in *M. (E.) heroides*, 9–10 and 5 in *M. (E.) floweri*, respectively). *M. (E.) floweri* has a much narrower spine and pygidial border than *M. (E.) nevadensis,* an evolution comparable to that of the two Scandinavian species.

Occurrence. – Only pygidia are known from Norway. They occur mostly in beds 1–4, (one small pygidium is labelled bed 6); Skarahaugen, Vestfossen railway station, Krekling-Stavlum. Lower part of the *Megistaspis (Paramegistaspis) planilimbata* Zone in Sweden (Limön, Västergötland, Närke, Dalarna, Jämtland).

Subgenus *Megistaspis (Paramegistaspis)* Balashova, 1976

(= Subgenus *Megistaspis (Varvaspis)* Tjernvik & Johansson, 1980)

Fig. 7. Megistaspis (Paramegistaspis) planilimbata (Angelin, 1851); (A, C–F, H–I): *Megistaspis (Paramegistaspis) planilimbata* sensu stricto; (B, G, J): *Megistaspis (Paramegistaspis) planilimbata* subsp. A; (K): *Megistaspis (Paramegistaspis) planilimbata* subsp. B: (A) Dorsal view of small cranidium. ×3.3, PMO 142.309, ~40 cm above base of the Hagastrand Member, Øvre Øren, Vikersund; (B) (subsp. A) Dorsal view of exoskeleton lacking free cheeks, lateral ends of most thoracic pleurae and anterior part of cranidium, damaged pygidium. ×1.9, PMO 143.183, Bed 2, Vestfossen railway station; (C) Dorsal view of pygidium. ×1.8, PMO 89746, uppermost part of the Hagastrand Member, Skarakrysset, Vestfossen; (D) Dorsal view of pygidium. ×1.8, PMO 89746, uppermost part of the Hagastrand Member, Skarakrysset, Vestfossen; (E) Dorsal view of small pygidium. ×3.8, PMO 142.075, Bed 6, Vestfossen railway station; (F) Dorsal view of pygidium. ×1.9, PMO 90415, Krekling; (G) (subsp. A) Dorsal view of incomplete pygidium. ×2, PMO 138.147, Bed 2, Vestfossen railway station; (H) Dorsal view of pygidium. ×2, PMU Vg 548, 0–12 cm above base of the M. (P.) *planilimbata* Zone, Oltorp, Västergötland, Sweden. Original of Tjernvik 1956, pl. 6, Fig. 7; (I) Dorsal view of meraspid pygidium. ×10 , RM Ar 12350, 'Shumardia Shale' (M. (P.) *planilimbata* Zone), Lanna, Närke, Sweden. Original of Wiman (1905, pl. 1, fig. 18); (J) (subsp. A) Dorsal view of incomplete pygidium showing the numerous pleura and prominent rachial ridge. ×4, PMO 1540, Krekling; (K) (subsp. B) Dorsal view of incomplete pygidium showing the very narrow border posteriorly. ×2.4, PMO 144.128/1, Uppermost part of the Hagastrand Member, Kårtveitbekken, Krekling.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Type species. – *Megistaspis (Paramegistaspis) planilimbata* (Angelin 1851), from the lowermost Arenig Megistaspis (Paramegistaspis) planilimbata Zone of Baltoscandia.

Remarks. – Tjernvik (1956) referred the trilobites of the *planilimbata*-group (Jaanusson 1956) to *Plesiomegalaspis,* Thoral, 1946, but in Harrington et al. (1959) these species were assigned to *Megistaspis* Jaanusson, 1956. It is clear that this group belongs in *Megistaspis*, being closer to *M. (Megistaspidella)* Jaanusson, 1956, rather than *M. (Megistaspis).* This is suggested by the great similarity between *M. (Paramegistaspis)* and *M. (Megistaspidella)* in the even-sided glabella and effacement of all furrows on the cranidium, while *M. (Megistaspis)* has a very deep occipital furrow and a pear-shaped glabella with distinct furrows. *Megistaspis* spp. B–C, described by Nielsen (1995) from the *Megistaspis (Megistaspis) polyphemus* Zone are possibly more closely related to *M. (Paramegistaspis)* than to *M. (Megistaspis)* (Nielsen 1995, pp. 161–164). Especially *Megistaspis* cf. *knyrkoi* (Schmidt, 1906) (Nielsen 1995, p. 160) is rather similar to *M. (P.) planilimbata* subsp. A (see below). Three different forms of *M. (Paramegistaspis)* are present in the Hagastrand Member (here treated as subspecies of *M. (P.) planilimbata*): *M. (P.) planilimbata* Angelin (beds 2–6), *M. (P.) planilimbata* subsp. A (beds 1–3), and *M. (P.) planilimbata* subsp. B. (only a few pygidia in the lowest beds). They may be different ecophenotypes of *M. (P.) planilimbata* as discussed by Nielsen (1995) for *M. (M.) limbata* but the number of specimens is too small to be sure.

Megistaspis (Paramegistaspis) planilimbata (Angelin 1851)

Fig. 7A, C–F, H–I

1851 *Megalaspis planilimbata* n. sp.; Angelin; p. 18, pl. 16, figs. 2–2a.
1882 *Megalaspis stenorachis* Angelin (partim); Brøgger, pp. 76–77, pl. 4, fig. 6.
1886 *Megalaspis planilimbata* Angelin; Brøgger, pp. 39, 41, pl. 2, fig. 21, *non* pl. 3, fig. 47.
1898 *Megalaspis planilimbata* Angelin; Kayser, pl. 16, fig. 5.
1901 *Megalaspis planilimbata* Angelin; Lindström, p. 61, pl. 5, fig. 8.
1905 *Megalaspis planilimbata* Angelin; Wiman, p. 8, pl. 2, figs. 5 (?), 6–10.
Non 1906 *Megalaspis planilimbata* Angelin; Schmidt, pp. 10–14, text-figs. 2, 3, Pl. 1, figs. 1–4, pl. 2, figs. 1–4.
1906 *Megalaspis planilimbata* Angelin; Moberg & Segerberg, p. 97, pl. 7, fig. 1.
?1951 *Megalaspis* sp. cf. *M. planilimbata* Angelin; Harrington & Kay, p. 665, pl. 97, fig. 21.
Non 1952 *Megalaspis planilimbata* Angelin; Skjeseth, pp. 158–160, text-fig. 6, pl. 1, figs. 9, 10.
1952 *Megalaspis planilimbata* Angelin; Tjernvik, p. 56, text-fig. 3A.
1956 *Plesiomegalaspis planilimbata* (Angelin); Tjernvik, pp. 235–238, text-fig. 38A, pl. 6, figs. 1–9.
1956 *Megistaspis planilimbata*-group; Jaanusson, p. 67.
1976 *Paramegistaspis planilimbata* (Angelin); Balashova, p. 77.
1980 *Megistaspis (Varvaspis) planilimbata* (Angelin); Tjernvik & Johansson, p. 195, figs. 6A, 8A–F.

Type specimen. – Tjernvik (1956, p. 236) noted that Angelin's original is lost, and topotype material is not good enough to provide a neotype.

Material. – Four cranidia, 1 hypostoma, 39 pygidia.

Remarks. – To the description of Tjernvik (1956, p. 235) can be added the low number of pygidial pleurae (7); the usually low convexity; the shape of the axis, which has its narrowest point well in front of the wider terminal portion; and the relatively wide, flattened pygidial border. These characters distinguish *M. (P.) planilimbata* proper from the slightly older *M. (P.) planilimbata* subsp. A (see below). *M. (P.) planilimbata* is a very common species in Sweden, but remarkably little was known about it until the modern description by Tjernvik (1956); several of the earlier descriptions are in fact of one of the other species of the same subgenus occurring later than *M. (P.) planilimbata* proper: *Megalaspis planilimbata* of Schmidt (1906) was assigned by Tjernvik (1956) to *Plesiomegalaspis estonica* (= *Megistaspis (Paramegistaspis) estonica*). The pygidium figured by Skjeseth (1952, pl. 1, fig. 10) was selected as the type specimen of *M. (P.) norvegica* by Tjernvik (1956, p. 240). This species occurs in the *Megalaspides dalecarlicus* Zone in Sweden. The poorly figured external mold of a pygidium in Harrington & Kay (1951, pl. 97, fig. 21) from Colombia, seems to be rather similar to *M. (P.) planilimbata*, having 8–9 axial rings and 6 pleural ribs. The pygidium figured by Brøgger (1882, pl. 4, fig. 6; Skjeseth 1952, p. 159) as *Megalaspis planilimbata* from Krekling belongs to *Megistaspis (Paramegistaspis) planilimbata* subsp. A (see below).

Occurrence. – Beds 2–6, all localities of the Hagastrand Member in Norway. Common throughout the unit in Sweden.

Megistaspis (Paramegistaspis) planilimbata subsp. A

Fig. 7B, G, J

1882 *Megalaspis stenorachis* Angelin; Brøgger, pl. 4, fig. 6, (7?).
1886 *Megalaspis planilimbata* Angelin; Brøgger, pl. 3, fig. 47.
1908 *Megalaspis planilimbata* Angelin; Wiman, p. 90, pl. 7, fig. 23.
1952 *Megalaspis planilimbata* Angelin; Skjeseth, pp. 158–160, text-fig. 6.
1956 *Plesiomegalaspis*? sp. no. 2. Tjernvik, p. 246, pl. 8, fig. 6.

Material. – One entire exoskeleton lacking the free cheeks, one cranidium, one hypostoma, eight pygidia.

Remarks: Description. – (Since no entire specimen has been illustrated before, I describe here certain features evident only from this specimen): Exoskeleton about half as wide as long (fig. 7A: L/W = 2.08); cephalon and thorax of about the same length, pygidium slightly longer (PMO 143.183; fig. 7A:17 mm/17 mm/ 20 mm).

Thorax almost even-sided (L/W = 0.65), only slightly wider at mid-length; axis narrow (trans.), constituting about 0.25 of total width and narrowing slightly backwards; the articulating half-ring are almost as wide (sag.) as the axial ring; pleurae are short (exsag.) and wide (trans.), L/W = 0.15, pleural furrow wider in the posterior part of the thorax than in the anterior part; adaxially it starts very near the anterior margin of each pleurae, having a slight backward angle to the median line, abaxially it lies at the centreline of each pleurae, ending at the down-bent part; in the posterior pleurae the furrow is almost perpendicular to the sagittal line. This may show that most of the flexing (and thereby the overlap between the lateral part of the segments) during enrolment took place in the forward part of the thorax.

