

Lower and Middle Cambrian trilobites from the Digermul peninsula, Finnmark, northern Norway

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Ten trilobite species are described. The only Lower Cambrian one is the olenellid *Kjerulfia lata* from the upper member (D2) of the Doulbasgaissa Formation, previously known from southern Norway. The Middle Cambrian species are from the two lower members (K1, K2) of the overlying Kistedal Formation. The trilobites from K1 are described as *Ellipsocephalus cf. hoffii*, *Eccaparadoxides cf. pusillus* and *Hydrocephalus cf. carens* and are compared to Czechoslovakian and Polish species. The trilobites from K2 are *Doryagnostus incertus*, first described from southern Norway, the subspecies *Peronopsis ferox sallesi*, earlier known from France and Spain, *Paradoxides davidis*, earlier known from various countries including southern Scandinavia, a new species, *Nassovia? mjollnir* n.sp., and two incompletely known forms, described below as *Ptychopariinae* gen. et sp. indet. and *Anomocarina?* sp.. Thus, both Middle Cambrian trilobite faunas differ from the very well documented contemporaneous ones in southern Scandinavia, but especially the fauna from K1. A striking difference is also the scarcity of agnostid trilobites.

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Introduction

Upper Cambrian and lower Tremadoc trilobites (all olenids) from the Digermul peninsula were described in an earlier paper (Nikolaissen & Henningsmoen 1985). The present paper on Lower and Middle Cambrian trilobites concludes the description of the hitherto known trilobites from the peninsula.

The Digermul peninsula (Digermulhalvøya) is situated in the Tana area, Finnmark county, northern Norway (Fig. 1). It is 30 km long and separates Langfjord from the inner part of Tanafjord.

An overall presentation of the geology in the Tana area was given by S. Føyn (1937). H.G. Reading (1965) gave a detailed account of the geology of the Digermul peninsula and described the stratigraphy of the Eocambrian (Vendian), Cambrian and Tremadoc rocks exposed.

Fossils were first found on the peninsula in 1934 by Sven Føyn (Føyn 1937) — brachiopods, a hyolithid and a trail of *Cruziana* type, described by Trygve Strand (1935) and assigned to the Middle Cambrian. The first trilobite, a paradoxidid, was collected by Harold G. Reading in 1950 (Reading 1965, p. 168). Upper Cambrian and lower Tremadoc olenid trilobites and lower Tremadoc graptolites were discovered in 1959 by R. Pattinson and J.K. Russell, who with H.G. Reading from Oxford

University carried out fieldwork financed by the Geological Survey of Norway. Further fossils were collected on expeditions from Oxford University in 1961 and 1963 (Reading 1965, pp. 168, 170) and subsequently presented to the Palaeontological Museum, University of Oslo. The present authors made their own collections in 1960 (Henningsmoen 1961) and again in 1963 when they were accompanied by Amanuensis Kari E. Henningsmoen. Fieldwork was financed by the Fridtjof Nansen Fond and associated funds.

In 1980 and later, collections have been made by B.-D. Erdtmann and others from the Georg-August-Universität, Göttingen, western Germany, and the trilobites from these have been presented to the Palaeontological Museum in Oslo.

The present study of the Lower and Middle Cambrian trilobites was initiated by the senior author (G.H.) in 1965, but the work was interrupted until 1984 when the junior author (F.N.) took over the task to complete and extend the description, with some participation by the senior author.

Techniques

Where necessary, specimens have been prepared using a vibro drill or needles. Linear