This subspecies is rather similar to *M. (P.) planilimbata* (see Tjernvik 1956, p. 237), but it differs in that the pygidium is more strongly convex; the pygidial pleurae are proportionately longer (trans.), and therefore the pleural fields are much wider and the border correspondingly narrower; the pleurae are more numerous (9 vs. 6–7); the axis is distinctly different, narrowing evenly backwards, whereas in *M. (P.) planilimbata* proper the narrowest point lies somewhat in front of the terminal portion; the axis is also more strongly elevated above the pleural fields than in *M. (P.) planilimbata*; the border is narrower with a stronger downward tilt. No variation is found in the cephalon.

Affinities. – *M. (P.) planilimbata* subsp. A shows some similarities to the specimens of *Megistaspis* cf. *knyrkoi* (Schmidt, 1906) described by Nielsen (1995, pp. 160–161, fig. 123) from the *Megistaspis (Megistaspis) polyphemus* Zone of Bornholm, especially in the ridge along the axis (Nielsen 1995, fig. 123B) and the wide pleural fields. The pygidium of *M.(P.) planilimbata* subsp. A also bears some similarity to that of *Basiliella carinata* Harrington, 1938 from Argentina (Harrington & Leanza 1957, fig. 62; 1, (2?), 3, 5, 7, 9) but differs in that the pleural fields are wider in the Norwegian material. The cranidia figured by Harrington & Leanza (1957, p. 144, fig. 61; 1–8) are also rather similar to *M. (P.) planilimbata* except for the prominent mid-line ridge on the preglabellar field and the upturned anterior margin. Harrington & Leanza (1957, p. 145) assigned the Argentinian species to *Basiliella* Kobayashi, 1934 without explanation. After comparing photographs of the material from Argentina with those in Kobayashi (1934, pls. 35–37), the only character present in the Argentinian material consistent with the genus *Basiliella* is the median ridge on the preglabellar field. Otherwise, the species of *Basiliella* figured by Kobayashi are rather *Asaphus*-like, both in their shorter preglabellar fields (usually lacking the ridge), and in the pear-shaped glabella. The median ridge is seen only on one of the specimens figured by Kobayashi (1934; *Basiliella minima*; pl. 37, fig. 7). Such a median ridge is also found on the cranidium of *Hunnebergia retusa* Tjernvik (1956, pl. 10, fig. 5). Pygidia figured by Harrington & Leanza (1957, fig. 62; 4, 8) are like that of *H. retusa* (Tjernvik 1956, pl. 10, fig. 6), and have relatively small pleural fields and a very wide doublure.

Occurrence. – Beds 1–3 (4?) at Skarahaugen and Vestfossen railway station, unknown level in the Hagastrand Member at Krekling and Øvre Øren.

Megistaspis (Paramegistaspis) subsp. B
Fig. 7K

Material. – Four pygidia.

Remarks. – A few pygidia found at Øvre Øren and Krekling are more convex than the specimens of *M. (P.) planilimbata* figured by Tjernvik (1956, pl. 6, figs. 6, 7), and have a narrower axis, occupying only about 0.14 of the total pygidial width at anterior end, narrowing only slightly backwards; in lateral view the axis is almost horizontal, exhibiting a distinct downward bend behind the border furrow. The pleural ribs terminate nearer to the lateral margin and the outermost horizontal part of the lateral border is much narrower. Posteromedially, the border is slightly emarginated and bent upwards. The slight median axial ridge is similar to that found in *M. (Ekeraspis) heroides* (Brøgger, 1882) and *M. (P.) planilimbata* subsp. A.

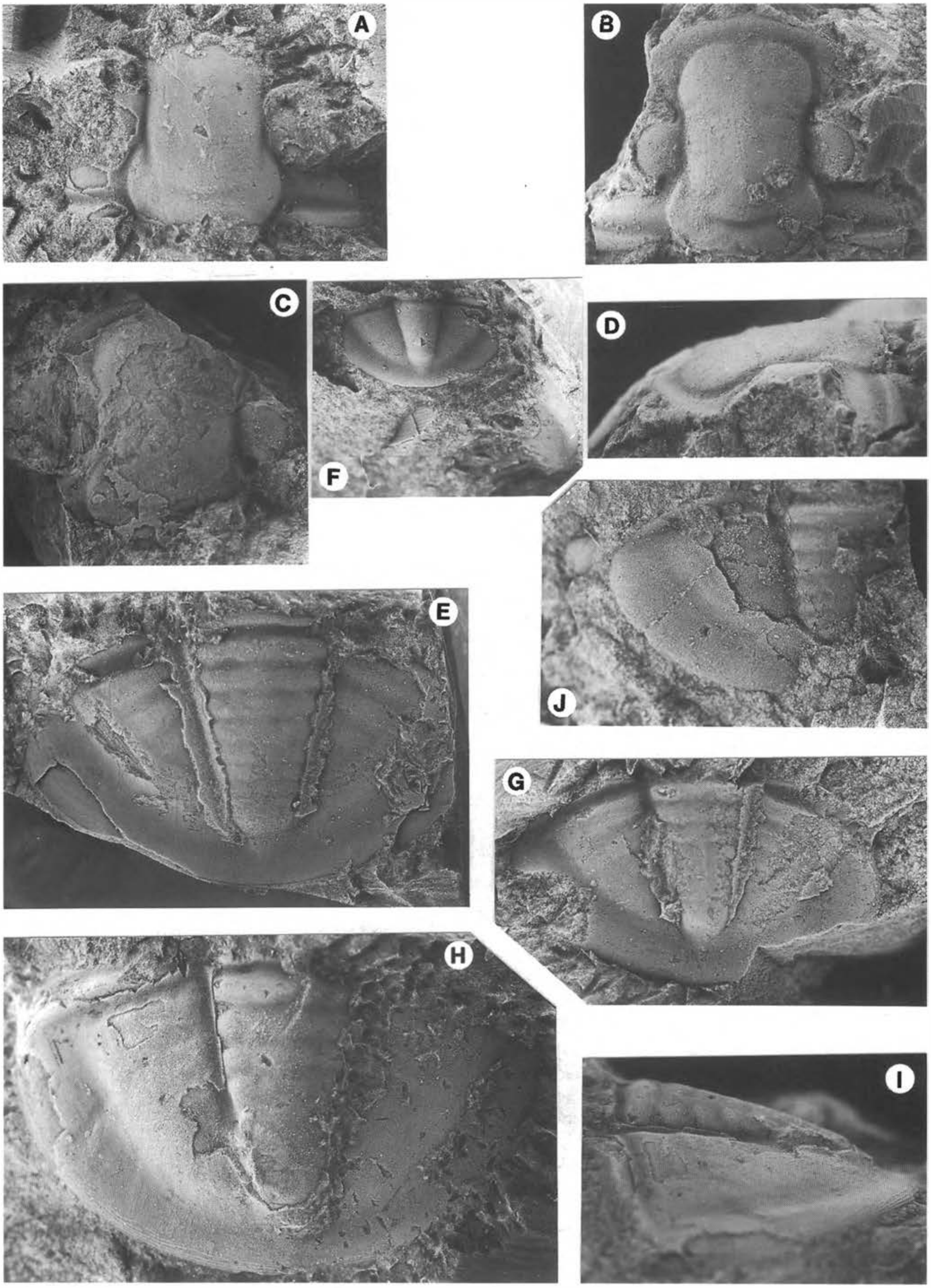
Subfamily Niobinae Jaanusson, 1959

Remarks. – Apart from the nominal genus, the following genera was included in the Niobinae by Jaanusson (*in* Harrington et al. 1959, p. O350); *Norinia* Troedsson, 1937; *Niobina* Lake, 1946; *Bohemopyge* Pribyl, 1950; *Lapidaria* Tjernvik, 1956 and *Yuepingia* Lu, 1956. A later addition was *Gog* Fortey, 1975. *Pogrebovites* Balashova, 1976 (type species *'Niobe' volborthi* Schmidt, 1907) was erected to accommodate a group of species already included in *Ottenbyaspis* Bruton, 1968, but according to Nielsen (1995, p. 326), *Pogrebovites* is probably a subjective synonym of *Panderia* Volborth, 1863, and thus belongs to the Panderiidae Bruton, 1968.

Genus *Niobe* Angelin, 1851

Type species. – *Asaphus frontalis* Dalman, 1827 (subsequently designated by Vogdes 1890) from the *Megistaspis (Megistaspidella) gigas* Zone (Lower Llanvirn) of Ljung, Östergötland, Sweden (See Bohlin 1955, p. 143).

Remarks. – Nielsen (1995, p. 165) only assigned 2 of 36 non-Baltic species to *Niobe (Niobe)*, these being *Niobe (Niobe) lignieresi* (Bergeron, 1895) (see Thoral 1935) and *Niobe (Niobe) yangtzeensis* Lu, 1975. *Niobe (Niobe?) chui* Sheng, 1934, *Niobe groenlandica* Poulsen, 1937 and *Niobe*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brevicauda Poulsen, 1937 may also belong to *Niobe (Niobe)*, the remainder belong to *Niobe (Niobella)*, or they are either too fragmentary or to poorly illustrated to be evaluated, especially the Russian and Chinese material. This being so, the morphological range of the illustrated forms is substantial, and a revision of the group is likely to produce new subgenera.

Nielsen (1995, p. 165) also listed 20 Baltoscandian species younger than the Lower Tremadoc, 9 of these belonging to *Niobe (Niobe)* and 11 belonging to *Niobe (Niobella)*. The oldest record is *Niobe (Niobella) aurora* Westergård, 1939 from the Upper Cambrian *Peltura scarabeoides* Zone of Västergötland. *N. (Niobella)* disappears in the middle of the *Asaphus 'raniceps'* Zone, while *Niobe (Niobe)* extends to the upper part of the uppermost Lower Ordovician *Megistaspis (Megistaspidella) gigas* Zone, just below the first appearance of *Ogygiocaris* (Jan Johansson pers. com.–1996). The extensive geographical range of the genus includes Baltoscandia, Siberia, China (Nielsen 1995), Northern Ural mountains (Burskij 1970), Great Britain (Salter 1866), France (Dean 1966), Bavaria (Barrande 1868), Spitsbergen (Fortey 1975), Greenland (Poulsen 1937), Newfoundland (Whittington 1965) and Nevada (Shaw 1966).

I agree with Nielsen (1995, p. 167) that *Niobe quadraticauda* Billings, 1865 and *Niobe morrisi* Billings, 1865 are not sexual dimorphs as suggested by Whittington (1965, p. 363). The pygidium of the former is unlike any assigned to *N. (Niobe)* or *N. (Niobella)*. The variation seen in Scandinavian species of *Niobe* suggests that their morphology may have been directed by environmental factors.

Stratigraphical range. – Upper Cambrian to Lower Llanvirn.

Subgenus *Niobe (Niobella)* Reed, 1931

Type species (by original designation). – Niobe homfrayi Salter, 1866 from the lower Tremadoc of Wales.

Niobe (Niobella) bohlini Tjernvik, 1956

Fig. 8A–I

1882 *Niobe laeviceps* Dalman; Brøgger, p. 66. (report of find probably from the Hagastrand Member, Krekling).
1905 *Niobe laeviceps* Dalman; Wiman, p. 10
?1905 *Niobe* sp. no. 1; Wiman, p. 10, pl. 2, fig. 14.
1906 *Niobe laeviceps* Dalman (partim); Moberg & Segerberg, p. 96, pl. 6, fig. 19.
1952 *Niobe* sp. aff. *obsoleta* Linnarsson; Tjernvik, p. 57, text-fig. 4A.
1956 *Niobella bohlini* n. sp.; Tjernvik; pp. 231–232, pl. 5, figs. 4–9, text-fig. 37B.

Material. – 10 cranidia, 20 pygidia.

Description. – Cranidium moderately convex, 0.77 as long as wide; preglabellar area rather short (sag.), about 0.07 total cranidial length, its width (measured perpendicular to the anterior margin of the glabella) widening towards the anterolateral corners to about twice the width it has at the median line; glabella moderately convex, long and narrow, length (sag.) 1.33 the width (trans.) at the level of palpebral lobes, emarginated in front, broadly rounded at anterolateral corners, constricted between palpebral lobes, its minimum width being 0.9 that of maximum width. The frontal surface of the glabella has a slight notch at median line, widening anteriorly. Glabella distinguished from preglabellar area only by an abrupt change in slope; three pairs of glabellar furrows visible on internal molds, the first (1P) a wide (trans.) and very short (exsag.) pit located at the mid-point of the palpebral lobes; the second (2P) starts at the frontal margin of the palpebral lobes and is directed adaxially forward at an angle of about 30° to the transverse; the third (3P) is very short (trans.), and starts at the point where the glabella widens and is directed forward-inward at an angle of about 35°; palpebral lobes longer (exsag.) than wide, not elevated above glabella; bacculae are rather large, but low and not well differentiated from the glabella; occipital furrow effaced for most of its length, bent backwards and deep medially; occipital ring narrow (sag.) occupying only 0.13 of total cranidial length; postocular fixed cheeks rather long (trans.) and narrow (exsag.); posterior border furrow wide and deep, transecting the postocular fixed cheeks at the middle of their width (exsag.), making the posterior border about as wide as the rest of the postocular fixed cheeks.

One of the cranidia (not figured) has a wider and more flattened glabella, and the occipital furrow extends out to the bacculae. This specimen is not unlike that of *Niobe morrisi* (Billings, 1865) from the Middle Ordovician Table Head Formation, Western Newfoundland (see Whittington 1965, pl. 28, figs. 1, 3, 4), which also has wider (trans.) fixed cheeks than is usual in *Niobe (Niobe)*. The latter also carries an ornamentation of small pits which is not present in the Norwegian specimens of *N.(Niobella) bohlini*, although this could be caused by most specimens being internal molds.

Free cheeks, hypostomata and parts of the thorax are not found in the Norwegian material.

Pygidium less than twice as wide as long (L/W = 0.6) on the largest specimens, proportionately slightly wider in the

Fig. 8. (A–I): *Niobe (Niobella) bohlini* Tjernvik, 1956. (A) Dorsal view of incomplete cranidium with preserved exoskeleton. ×3.6, PMO 142.102, Bed 3, Klunderud, Krekling; (B, D) Dorsal and lateral view of exfoliated cranidium showing muscle impressions. ×3.8, PMO 20087, Krekling; (C) Dorsal view of incomplete, exfoliated cranidium. ×4 , PMO 20088, Krekling; (E) Dorsal view of largely exfoliated pygidium. ×3.5, PMO 143.350, Bed 4, Skarahaugen, Vestfossen; (F) Dorsal view of small, complete pygidium. ×4, PMO 139.373, Bed 1, Vestfossen railway station; (G) Dorsal view of largely exfoliated pygidium. ×3.5, PMO 138.188, Bed 4, Skarahaugen, Vestfossen; (H–I) Dorsal and lateral view of pygidium retaining the exoskeleton. ×3.3, PMO 143.349, Bed 4, Skarahaugen, Vestfossen; (J) *Niobe (Niobella)* sp. aff. *obsoleta* (Linnarsson, 1869). Dorsal view of small, incomplete pygidium. ×6.5, PMO 139.351, Bed 6 *'o'* , Skarahaugen, Vestfossen.

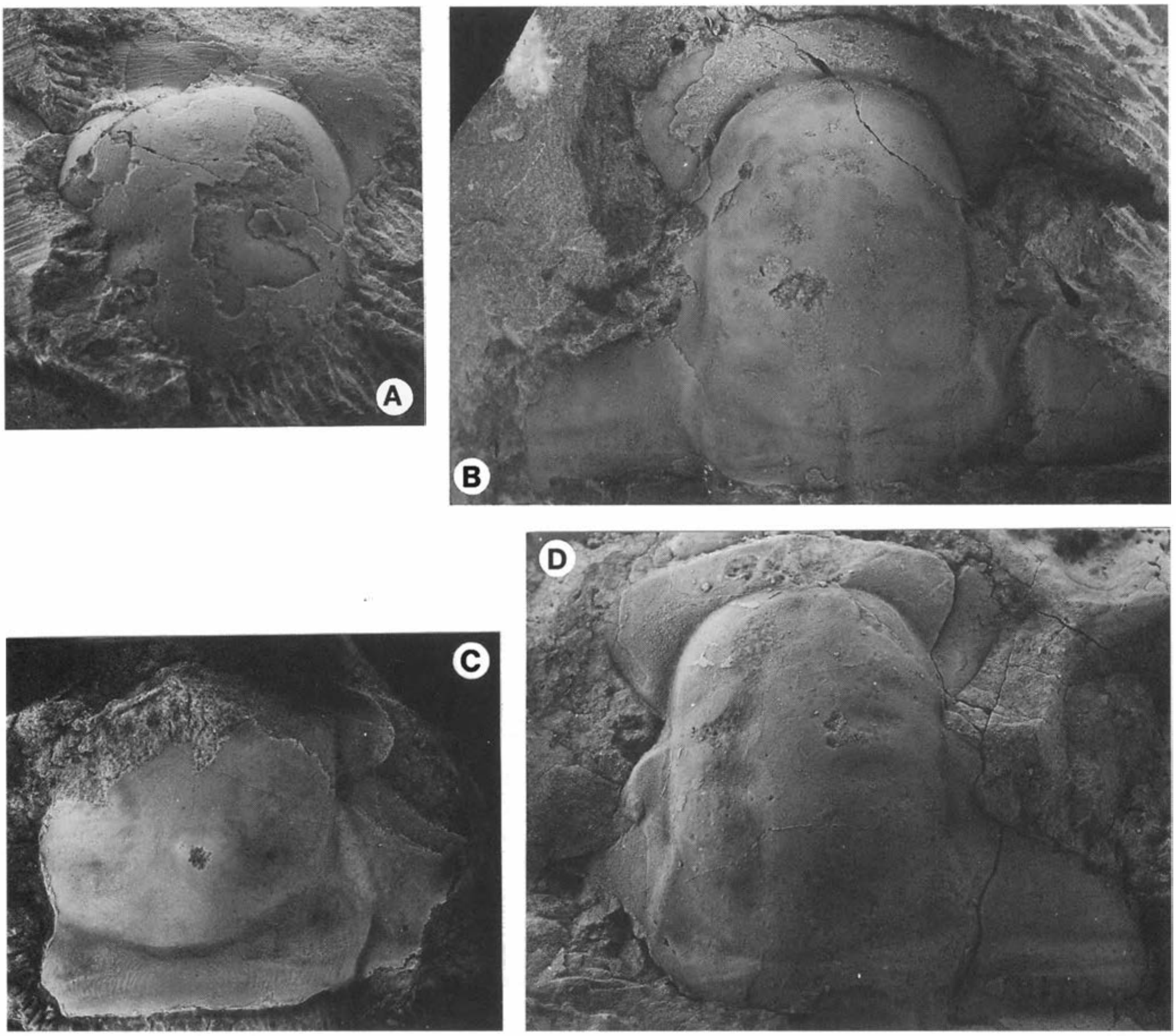


Fig. 9. (A, C) *Niobe (Proxiniobe) longicauda* n.subgen. et sp.: (A) Anterior portion of cranidium. ×1.9, PMO 144.135, uppermost part of the Hagastrand Member, Kårtveitbekken, Krekling; (C) Posterior portion of cranidium. ×2, PMO 138.156, Bed lB *'o'*, Skarahaugen Farm, Vestfossen; (B, D) Swedish cranidia possibly belonging to *Niobe (Proxiniobe) longicauda* n.subgen. et sp.: (B) Dorsal view of large cranidium with weak glabellar furrows, deeper preglabellar furrow and rounded anterolateral corners of the preglabellar area. ×1.9, PMU N 836, 57–61 cm in the profile of Holmstorp, Hagaberg, Närke, Sweden; (D) Dorsal and lateral view of large, exfoliated cranidium, showing deep glabellar furrows, shallow preglabellar furrow and angular anterolateral corners of the preglabellar area. Associated with a pygidium of *Niobe (Proxiniobe) longicauda* n.sp. ×1.8, PMU Vg 479, 26–63 cm in the profile in Tjernvik (1956, p. 123), Stenbrottet, Västergötland, Sweden.

the smaller ones, the widest having L/W = 0.55; width of axis varying between about 0.2 and 0.28 of total width at anterior margin, tapering backward, the axial furrows enclosing an angle of about 15°, with half ring, 7 or 8 axial rings and terminal portion, separated by almost straight or slightly undulating transverse furrows often largely effaced medially, especially on the posterior part of the axis; pleural fields moderately convex, occupying (together with the axis) 0.8 of total width, outer surface smooth, internal mold with four pleural lobes of rectangular section, reaching to paradoublural line, each with faint pleural furrow; border wide (trans.) and only slightly convex, widest anterolaterally, at the level of the second pleura, narrowing posteriorly, its width (sag.) at posterior margin (median line) half that at the widest point; doublure rather wide, its inner margin crossing the pleural fields about halfway between the axis and the inner margin of the border and running into the axis at about the level of the terminal portion.