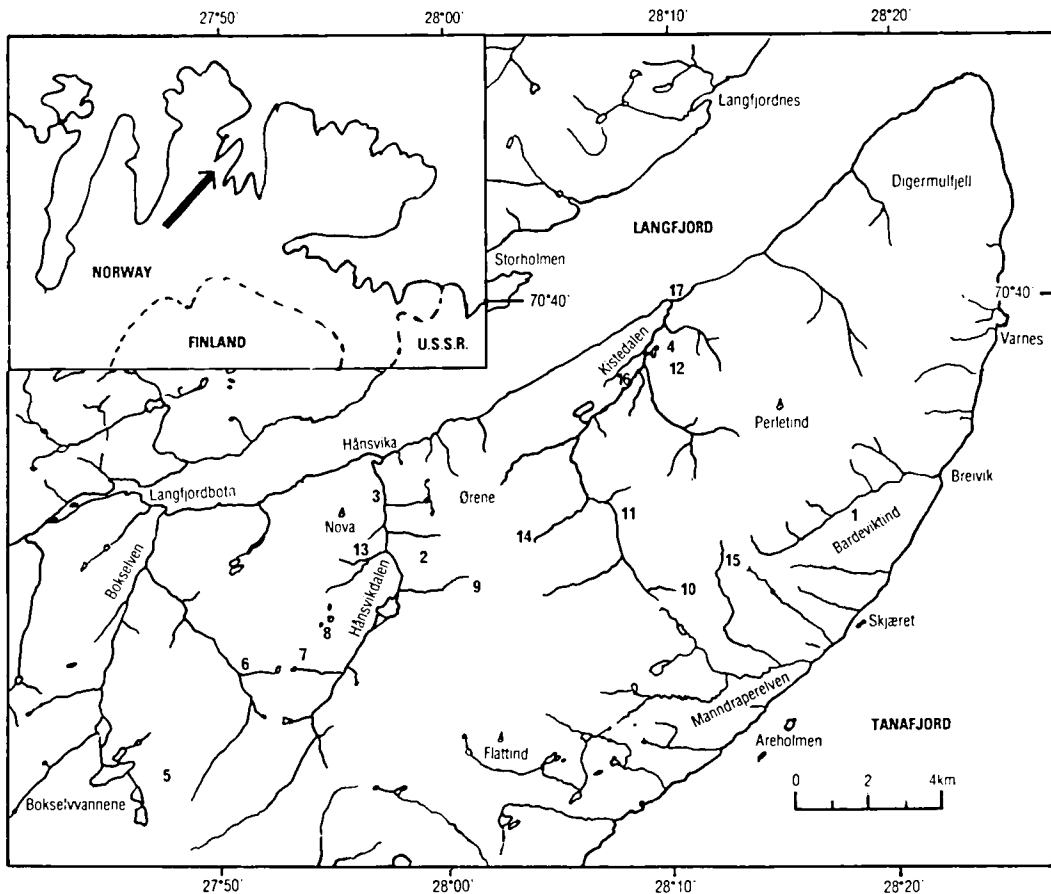


Fig. 1. Sketch map of Digermul peninsula (Digermulhalvøya), Tanafjord, Finnmark, northern Norway, with main sampling sites (1-17) for Lower and Middle Cambrian trilobites. Inset map shows location of the Digermul peninsula (arrow). Concerning geographical names in Finnmark, both Lappish and Norwegian names are official, but only the latter are used here.

1. Lower Cambrian. Greenish-grey micaceous siltstone with flakes of greenish shale interbedded in the middle part of the massive bedded quartzite member (D2) of the Doublasgaissa Formation. Scree at outcrops on the northwestern slope of Bardeviktind.

2-4. Lower Middle Cambrian. Quartzite and shale member (K1) of the Kistedal Formation.

2. Grey or green siltstones interbedded with thin quartzite beds. Eastern slope of Hånsvikdal, 1 km northwest of Nova.

3. Sediments as in locality 2. Section in creek in northern part of Hånsvikdal, about 1 km south of the sea-shore.

4. Alternating bands of grey quartzite and sandstone with greenish-grey shales, approximately 3 m above the top white quartzite of the Doublasgaissa Formation. Southeastern slope of Kistedal, 600 m east of small 'sausage-shaped' pond.

5-17. Middle and upper Middle Cambrian. Quartzite and shale member (K2) of the Kistedal Formation.