Remarks. – This is one of the most common species in the *Megistaspis (Paramegistaspis) planilimbata* Zone in both Sweden and Norway. It is distinguished from the older *N. (Niobella) obsoleta* by having a longer, slimmer cranidium with the glabella wider in front and the posterior border of equal width (exsag.). The pygidium has a smaller length/width ratio, a slightly wider axis, shorter pleurae, wider doublure and a border of unequal width. Nielsen (1995, p. 178) reported two specimens of *N. (Niobella)* sp. aff. *lindstroemi* from the *Megistaspis (Megistaspis) polyphemus* Zone at Slemmestad with maximum border width posterolaterally and anterior half-rib raised above pleural fields. Nielsen claims that these traits are distinctive of *N. (Niobella) bohlini*, but in the present material of *N. (Niobella) bohlini* the widest part of the border is situated more anteriorly than the specimens figured by Nielsen, suggesting that the latter are more like *N. (Niobella) lindstroemi*.

Occurrence. – *Megistaspis (Ekeraspis) armata* Zone and *M. (Paramegistaspis) planilimbata* Zone of Sweden, all limestone beds of the lower Hagastrand Member at Krekling and Vestfossen.

Niobe (Niobella) sp. aff. *obsoleta* (Linnarsson, 1869)
Fig. 9J

1956 *Niobella* sp. aff. *obsoleta* no. 2; Tjernvik, p. 231, pl. 5, fig. 3.

Material. – One incomplete pygidium.

Description. – This single pygidium is only about 0.5 cm long, has a L/W ratio of 0.4 (as opposed to 0.55–0.6 in *N. (N.) bohlini*); the pleural fields are proportionately narrow (trans.), occupying together with the axis 0.77 of total width, bearing only three or four pleural furrows; the axis is short, with five transverse furrows; border is comparatively wide (trans.), when compared with small specimens of *N. (N.) bohlini* (see Fig. 8F).

Remarks. – In Sweden, *Niobella* sp. aff. *obsoleta* occurs in the Transition Beds (*Megistaspis (Paramegistaspis)* aff. *estonica* Zone), lower part of the Billingen Substage (see Nielsen 1995, p. 165), and its occurrence in the uppermost bed (6 *o*) at Skarahaugen may indicate that the upper limestone beds of the lower Hagastrand Member may belong to this Zone, and suggests that the depostion of black shale started slightly later at Vestfossen than at Krekling. At Krekling, the lowest shale beds in the overlying Galgeberg Member contain *Tetragraptus phyllograptoides*, and thus belong to the *M. (P.) planilimbata* Zone (Upper Hunneberg Substage).

Subgenus *Niobe (Proxiniobe)* n. subgen.

Type species: *Niobe (Proxiniobe) flabellifera* Fortey, 1975.

Name. – From Latin *Proximus* (nearby), referring to the taxonomical position near to both *Niobe (Niobe)* and *Niobe (Niobella)*.

Occurrence. – Lower Ordovician (Uppermost Tremadoc (?) -Upper Arenig (*Phyllograptus typus* Zone and *Phyllograptus anna* Zone)): Scandinavia, Spitsbergen, Kazakhstan.

Diagnosis. – Large, flattened niobinid cranidium with relatively wide postocular fixed cheeks. Pygidial doublure broad; axis tapering rapidly anteriorly, posteriorly being almost even-sided, making it look more or less like one half of an hour-glass, with undulating, transverse furrows in some species effaced medially; 5–7 pairs of pygidial pleural furrows, the first much longer than the others, reaching well beyond the paradoublural line; pygidial pleural lobes broad and flat in cross-section, reaching beyond the paradoublural line and merging smoothly into the border; border broad and concave, usually as wide as the pleural fields, and set off from these without a distinct change in slope.

Species included. – *Niobe (Proxiniobe) flabellifera* Fortey, 1975; *N. (P.) occulta* Fortey, 1975, both from the *Didumograptus gibberulus* Zone (Upper Arenig) of Spitsbergen; *N. (P.) ornata* (Reed 1945) (see Fortey 1975, pl. 6, fig. 3) from the same level in Ireland; *N. (P.) longicauda* n. sp. from the lowermost Arenig of Sweden and Norway and possibly *N. (P.) fourneti* Thoral, 1946 from the Llanvirn (?) of Montaigne Noir, France. In addition, the pygidium figured as *Niobe brevicauda* (?) n. sp. (Poulsen 1937, pl. 7, fig. 13) from the Lower Ordovician of Greenland, may belong to this subgenus. It does not seem to be conspecific with *Niobe brevicauda* (Poulsen 1937, pl. 7, figs. 9,10). Both *Niobe groenlandica* Poulsen, 1937 and *Niobe brevicauda* (Poulsen 1937, pl. 7, fig. 11) may belong to *Niobe (Niobe)*, but also could belong to *Bathyurellus*.

Discussion. – Fortey (1975, p. 30) noted that *Niobe occulta* Fortey, 1975 and *Niobe flabellifera* Fortey, 1975 are closely related, but ruled out the possibility that they are sexual dimorphs for stratigraphical reasons. They are distinguished from the more typical *Niobe (Niobe)* species from the Late Tremadoc-Llanvirn of Scandinavia such as *N. (N.) insignis* Linnarsson, 1869, *N. (N.) incerta* Tjernvik, 1956, *N. (N.) emarginula* Angelin, 1851 and *N. (N.) frontalis* (Dalman, 1827) by the short pleural furrows, ill-defined, very broad, flattened pygidial border and the extensive sculpture of fine, anastomizing lines on the whole test. The pleural lobes of *N. (P.) longicauda* n. sp. show some similarities to *N. (Niobella)* in that they are broad and flat, with a hint of a rib furrow, and reaching to or slightly beyond the inner edge of the doublure before blending imperceptibly into the border. The overall shape of the pygidium of *N. (P.) longicauda* is not typical for *Niobella,* however, the length/width ratio being about 3/4, while in *N. (Niobella) obsoleta* this is 2/3, in *N. (Niobella) bohlini* 3/5, and later species become more than twice as wide as long. In *N. (Niobe) incerta*, on the other hand, the length/width ratio is about 3/4, which in this respect makes *N. (P.) longicauda* close to *N. (Niobe)*. The pygidium of *Niobe morrisi* (see Whittington 1965, pl. 27, figs. 10–13) is similar to *N. (P.) longicauda* n. sp. in having a relatively long axis and similar pleural lobes, but the very narrow posterior border and the transverse axial furrows, deepest at the median line, make it more similar to *Niobe (Niobella)*. According to Nielsen (1995), such a reduced border can be controlled by environmental factors and may not be of taxonomic importance. If this is the situation, it follows his conclusions that the intensive ornament of terrace lines and the narrow posterior border indicate deeper water. This is also in accordance with the transgressive nature of the middle Table Head Formation, containing *Niobe morrisi*. *Niobe fourneti* Thoral, 1946 is somewhat intermediate between *N. (Niobe)* and *N. (Proxiniobe)* in having a rather wide axis as in *N. (Niobe)*, but pleural lobes with distal lateral ends blending into the border, as in *N. (Proxiniobe)*. *Niobe ornata* (Reed, 1945) may be a senior synonym to one of the species from Spitsbergen, each occurring together with the pelagic trilobites *Opipeuter inconnivus* and *Oopsites hibernicus* (see Fortey 1975, p. 31). *Niobe tenuistriata* Chugaeva, 1958 has a wide cranidium similar to that of *N. (P.) flabellifera*. The proportionately long pygidium with a poorly defined border is also reminiscent of *Niobe (Proxiniobe)*. The pleural furrows are longer and deeper, reaching past the paradoublural line. Nielsen (1995) assigns *Niobe tenuistriata* to *Gog* Fortey, 1975. It is reminiscent of *G. explanatus* (Angelin) except for the shorter pleural furrows, but is probably more closely related to *G. vogti* (Strand 1949) (see discussion of *Gog* below).

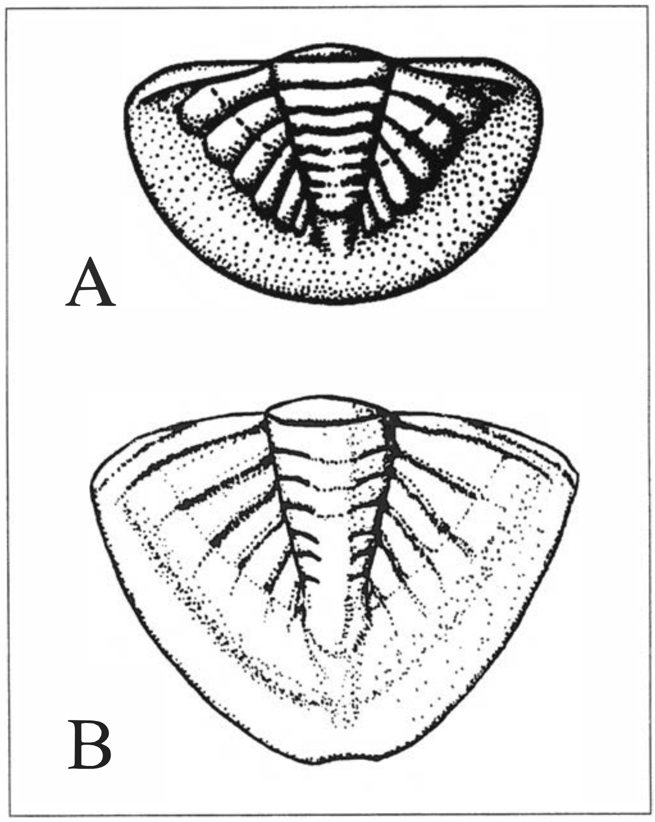


Fig. 10. Comparison between the pygidia of A: *Niobe (Niobe) emarginula* Angelin, 1851 and B: *Niobe (Proxiniobe) longicauda* n. sp.

***Niobe (Proxiniobe) longicauda* n. sp.**
Figs. 9,10, 11A–D, H

1905 *Niobe* sp. N:o. 2; Wiman p. 10, pl. 2, fig. 12.