5. Thin-bedded sandstone and grey/greenish-grey shale. About 1 km east of the small lakes Bokselvannene.

6. Sediments as in locality 5. Creek section 5 km south-southwest of Nova.

7. Sediments as in locality 5. Loose specimens and specimens collected in various horizons from about 25 m to about 50 m above the quartzite and shale member (K1). Section in a small stream flowing down into Hånsvikdal, 4 km south of Nova.

8. Sediments as in locality 5, horizons as in locality 7. Southeastern hillside about 800 m northeast of locality 7.

9. Sediments as locality 5, horizon as in locality 7. The most southeasterly tributary to Hånsvikdal, 2 km south of Ørene.

10. Sediments as in locality 5, horizons as in locality 7. The most southerly tributary of Kistedal, nearly 6 km south-southwest of the summit of Perletind (Berlogaissa).

11. Sediments as in locality 5, probably horizons as in locality 7. Loose specimens from the hillside 3 km northwest of locality 10.

12. Sediments as in locality 5, horizons as in locality 7. Eastern slope of Kistedal, about 700 m southeast of small 'sausage-shaped' pond.

13. Sediments as in locality 5. Various horizons from about 55 m to about 75 m above the top of the quartzite and shale member (K1). Western slope of Hånsvikdal, 2 km south-southeast of Nova.

14. Sediments as in locality 5, horizons as in locality 13. Southwest of Kistedal, about 4 km southeast of Ørene.

15. Yellowish shale with articulate brachiopods in abundance. Horizon probably as in locality 13. Loose specimens at northern tributary to Manndraperelva, 5 km south-southwest of the summit of Perletind (Berlogaissa).

16. Darker grey, shaly mudstones. Possibly somewhat younger than the horizons in locality 13. Section along the river in Kistedal, 1 km northeast of the largest lake in the valley.

17. Darker micaceous mudstone. Probably high up in the quartzite and shale member. Scree along the eastern shore of Kistedal.

measurements have been made using either a micrometer ocular or vernier calipers. Angles were measured using a protractor and are given to the nearest 5°.

All specimens have been coated with ammonium chloride before photographing. A fluorescent ring-light illuminator and an additional northwest source were utilised for illumination. The photographs are not retouched. The drawings in this and the 1985 paper were made by the junior author.

Systematic descriptions

Terminology

The terminology mainly follows that of Harrington et al. (1959, pp. O117-O126). For brevity the symbols 'L1-L4' are used for the lateral glabellar lobes and 'S1-S4' for the furrows, as suggested by Jaanusson (1956, p. 37; also Henningsmoen 1957, p. 12). Other terms applied are those given by Henningsmoen (1957, pp. 12-14; 1959, pp. 154-157) and Öpik (1967, pp. 52-62), but following the recommendations given by Whittington & Kelly (1983a, pp. 1-29; 1983b, pp. 1-9, Pls. 1-7). However, for the longitudinal furrow dividing the anterior and posterior palpebro-ocular ridges we apply the term 'epipalpebral furrow' introduced by Cowie & McNamara (1978, p. 616; also McNamara 1978, p. 636) in preference to 'ocular furrow' introduced by Szdzy (1978, p. 93) and to 'palpebral ledge' as suggested for a corresponding deep and strong groove in *Lophosauka* by Shergold (1972, p. 15). We also accept the term 'metagenal ridge' extending from the axial furrow to the metagenal spine in olenellids as introduced by Bergström (1973b, Fig. 1; also 1973c, p. 284). Finally, we employ the term 'deltoid area' introduced by Robison (1978, p. 5) for the triangular depression formed by the expansion of the anterior border furrow at its junction with the preglabellar median furrow in agnostids.

Classification

The systematic classification mainly follows that of Harrington et al. (*in* Moore 1959), but with a few modifications according to more recent studies. We thus prefer mainly to follow Öpik's (1967; 1979) classification of agnostids. We fully agree with Bergström (1973a, p. 37) that the olenellids and redlichiids should be grouped in separate orders, thus re-establishing

their assignment to taxa of highest equal rank within the Trilobita.