Holotype. – Pygidium PMO 139.371-PMO 139.372 (Part and counterpart) from bed 3–4 (Hagastrand Member) at Skarahaugen, Vestfossen. Fig. 12B–C herein.

Name. – From Latin: *longus* (long) and *cauda* (tail of an animal), referring to the anomalously large length/width ratio of the pygidium.

Norwegian material. – Two incomplete cranidia; four additional pygidia; one possible hypostoma and two incomplete thoracic segments.

Swedish material. – Two cranidia and 12 pygidia from Tjernvik's collection in the Paleontological Institution of Uppsala, and from the private collection of M. Høyberget have been studied. (Specimens of *Niobe (Niobe) emarginula* Angelin, 1851 are also figured for comparison).

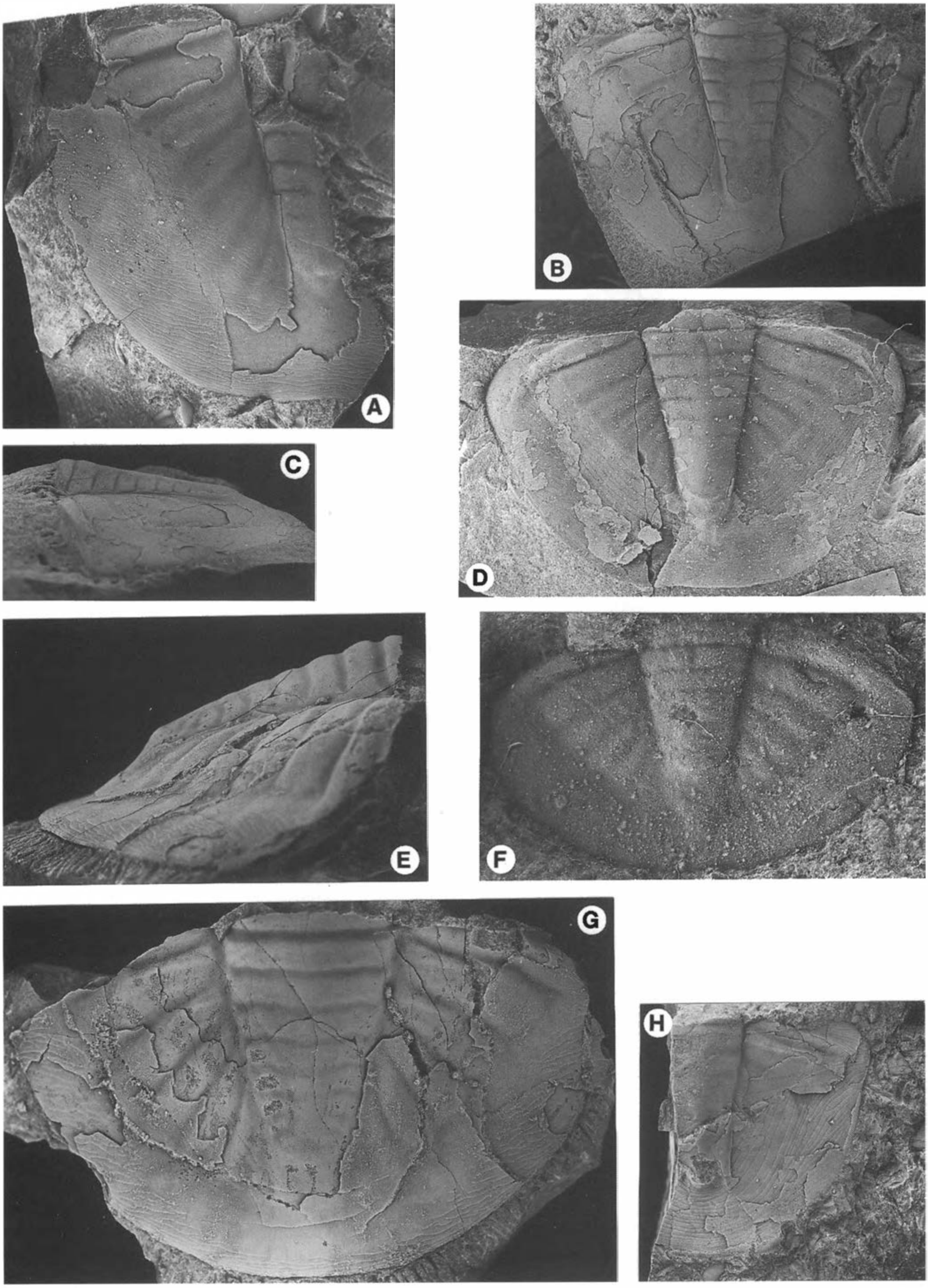
Diagnosis. – A species of *Niobe (Proxiniobe)* having a long pygidium with five or six square pleural lobes blending smoothly into border. Axis with eight transverse furrows bent inwards and backwards, of which the six posterior ones are obliterated medially. Posteriormost part of margin straight.

Description. – Cranidium probably identical or very similar to that figured by Tjernvik (1956, pl. 4, fig. 14) as the lectotype of *Niobe (Niobe) emarginula* Angelin, 1854.

Fragmentary material suggests that the free cheeks are very wide (trans.).

Hypostoma very like that of *N. (N.) emarginula*; frontal margin broadly rounded; frontal area very short (sag.); median body rather flat; frontal lobe pear-shaped, occupying 9/10 of the length of median body, posterior end very constricted, with a median tubercle or short keel at the transition to the posterior lobe; posterior lobe a small transverse bar with maculae at lateral ends; separated from lateral border by two deep pit-like furrows; lateral border present only outside the posterior half of median body; lateral margin swinging slightly inwards and upwards

Fig. 11. (A–D) *Niobe (Proxiniobe) longicauda* n. sp.: (A) Dorsal view of pygidium, long form with six pairs of pleural furrows, prominent terrace lines and emarginated posterior margin. ×2, PMO 139.365, Bed 1C *'u'*, Skarahaugen; (B–C) Holotype. Dorsal and lateral view of pygidium, showing shape of rachis, five pairs of pleural furrows and terrace lines. ×2, PMO 139.371, Bed 3, Skarahaugen, Vestfossen; (D) Dorsal view of small, slightly flattened pygidium. ×3.5, RM Ar 12424. 'Shumardia Shale' (*M. (P.) planilimbata* Zone), Lanna, Närke, Sweden. Original of Wiman (1905, pl. 2, fig. 12); (E–G) *Niobe (Niobe) emarginula* Angelin, 1851 (for comparison): (E, G) Lateral and dorsal view of large pygidium. ×1.7, PMU Vg 607, Stenbrottet, Västergötland, Sweden. Original of Tjernvik (1956, pl 4, fig. 16); (F) Dorsal view of small pygidium. ×9.5, RM Ar 12425. 'Shumardia Shale' (*M. (P.) planilimbata* Zone), Lanna, Närke, Sweden. Original of Wiman (1905, pl. 2, fig. 14); (H) *Niobe (Proxiniobe)* sp.: Dorsal view of partial pygidium. ×2, PMO 143.181, Lower part of the Bjørkåsholmen Formation, Prestenga bus-stop, Slemmestad.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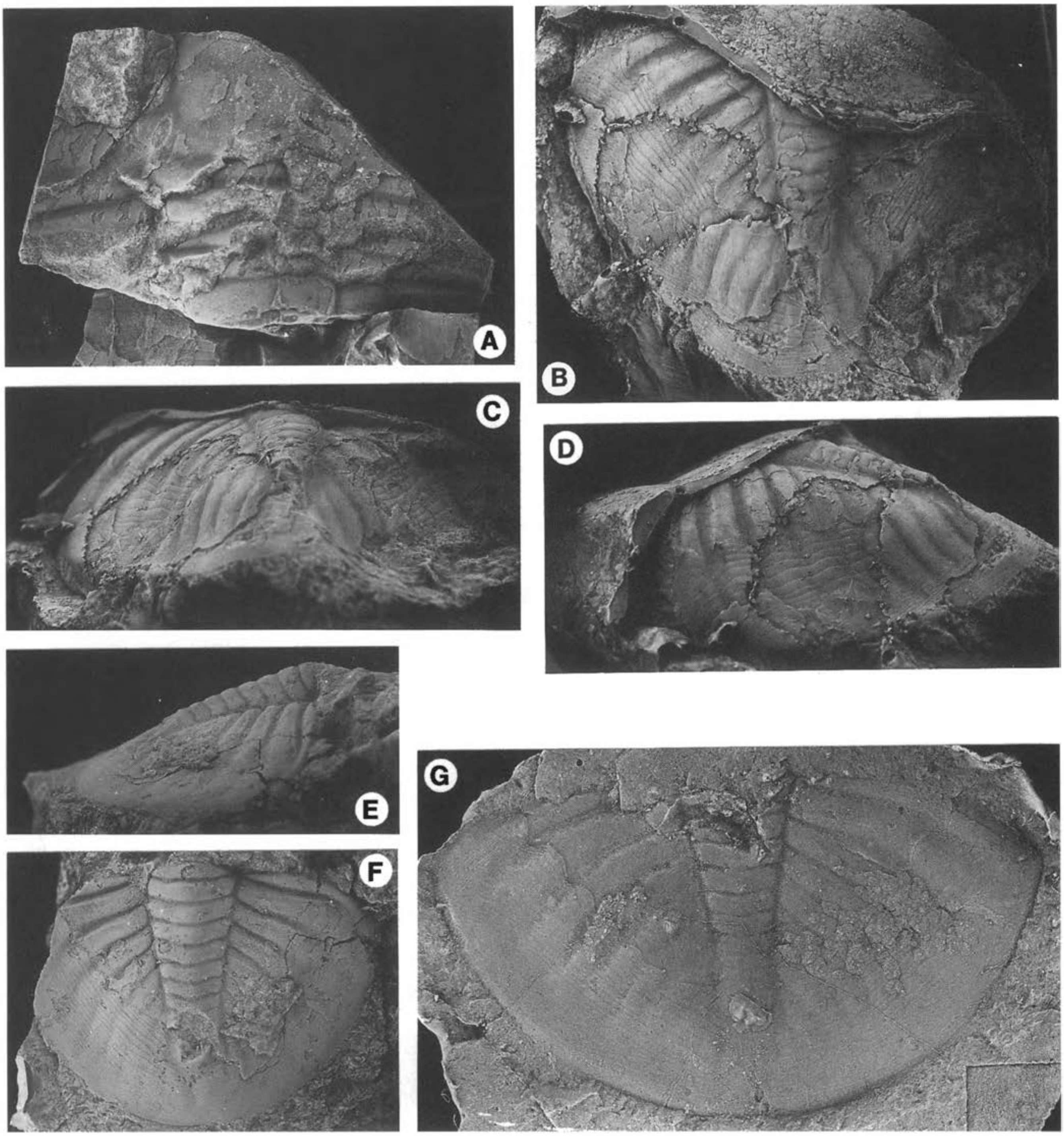

Fig. 12. Gog n. sp.: (A) Dorsal view of incomplete cranidium showing bacculae of glabella and left fixed cheek, with three attached thoracic segments. ×1.8, PMO 142.303, Hagastrand Member, Øvre Øren, Vikersund; (B–D) Dorsal, posterior and lateral views of latex cast of slightly distorted, incomplete pygidium. ×2, PMO 139.378, Beds 3–4, Skarahaugen, Vestfossen; (E–F) Lateral and dorsal views of well-preserved pygidium. ×1.8, PMU Vg 347, 56–68 cm in profile in Tjernvik (1956, p. 123) (*M. (E.) armata* Zone), Stenbrottet, Västergötland, Sweden; (G) Dorsal view of small pygidium. ×3.6, RM Ar 13174. 'Shumardia Shale' (*M. (P.) planilimbata* Zone), Lanna, Närke, Sweden. Original of Wiman (1905, pl. 2, fig. 13.)

anteriorly, widening posteriorly into rounded posterolateral angles; posterior margin probably notched at median line; terrace lines on the whole surface.

Thoracic segments rounded distally, displaying fine anastomizing lines parallel to the axis.

Pygidium much longer than usual in *Niobe*; in the holotype the length is about 2/3 the width, in some specimens it is about 3/4; Axis wide in front, its width at anterior margin slightly less than 1/4 of the total width, its length about 3/4 total pygidial length, anterior part (3/4 the length) tapering rapidly backward, last 1/4 almost not tapering; with 7 or 8 transverse furrows (7 or 8 rings and terminal portion), all but the two anteriormost effaced at the median line, bending adaxially rearwards, the effaced part of the axis becoming wider (trans.) posteriorly; pleural fields with 5 or 6 pleural furrows, reaching slightly beyond paradoublural line, pleural lobes wide (sag.) and flat with a hint of a rib furrow, adaxially bent backwards, towards the middle of the pleural field bending slightly forwards, then again turning backwards before distally merging smoothly into the border about halfway between the axis and the lateral margin; lateral border wide, flat and slightly concave, of about the same width both laterally and posteriorly; doublure wide, occupying at least 2/3 of the area between the axis and the lateral margin; posterior margin probably emarginated, making the outline not unlike that of *Hunnebergia retusa* Tjernvik, 1956.

Discussion. – The pygidium of *N. (P.) longicauda* n. sp. is distinguished from *N. (N.) emarginula* Angelin, 1854 by the larger length/width ratio, the narrower axis with discontinuous transverse furrows, the lower pleural lobes without distinct lateral terminations and the much wider border, especially posterior to the axis (see Fig. 10). Wiman (1905, p. 10) described *'Niobe* sp. N:o 2' from Lanna in Närke as being ['very long for a *Niobe* species. It is emarginated at the posterior end. The axis is short, indistinctly furrowed. The pleural fields sport five very low pleurae.'(transl.)]. I regard this material to be conspecific with *N. (P.) longicauda* n. sp. (Wiman's original is here figured as 11D.

Some variation seems to be present in this species; one pygidium (Fig. 11A) from the lowest part of the Hagastrand Member at Skarahaugen, has the same length/width ratio as the holotype, but differs in having six pleural lobes instead of five as on the holotype. The sculpture of fine lines also seems to be more extensive and distinct.

I have failed to identify specimens of *Niobe (Niobe)* in the Tøyen Formation of Norway. *N. (N.) insignis* is very common in the underlying Bjørkåsholmen Formation (Ebbestad 1993), and *N. (N.) schmidti* Balashova, 1976 occurs sparsely in the overlying Huk Formation (*Asaphus expansus* Zone, Nielsen 1995, p. 173). *N. (N.) emarginula* is also found in beds coeval to the Tøyen Formation in Sweden, where *N. (Niobe)* and *N. (Proxiniobe)* occur together in Närke and Västergötland. Examination of the material in Tjernvik's collection in Uppsala showed that more than 60% of the pygidia assigned to *Niobe (Niobe) emarginula* can now be assigned to *Niobe (Proxiniobe) longicauda* n. sp. Pygidia of *N. (Niobe) emarginula* (*sensu* Tjernvik 1956) have not yet been found in Norway, but the cranidia available closely resemble the lectotype cranidium (Tjernvik 1956, pl. 4, fig. 14). This perhaps suggests that the cranidia belonging to the two different pygidia may be very similar, or alternatively that the pygidium assigned by Tjernvik to *N. (N.) emarginula* may not belong to the lectotype cranidium of *N. (N.) emarginula*, while the pygidium called *N. (P.) longicauda* herein does. This problem can only be resolved by finding complete specimens. The presence of two such similar trilobites in Sweden suggests that they could be dimorphs, but since only one type is present in Norway this is less probable. In addition, the two forms are not known to occur in association on the same bedding plane, and this makes it possible that the morphological differences between the two species (wide border and flattened exoskeleton of *N. (P.) longicauda*, shorter, more vaulted pygidia with stronger pleural ribs in *N. (N.) emarginula* (*sensu* Tjernvik 1956) are adaptations to different bottom conditions; pygidia of *N. (Niobe) emarginula* are found mostly in the eastern (more shallow water) parts of Sweden (Östergötland and Öland), while pygidia of *N. (Proxiniobe) longicauda* n. sp. are collected mainly from the deeper-water areas of Dalarna, Uppland and Jämtland. Nielsen (1995, p. 69) suggested that *N. (Niobella)* also preferred deeper water.

A species similar to *N. (P.) longicauda* occurs in the lower part of the Bjørkåsholmen Formation (*Apatokephalus serratus* Zone) in Asker (Fig. 11H). Ebbestad (1993, fig. 11I, L) identified such specimens as *N. (Niobella) obsoleta.* Ebbestad (1993, fig. 11L) also figured a pygidium similar to those figured by von Post (1906, figs. 1, 2) from Orreholmen in Fallbygden, Sweden and later assigned by Tjernvik (1956, p. 230) to *Niobella* sp. aff. *obsoleta* no. 1. These pygidia are probably more closely related to *N. (Proxiniobe).*

The pygidium of *Ogygites almatyensis* (Chugaeva 1958, pl. 4, fig. 4) from the Middle Ordovician of Kazakhstan resembles that of *N. (P.) longicauda* in the overall form, and shape and number of the pleurae (5–6), but differs in having a longer axis with more axial furrows.

Dimensions. – The largest specimen (PMO 139.977, an incomplete pygidium) has a width of at least 8–9 cm (which gives a pygidial length of over 6.5 cm and a total body length of nearly 20 cm.). Large size is a trait shared with the species of *Niobe (Niobe).*

Occurrence. – Bjørkåsholmen Formation, Norway. Hagastrand Member (except the lowest and highest beds); *Norway*: Krekling, Vestfossen, Øvre Øren, Slemmestad, Vekkerø, Tøyen. *Sweden*: Närke, Västergötland, Dalarne, Uppland, Jämtland.

Genus *Gog* Fortey, 1975

Type species. – By original designation: *Gog catillus* Fortey, 1975 from the middle part of the Olenidsletta Member, Valhallfonna Formation (Upper Arenig) of Spitsbergen.

Discussion. – This genus is peculiar in that it contains characters of both *Niobe* and *Ogygiocaris.* Fortey (1975) suggests that the ogygiocaridids derived from a *Gog*-like ancestor. Specimens of *Gog* usually constitute a rather small part of the total fauna. I have certain knowledge of only one specimen from the *Megistaspis (Ekeraspis) armata* Zone and one from the *Megistaspis (Paramegistaspis) planilimbata* Zone from Sweden. In Norway only four specimens have been found in the *Megistaspis (Paramegistaspis) planilimbata* Zone. Fortey (1975) included the following species: *Gog explanatus* (Angelin 1851, p. 15, pl. 11, fig. 4; pl. 12, fig. 2) from the *Megi staspis (Megistaspis) limbata* Zone (uppermost Arenig); *Gog catillus* Fortey (1975, p. 23, pls. 1–3, fig. 3) from the *bifidus* Zone (Upper Arenig) of Spitsbergen and possibly north Arctic Urals (Burskij 1970, pl. 14, figs. 6, 9); *Gog* n. sp. from the *Megistaspis (Paramegistaspis) planilimbata* Zone at Andersön, Jemtland, central Sweden (Fortey 1975, pl. 4, fig. 3). I agree with Nielsen (1995, p. 191) that the latter is not conspecific with the pygidium described by Wiman (1905, pl. 2, fig. 13) from Närke. Here, Wiman's specimen is considered to be identical to *Gog* n. sp., as are specimens figured as *Ogygiocaris* sp. N1 and N2 and *Ogygiocaris* aff. *sarsi* (Burskij 1970, pl. 15, figs. 1, 6, fig. 2, *non* pl. 16, fig. 7).

In addition to Scandinavia, *Gog* occurs in Spitsbergen (Fortey 1975, 1980), NW China (Zhou *in* Zhou et al.1982), Northern Ural (Burskij 1970), Central Asia (*Niobe tenuistriata* Chugaeva, 1958) and possibly Alaska (Ross 1965).

Niobe vogti Strand, 1949, from the Arenig–Llanvirn Hølonda Limestone, Trondheim region, (see also Neumann & Bruton 1974, fig. 16F, H) also belongs to *Gog*, and is rather similar to *G.* cf. *catillus* (Nielsen 1995, p. 195, fig. 143) and *G. tenuistriata* (Chugaeva, 1958). These three species form a group distinguished by the pleural furrows being deepest at the point where they reach the border. The pleural furrows are also seemingly slightly undulating in width (exsag.), and die out before they reach the margin. In the typical group of *G. catillus, G. explanatus*, *G.* n. sp. (of Fortey 1975) and *G.* n. sp. (of this publication) the pleural furrows are deepest inside the paradoublural line and shallow towards the margin. This could indicate that *G. tenuistriata*, *G. vogti* and *G.* cf. *catillus* belong to another subgenus than the typical species of *Gog*.