Order Agnostida Kobayashi, 1935

Suborder Agnostina Salter, 1864

Superfamily Agnostacea M'Coy, 1849

Family Agnostidae M'Coy, 1849

Subfamily Quadragnostinae Howell, 1935(a)

Genus *Peronopsis* Hawle & Corda, 1847

Synonyms. — *Mesospheniscus* Hawle & Corda, 1847 (type species by monotypy: *Battus cuneifer* Barrande, 1846), *Diplorrhina* Hawle & Corda, 1847 (type species by subsequent designation by Snajdr 1958: *D. triplicata* Hawle & Corda, 1847 = subjective junior synonym of *Battus cuneifer* Barrande, 1846), *Mesagnostus* Jaekel, 1909 (type species by original designation: *Battus integer* Beyrich, 1845), *Pseudoperonopsis* Harrington, 1938 (type species by original designation: *Agnostus Sallesi* Bergeron, 1889), ?*Acadagnostus* Kobayashi, 1939a (type species by original designation: *Agnostus acadicus* Dawson, 1868).

Type species. — *Battus integer* Beyrich, 1845.

Peronopsis ferox (Tullberg, 1880) *sallesi* (Bergeron, 1889).

Fig. 6:A-G

- 1888 *Agnostus Sallesi* n. sp. — Munier-Chalmas & Bergeron, p. 376 (nomen nudum).
- 1888 *Agnostus Sallesi* Munier-Chalmas et Bergeron — Bergeron, p. 284 (nomen nudum).
- 1889 *Agnostus Sallesi* Mun.-Chalm. et J. Berg. — Bergeron, pp. 337-338, Pl. 3, fig. 5 (descr. and fig. of dorsal exoskeleton).
- 1935 *Peronopsis sallesi* (Munier-Chalmas and Bergeron) — Howell, pp. 226-227, Pl. 22, figs. 17-18 (descr. and figs. of two dorsal exoskeletons).
- 1935 *Peronopsis Sallesi* Munier-Chalmas et Bergeron — Thorø, pp. 38-39 (remarks).
- 1938 *Pseudoperonopsis sallesi* (M. Chalmas et Bergeron) — Harrington, p. 151 (erects *Pseudoperonopsis* with *A. Sallesi* as type species).
- 1939a *Peronopsis sallesi* (Munier-Chalmas and Bergeron, 1889) — Kobayashi, p. 115 (listed).

- 1939b *Peronopsis (Pseudoperonopsis) sallesi* (Munier-Chalmas et Bergeron) — Kobayashi, p. 579 (remarks on the systematic position of *Pseudoperonopsis*).
- 1958 *Peronopsis fallax sallesi* (Munier-Chalmas & Bergeron 1889) — Lotze, pp. 732, 738 (listed).
- 1961 *Peronopsis fallax sallesi* (Munier-Chalmas & Bergeron 1889), — Sdzuy, pp. 523-524 (241-242), Pl. 2, figs. 1-8, Pl. 28, fig. 15 (comparison with *P. f. ferox* and figs. of cephalo and pygidia).
- 1961 *Peronopsis fallax* — Henningsmoen, p. 94 (recorded from Finnmark).
- 1965 Agnostids [partim.] — Reading, p. 175 (listed from Finnmark).
- 1967 *Peronopsis sallesi* M.Ch. et Berg. — Courtessole, pp. 492 (2), 515 (23), 519 (25), 521 (27) (listed).
- 1971 Agnostids [partim.] — Henningsmoen, p. 90 (reported from Finnmark).
- 1973 *Peronopsis fallax sallesi* (Munier-Chalmas y Bergeron 1889) — Courtessole, pp. 116-117, Pl. 2, figs. 4-14, text-fig. 21/5 (descr. and figs. of dorsal exoskeletons, cephalo and pygidia).
- 1974 Agnostids [partim.] — Martinsson, p. 237 (mentioned from Finnmark).
- 1981 *Peronopsis fallax sallesi* (Munier-Chalmas y Bergeron, 1889) — Gil Cid, pp. 118-119, Pl. 1, fig. 3 (descr. and fig. of pygidium).
- 1982 *Peronopsis fallax sallesi* (Munier-Chalmas and Bergeron) — Robison, p.155 (considered a synonym of *P. ferox*).
- 1986 *Peronopsis ferox* (Tullberg, 1880) — Liñán & Gozalo, pp. 42-43, stratigraphical distribution in sections in Figs. 10 (p. 23), 11 (p. 25), 12 (p. 26), Pl. 2, figs. 11-14.