Gog n. sp.

Fig. 12

1905 Pygidium no. 1.: Wiman; p. 10, pl. 2, fig. 13.
1956 *Niobe*? sp.: Tjernvik; p. 173 (recording of find)
1970 *Ogygiocaris*? sp. N 1. & *Ogygiocaris*? sp. N 2 & *Ogygiocaris* aff. *sarsi* (Angelin): Burskij; pp. 123–124, pl. 15, figs. 1, 2, 6, pl. 16, fig. 7.
?1975 *Gog* n. sp.: Fortey; p. 27; pl. 4, fig. 3.

Material. – One fragmentary cranidium, five pygidia. In addition, a pygidium (PMU Vg 347) from the *Megistaspis (Ekeraspis) armata* Zone at Stenbrottet, Västergötland, was used.

Description. – Of the cranidium, only the posterior part is known. It is rather similar to *Gog catillus* Fortey 1975; glabella broad, with at least two pairs of glabellar furrows developed as pits, widening at the posterior end; occipital furrow straight, shallow and narrow (sag.) at the median line, widening towards the fixed cheeks; bacculae well developed, but smaller than in *G. catillus*; occipital ring wide (sag.), being 1/4 the glabellar width (trans.); fixed cheeks wide (sag.), with a well-developed posterior border furrow, outer part not preserved on my material; eyes seemingly rather small but badly preserved.

Width of axis on thoracic segments about 0.36 of total width (measured on the third or fourth segment); well-developed articulating half rings; sagittal length of each segment is 0.14 the total pleural width (trans.); pleurae with narrow and deep pleural furrows which are almost parallel to the anterior margin of the pleura.

Pygidium subtriangular in outline and rather convex in well-preserved material, more semicircular in flattened specimens, proportionately long compared to *G. catillus*, its length being between 0.61 and 0.75 times the width; axis narrow, widening slightly forwards, occupying at anterior margin 0.22 of total width, the axial furrows enclosing an angle of about 15°, bearing about 12 furrows, which are bent backwards medially; pleural fields with 7–8 long pleural furrows (delimiting 8–9 pleural lobes) bent slightly backwards at half length, rather deep and well defined out to the paradoublural line, then becoming progressively more shallow towards the margin, reaching to extremely near the lateral margin before disappearing smoothly; pygidial doublure wide, covering about half of the ventral side at anterior margin, its inner, undulating margin being subparallel to the lateral margin until reaching the posterior end of the axis, with seven terrace lines per 5 mm; the terrace lines are subparallel to the margin, bowing inwards when crossing a pleural lobe, creating the undulating look typical of ogygiocarids; pygidial surface smooth, with thin anastomizing lines at posterior and lateral margins only.

Remarks. – This is a species of *Gog* with a proportionately longer pygidium than the type species, with 8–9 pleural lobes and very narrow pygidial axis. The cranidium has smaller bacculae than the type species.

A pygidium (Fig. 14G) from the *Megistaspis (Paramegistaspis) planilimbata* Zone in Närke, Sweden, described by Wiman (1905, p. 10), as ['almost absolutely flat. The axis is very narrow, showing twelve rings. The pleural field show nine pleurae, which reach long out into the wide, but not very distinctly marked border.' (transl.)], is assigned to *Gog* n. sp. Unfortunately, the pygidium figured by Fortey (1975, pl. 4, fig. 3) from Andersön, Jämtland, disappeared from the collections in Uppsala after the death of Torsten Tjernvik and is no longer available for study. Fortey (1975, p. 27) suggested that the specimen from Jämtland is conspecific with Wiman's specimen from Närke, but Nielsen (1995, p. 191) disagrees, because the latter has a narrower axis (axial width/total width = 0.19) than the specimen from Jämtland (axial width/total width = 0.22). Tjernvik & Johansson (1980, p. 185) state that pygidia are less common in southern Sweden than they are in the north (Jämtland). While studying the collections at the Paleontological Museum in Uppsala, I identified a pygidium of *Gog* n.

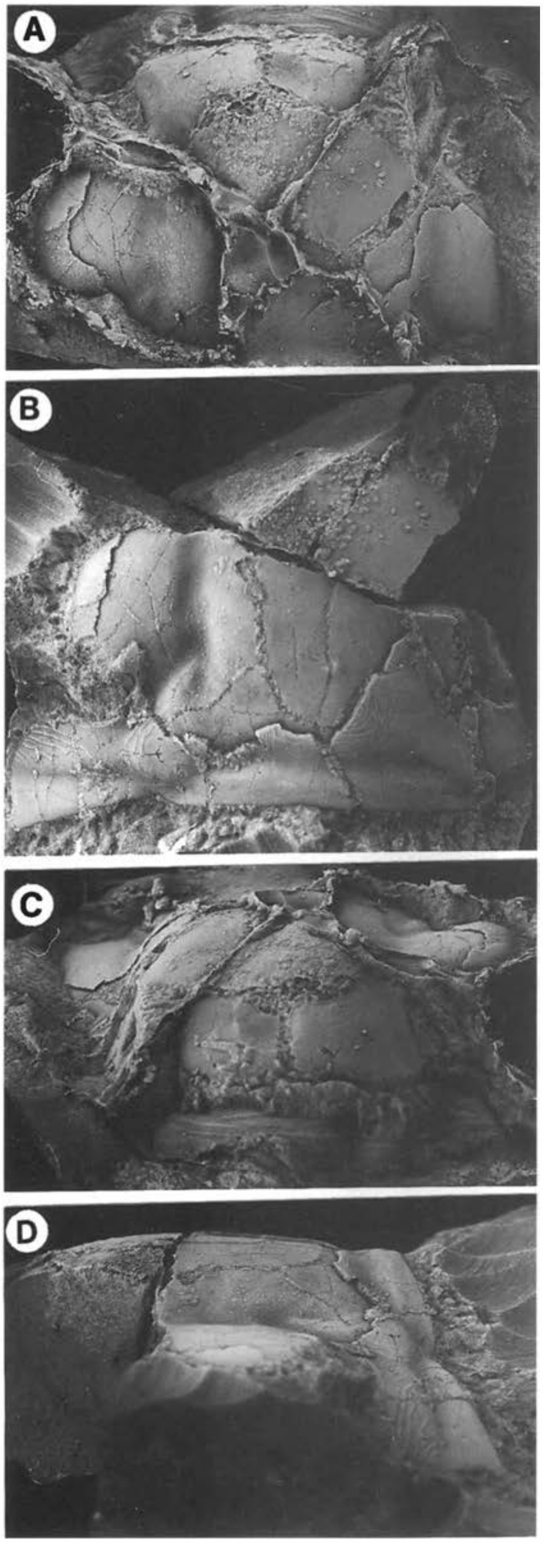

Fig. 13. Lapidaria rugosa Tjernvik, 1956: (A, C) Dorsal and anterior view, latex cast of anterior portion of large cranidium. × 1.9, PMO 143.186 (counterpart of fig. 13B, D); (B, D) Dorsal and lateral view of posterior portion of same cranidium with part of the test intact. × 1.9, PMO 143.185. Bed 4A, Skarahaugen, Vestfossen.

sp. (Fig. 12E–F) from the *Megistaspis (Ekeraspis) armata.* Zone in Västergötland. Nielsen (1995, p. 191) believes that in Scandinavia, *Gog* is confined to the marginal facies of Jämtland, Scania, Bornholm and Norway, but the pygidium from Västergötland contradicts this claim.

Occurrence. – Beds 3–4, *Megistaspis (Paramegistapis) planilimbata* Zone of Skarahaugen, Vestfossen railway station and Øvre Øren; possibly Andersön, Jämtland; *Megistaspis (Ekeraspis) armata* Zone of Stenbrottet, Västergötland.

Genus *Lapidaria* Tjernvik, 1956

Type species. – By original designation *Lapidaria tenella* Tjernvik, 1956, from the *Megistaspis (Ekeraspis) armata* Zone (Uppermost Tremadoc) at Stenbrottet, Västergötland, Sweden.

Remarks. – This genus was erected for *Lapidaria tenella* from the *Megistaspis (Ekeraspis) armata* Zone and *L. rugosa* from the overlying *Megistaspis (Paramegistaspis) planilimbata* Zone of the Hunneberg Substage of Västergötland, Sweden. So far, *Lapidaria* seems to be endemic to Scandinavia, where it ranges up to the lower part of the *Megistaspis (Paramegistaspis) planilimbata* Zone. Neben & Krueger (1971, pl. 2, fig. 11) figured a cranidium of a *Lapidaria* along with other species from the *Megistaspis (Megistaspis) polyphemus* Zone and the *Megistaspis (Megistaspis) simon* Zone, but all their material is from erratics, and cannot be taken as conclusive evidence for a younger distribution. Their small specimen resembles *L. rugosa* except in lacking a prominent preglabellar area (see Tjernvik 1956, p. 223).

Niobella kanauguki Ross, 1965, from the Seward Peninsula, Alaska, may belong to *Lapidaria* because of the large palpebral lobes and the course of the anterior facial suture near the glabella, but the pygidium has a rounded outline like *N. (Niobella).*

Lapidaria rugosa Tjernvik, 1956

Fig. 13

1956 *Lapidaria rugosa* n. sp. Tjernvik; pp. 222–223, pl. 4, figs. 8, 9

Material. – One cranidium (part and counterpart).

Remarks. – The only cranidium shows the specific characters described by Tjernvik (1956): Frontal end of the glabella strongly convex, sagittal length of palpebral lobes 1/3 the total cranidial length and postocular fixed cheeks wide (trans.), about 4/3 the transverse width of the palpebral lobes. It is distinguished from the type species by the large size, the occipital furrow being of equal depth across the median line and the smaller size of the palpebral lobes. The whole cranidium is about 27 mm long, 6 mm less than the holotype, and about 33 mm wide at the palpebral lobes, 5.5 mm less than the holotype.

PMO 143.185–186: Width/length = 1.222

Holotype: PMU N627:Width/length = 1.167

This is a rare species being known from one single specimen in Norway and a total of less than 10 specimens in Sweden.