Type specimen. — Holotype by monotypy is the dorsal exoskeleton from an uncertain Middle Cambrian zone in Montagne Noire, France, figured by Bergeron 1889, Pl. 3, fig. 5, preserved at the Laboratoire de géologie de la Sorbonne, Paris, France.

Finnmark material. — Sixteen more or less fragmentary cephalo, one external mould of a pygidium with articulated but poorly preserved thorax and thirteen other pygidia, all from the middle Middle Cambrian shale and sandstone member (K2) of the Kistedal Formation at localities 7, 11 and 12.

Dimensions: — The largest cephalon (PMO 111.589) is 3.4 mm long and 4.0 mm wide, and the largest pygidium (PMO 111.588) is 4.0 mm long and 4.3 mm wide (twice the width of right half).

Remarks. — Pygidia in the Finnmark material agree almost to the finest details with pygidia from Montagne Noire, southwestern France, as described and figured by Courtessole (1973, pp. 116-117, Pl. 2, figs. 4-6, 8-9, 11, 13) and from Los Barrios de Luna, northwestern Spain as figured by Sdzuy (1961, Pl. 2, figs. 4-8) and Gil Cid (1981, Pl. 1, fig. 3). The only difference that may be observed is that the marginal spines are more slender in the Finnmark material.

We agree with Robison (1982, pp. 153-155) in that several forms hitherto referred to as subspecies of *P. fallax* (Linnarsson, 1869), and among them *P. fallax ferox*, should warrant elevation to specific rank. On the other hand, we do not follow him (op. cit. p. 155) in considering *P. fallax sallesi* to be a synonym of *P. ferox*. The differences between pygidia of *P. ferox* and those of the French-Spanish form seem fairly obvious and quite well defined. However, we do not regard these differences as reflecting specific, but rather subspecific characteristics. Sdzuy (1961, pp. 523-524) did not, as stated by Öpik (1979, p. 43) regard *P. sallesi* as a subspecies of *P. ferox* but of *P. fallax*. Sdzuy did, however, point out the close similarity and presumed relationship between *P. sallesi* and *P. ferox*. *P. ferox ferox* occurs in dark, fine-grained shales, whereas *P. f. sallesi* is found in lighter shales embedded in sandstones or quartzites both in southwestern Europe and in Finnmark. Thus, it may well be that the two subspecies have been confined to two different types of environments.

Both Munier-Chalmas & Bergeron's (January 1888) and Bergeron's (February 1888) publications were only short reports without descriptions or illustrations. The specific taxon *sallei* therefore became valid with Bergeron's (1889) description and illustration of an almost complete dorsal exoskeleton. The latter work was written solely by Bergeron and hence he is the only author attributed to the taxon. Öpik (1979, p. 43) discussed the validity of the use of the name *P. sallesi* according to Howell's (1935, p.226) information on the inaccurate original description and illustration. Öpik

stated, however, on the basis of subsequently described and figured plesiotype material by Howell (1935, pp. 226-227, Pl. 22, figs. 17-18) and Sdzuy (1961, pp. 523-524 [241-242], Pl. 2, figs. 1-8, Pl. 28, fig. 15) that "the name *sallei* attributed to it is a reasonable but subjective inference". Nevertheless, Öpik maintained Harrington's (1938) generic name *Pseudoperonopsis* while waiting for the holotype of *P. sallesi* to be redescribed and refigured. Accepting the plesiotype material to be sufficient for the recognition of the name *P. sallesi*, we prefer to reject the name *Pseudoperonopsis* because material of this fulfils the generic concept of *Peronopsis* as given by Robison (1964, p. 530), but also Öpik's own (1979, p. 53), except for his statement that "(11) the posterior axial node is laterally expanded and its flanks are convex". This latter character is fairly vague even in the type species and is also only very faintly present in some specimens in the Finnmark material (Fig. 6:C) and in Sdzuy's material (1961, Pl. 2, fig. 6).

Furthermore, Öpik (1979, pp. 43-44) emphasized the similarity between *Linguagnostus perplexus* Robison, 1964 (transferred to *Pseudoperonopsis* by Öpik) from the *Bolaspidella contracta* Subzone in western Utah and V-Creek Limestone, Quita Formation of Queensland, Australia, and *P. f. sallesi*. *L. perplexus* differs, however, from the latter in having a wider pygidial axis, and a slightly shorter (sag.) postaxial field and a better defined anterior pygidial segment.

P. bifidus Khajrullina (in Repina et al. 1975, pp. 109-110, Pl. 9, figs. 12-15, Pl. 10, figs. 1-3) from the upper Middle Cambrian Amginsk and Majsk Formations in the northern submontane belt of Turkestan is rather similar to *P. ferox sallesi*. Their cephalons can hardly be separated, but pygidia of *P. f. sallesi* differ from those of the Turkestan species in having a wider axis and narrower (sag.) postaxial field and in having the posterior border far less distinctly zoned (see definition by Öpik 1967, p. 69).

Strikingly similar to the present form are both the holotype of *P. majiangensis* Lu & Chien (in Lu et al. 1974, p. 100, Pl. 39, fig. 2; also Lu & Chien in Yin & Li 1978, p. 390, Pl. 144, fig. 27) and additional conspecific material (Lu & Qian 1983, pp. 21-22, Pl. 1, figs. 13-14, Pl. 2, fig. 9) from the southeast Guizhou, southwestern China, and the pygidium from the Yangliugang Formation at Duibian in

Jianshan, Zhejiang, China, figured by Yang (1982, Pl. 2, fig. 3) as *P. taitzuhoensis* Lu (1957, p. 258, Pl. 137, figs. 4-5; also Lu et al. 1965, p. 49, Pl. 5, figs. 21-22). Both Chinese forms are rather small and reliable differences between them and *P. ferox sallesi* can hardly be given here. The pygidium of *P. taitzuhoensis* (which lacks the posterior axial furrow as seen in Lu's original) seems, however, to be slightly shorter than that of the Finnmark form.

Subfamily Euagnostinae Öpik, 1979

Genus *Doryagnostus* Kobayashi, 1939(a)

Synonym. — *Ceratagnostus* Whitehouse, 1939 (type species by original designation: *C. magister* Whitehouse, 1939).

Type species. — *Aagnostus incertus* Brøgger, 1878 by original designation.

Doryagnostus incertus (Brøgger, 1878)

Figs. 2a-c, 6:H-M

1878 *Aagnostus incertus*, n. sp. — Brøgger, pp. 70-71, Pl. 6, figs. 4a-b (descr. and figs. of cephalon and pygidium).

1880 *Aagnostus incertus* Brøgger — Tullberg, p. 19, Pl. 1, figs. 6a-b (descr. and figs. of cephalon and pygidium).

1883 *Aagnostus incertus* Brøgger — Linnarsson, p. 32 (recorded).

1890 *Aagnostus incertus* Brøgg. — Holm, p. 267 [13] (listed).

1902 *Aagnostus incertus* Br. — Grönwall, pp. 52-53 (recorded).

1907 *Aagnostus incertus*, Brøgger — Lake, pp. 29-30, Pl. 3, figs. 1-3 (descr. and figs. of cephalon and pygidium).

non 1916 *Aagnostus* cf. *incertus* Brøgger — Illing, p. 407, Pl. 28, fig. 10 (remarks and fig. of pygidium) [= *Peronopsis scutalis* (Hicks, 1872) according to Rush-ton 1979, p.50].

1929 *Aagnostus incertus* Br. — Strand, pp. 344-345 (remarks).