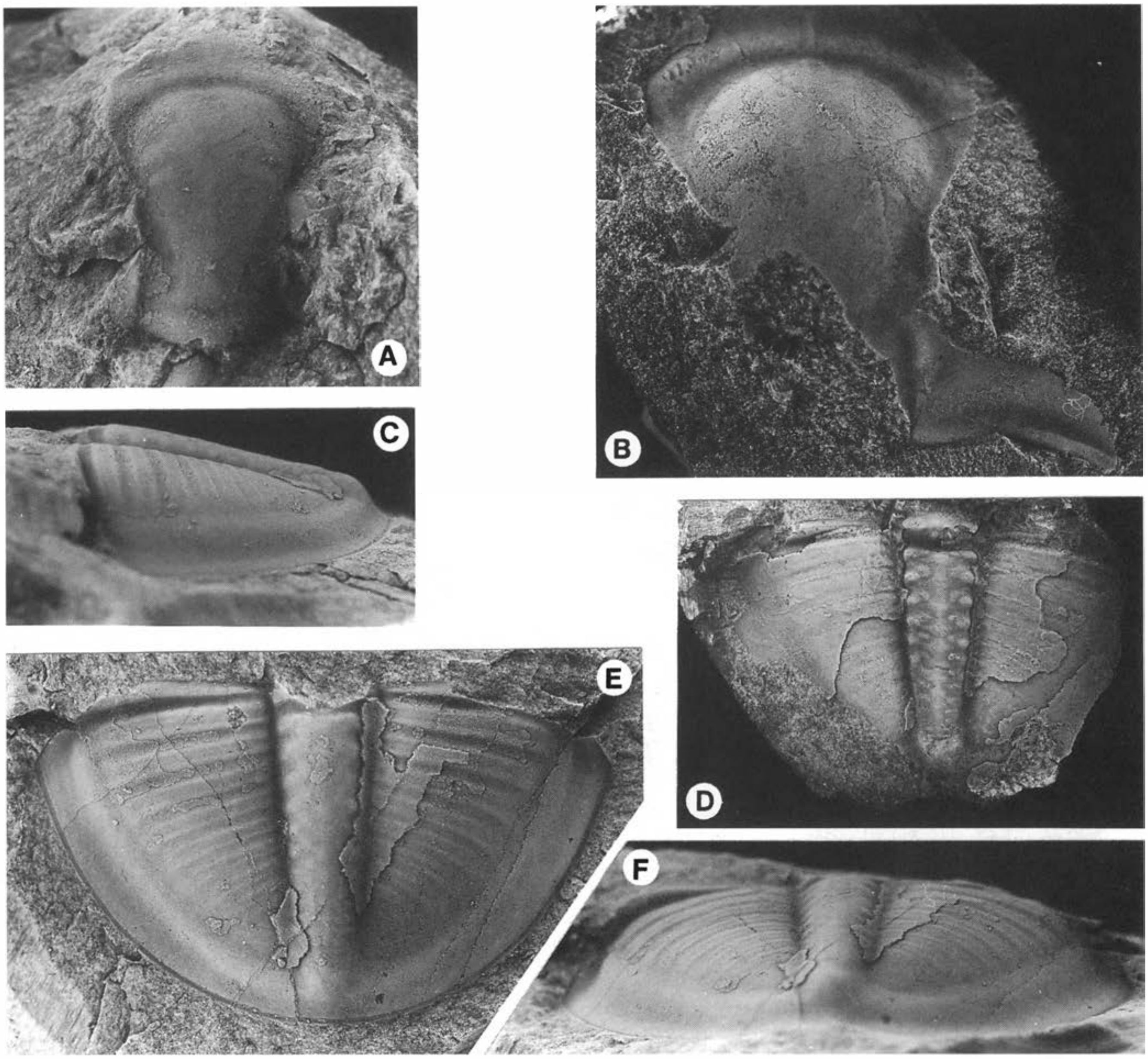

Fig. 14. Promegalaspides (Borogothus) stenorachis (Angelin, 1851): (A) Dorsal view of incomplete cranidium showing the shape of the glabella. × 3.5, PMO 1537, Hagastrand Member, Krekling; (B) Dorsal view of incomplete cranidium showing the right posterior fixed cheek. × 3.3, PMO 138.191, Bed 2 B *'o'*, Skarahaugen, Vestfossen; (C, E–F) Lateral, dorsal and posterior views of well-preserved pygidium. × 3.3, PMO 143.585, 100 cm above base of the Hagastrand Member, Krekling Farm; (D) Dorsal view of partially exfoliated pygidium showing the rachial ornamentation and rather smooth pleural fields. × 2, PMO 139.982, bed 4, Vestfossen railway station.

Subfamily Promegalaspidinae Jaanusson, 1959
Genus *Promegalaspides* Westergård, 1939

Type species. – Promegalaspides kinnekullensis Westergård, 1939 from the Upper Cambrian *Peltura scarabaeoides* Zone at Kinnekulle, Västergötland, Sweden.

Remarks. – This genus was erected for the type species from the Upper Cambrian of Kinnekulle, Västergötland. Later Tjernvik (1956) erected *Promegalaspides (Promegalaspides)* containing the type and a second species, *P. pelturae* Westergård, 1939, from the Upper Cambrian of Sweden, and *Promegalaspides (Borogothus)* for *P. (B.) stenorachis* (Angelin 1851), *P. (B.) intactus* (Moberg & Segerberg 1906) and *P. (B.) goniopleura* (Thoral 1935), all from the Late Tremadoc–early Arenig.

Subgenus *Promegalaspides (Borogothus)* Tjernvik, 1956

Type species. – Megalaspis stenorachis Angelin, 1851 from the *Megistaspis (Paramegistaspis) planilimbata* Zone at Husbyfjöl, Östergötland, Sweden.

Remarks. – Tjernvik erected this subgenus because cranidia are less niobe-like; the suture approaches a more isotelliform pattern, the glabella is more pear-shaped and Ordovician species lack *Niobe*-like basal lobes. Instead, a pair of bulbous bacculae is developed in *P. (B.) intactus* (see Tjernvik 1956, pl. 10, fig. 1) while in *P. (B.) stenorachis* they become more distinctly elongated and separated from the glabella by a furrow, in a manner resembling those in *Gog* Fortey, 1975. The pygidium is very distinctive; the anterior axial (half-) ring is large and well set off from the rest of the axis by a deep furrow, the axis is clearly segmented, but with the transverse furrows developed as pits on either side of the axis.

***Promegalaspides (Borogothus) stenorachis* (Angelin, 1851)**
Fig. 14

1851 *Megalaspis stenorachis* n. sp.; Angelin 1851, p. 17, pl. 16, fig. 1.
1882 *Megalaspis stenorachis* Angelin; Brøgger, p. 76, pl. 4, fig. 7.
?1905 Pygidium N:o 2; Wiman, p. 10, pl. 2, fig. 11.
1906 *Megalaspis stenorachis* Angelin; Moberg & Segerberg, p. 97.
1952 *Megalaspis planilimbata* Angelin [partim] and *Ptychopyge* sp.; Skjeseth, pl. 1, fig. 9, pl. 4, fig. 7.
1956 *Promegalaspides (Borogothus) stenorachis* (Angelin); Tjernvik, p. 253, pl. 9, figs. 6–14, text-fig. 41A.

Non in press *Promegalaspides (Borogothus) stenorachis* (Angelin); Ebbestad, figs. 53B, 54.

Type specimen. – Angelin's type specimen from Husbyfjöl in Östergötland is lost. A neotype needs to be selected but available topotype material is poor.

Material. – Three fragmentary cranidia, 2 free cheeks, 2 hypostomata and 13 more or less complete pygidia.

Emended description. – Preglabellar area delimited from the glabella by a deep preglabellar furrow, usually exhibiting a prominent median ridge from the preglabellar furrow to the anterior margin (fig. 14B); posterior part of glabella bordered by slender bacculae, very small in small specimens, becoming proportionately larger and more distinct in larger specimens, positioned at an angle of about 10° to the mesial line, directed abaxially rearwards. Pygidial length/width = 0.55–0.7; axis narrow, occupying 0.15 of total width at anterior margin, tapering only slightly backwards for 0.9 of the length, then narrowing faster, widening again to make the distinct knob at the posterior end; sometimes the transverse axial furrows are continuous across the axis, in which case a low ridge along the mesial line can be seen, especially in larger specimens; no Norwegian specimens have been found with more than 12 axial furrows behind the first and deep furrow. There is an amount of variation in the species; two kinds of pygidia can be distinguished by the width and depth of the dorsal furrow. This difference is seen in both small and large specimens. Some specimens have pleural fields sloping evenly down from the axis, distinguished from it only by an abrupt change in slope. This is as described by Tjernvik (1956). In other pygidia, the presence of a very deep axial furrow makes the pleural field appear to bulge upwards before sloping down and outward (fig. 14F). The Norwegian specimens seem to have only eight pleural ribs; in some specimens the interpleural and pleural furrows are of equal depth (fig. 14D).

Remarks. – Pygidia from the Bjørkåsholmen Formation figured by Ebbestad (in press, fig. 54) have a smaller number of pleural ribs (6), and are proportionately wider than the specimens from the lower part of the Tøyen Formation (8 ribs). The border is also twice the width of that of *P. (B.) stenorachis* sensu stricto. These older specimens may represent a new species. However, the material is too poor to be certain of this.

A pygidium strongly resembling *P. (B.) stenorachis* was figured as *Ogygiocaris? inflexicostata* n. sp. by Thoral (1946, pl. XV, fig. 2) from the lower Middle Arenig of the Cabrières, Montagne Noire, France, but I have no doubt that it belongs to *Promegalaspides (Borogothus)*. This species has 9 pygidial pleurae and about 12 axial segments with the axial furrows almost obliterated at the mid-line. The first axial ring is separated from the rest of the axis by a deep furrow and stands above the succeeding axial rings. This is a very distinct character of the subgenus. The terminal portion of the axis reaches out onto the narrow border and bears a knob, as in *P. (B.) stenorachis*. Regrettably, no other specimen of this species seems ever to have been illustrated. *Megalaspis goniopleurae* Thoral (1935, pl. 24, figs. 7, 8) from the Upper Tremadoc of Le Mas-Neuf and NE of the St Chinian, Montagne Noire, France is very similar to *Promegalaspides (Borogothus) intactus* (Moberg & Segerberg, 1906). It has five or six pygidial pleurae, the axis is almost devoid of segmentation, except for a well-defined first ring, and bears a knob on the terminal portion. The outer part of the last thoracic segment seems to be bent strongly backwards, and probably bore a long spine as in *P. (B.) stenorachis* (see Tjernvik 1956, pl. 9, fig. 13).

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