1930 *Aagnostus incertus* Brøgg. — Wallerius, pp. 52, ?54 (recorded).

1935 *Aagnostus incertus* Brøgger — Thorslund, p. 107, Pl. 1, figs. 9-10 (recorded and figs. of cephalon and pygidium).

- 1939a *Doryagnostus incertus* (Brögger) — Kobayashi, p. 148 (erection of *Doryagnostus*).
- 1946 *Doryagnostus incertus* (Brögger, 1878) — Westergård, pp. 83-84, Pl. 12, figs. 20-23, Pl. 13, figs. 1-3 (remarks and figs. of cephalon and pygidia).
- 1948 *Doryagnostus incertus* (Brögger) — Strand, p. 92 (recorded).
- 1960 *Doryagnostus incertus* (Brögger) — Pokrovskaya (in Chernysheva), Pl. 1, figs. 15-16 (copies of Westergård 1946, Pl. 12, figs. 22-23).
- 1961 *Doryagnostus incertus* — Henningsmoen, p. 94 (recorded from Finnmark).
- non 1962 *Doryagnostus incertus* (Brögger) — Hutchinson, p. 87, Pl. 10, figs. 9-11 (remarks and figs. of cephalon and pygidia) [= *D. magister* (Whitehouse, 1939) according to Öpik 1979].
- 1965 Agnostids [partim.] Reading, p. 175 (listed from Finnmark).
- 1971 *Doryagnostus incertus* — Henningsmoen, p. 90 (reported from Finnmark).
- 1974 Agnostids [partim.] — Martinsson, p. 237 (listed from Finnmark).
- non 1977 *Doryagnostus incertus* (Brögger) — Zhou et al., p. 111, Pl. 36, figs. 20-21 (short descr. and figs. of cephalon and pygidium) [? = *D. notalibrae* Öpik, 1979].
- non 1978 *Doryagnostus incertus* (Brögger) — Robison, p. 7, Pl. 2, figs. 1-2, 8 (descr. and figs. of dorsal exoskeletons) [= *D. magister* (Whitehouse, 1939)].
- non 1978 *Doryagnostus incertus* (Brögger) — Yang, pp. 20-21, Pl. 1, figs. 11-12 (short descr. and copies of figs. of Zhou et al.) [? = *D. notalibrae* Öpik, 1979].
- 1979 *Doryagnostus incertus* (Brögger, 1878) — Öpik, p. 82 (remarks and comparison with *D. magister* Whitehouse, 1939).
- 1984 *Doryagnostus* — Henningsmoen, pp. 23-24 (mentioned and fig. of cephalon from Finnmark).
- 1985 *Doryagnostus incertus* — Berg-Madsen, p. 359 (listed).

Type material. — Brögger (1878) based his description of the species on isolated cephalon and pygidia in black shale from Krekling, Eiker-Sandsvær area, Oslo Region. He thus did not base his description on a single specimen, but did give drawings of a cephalon and a cranidium. The drawings appear somewhat schematic (and are possibly somewhat resto-

red) and do not show any details that could help to identify the specimens, and no catalogue numbers were given.

Westergård (1946, p. 83-84) remarked that the pygidial axis varies in breadth in his specimens of *D. incertus* from Sweden, but that none of them had an axis as broad as in Brögger's figure. The same is, however, true of the specimens from Krekling in our collections; the axial width may have been exaggerated in Brögger's drawing.

A lectotype (PMO 28200, Fig. 2a) and two paralectotypes (PMO H2646, Fig. 2b and PMO H2646, Fig. 2c) are selected here among specimens collected by Brögger at Krekling in 1877. They are accompanied by a label with Brögger's own handwriting.

Robison (1978) quoted a statement from the Paleontological Museum in Oslo that representatives of *Agnostus incertus* collected by Brögger were missing in its collections. Luckily, quite a number of specimens have now been traced, — partly labelled as such by Brögger and partly (PMO H2646) on a piece of shale labelled *Paradoxides rugulosus* by Brögger (with the cranidium figured by Brögger 1878, Pl. 2, fig. 1). Other specimens do not have labels written by Brögger, but it is stated that they were collected by Brögger (alone or with co-collectors). Further specimens have been added to the collections subsequently.

Finnmark material. — Sixteen more or less complete cephalon, thirteen more or less fragmentary or distorted pygidia, and one pygidium articulated with but very fragmentary thorax and posterior part of the cephalon, all preserved in greenish shale of the Middle Cambrian shale and sandstone member (K2) of the Kistedal Formation at localities 7, 11, 14, 15 and 18.

Dimensions. — The largest cephalon (PMO 86437) is 4.8 mm long and 5.2 mm wide (twice the width of the right half). The largest pygidium (PMO 111.605) is 5.8 mm long and 6.0 mm wide.

Remarks. — The Finnmark material agrees very well with the material from southern Norway housed in the Paleontologisk Museum in Oslo and that from Scania, Sweden, as described and figured by Westergård (1946, pp. 83-84, Pl. 12, figs. 20-23, Pl. 1-3, figs. 13). Although the distance from the posterior end of the pygidial axis to the posterior border

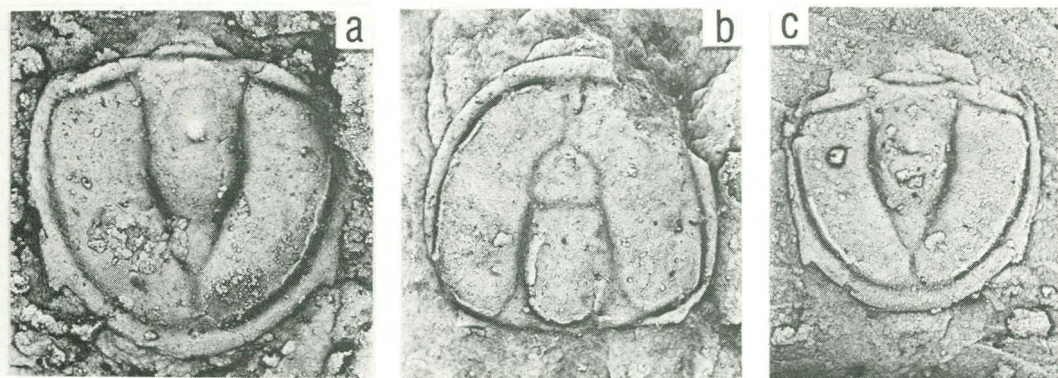


Fig. 2. *Doryagnostus incertus* (Brøgger, 1978). Black alum shale, Zone of *Ptychagnostus punctuosus*, *Paradoxides paradoxissimus* Stage, middle Middle Cambrian. Railroad section at Krekling Station, southern Norway. a. dorsal view of lectotype, almost complete but flattened pygidium. PMO 28200. Dorsal views of b. paralectotype, incomplete and flattened cephalon, and c. paralectotype, practically complete but flattened pygidium, both occurring on the same piece of shale as the cranidium figured by Brøgger 1878, Pl. 2, fig. 1 as *Paradoxides rugulosus* Corda, 1847 [= *Eccaparadoxides brachyrachis* (Linnarsson, 1882)]. PMO H2646. All latex casts of external moulds, x 8.

furrow is slightly longer in the Finnmark specimens than in those from southern Scandinavia, we do not find any reason to regard this rather minor difference as being more than natural variation between separated populations, and do not hesitate to include our material in the same species.

Argumentation for a synonymy of *D. incertus* and the Australian species *D. magister* (Whitehouse, 1939, pp. 256-257, Pl. 25, fig. 27) was brought forward by Westergård (1946, pp. 82-83) and more recently by Robison (1978, p. 7) who re-illustrated Whitehouse's type specimens together with additional topotypes. Öpik firstly concurred with (1957, p. 14) but later challenged (1979, p. 82) Westergård's view. He stated that *D. magister* differs from *D. incertus* in having large, undeflected, curved, pygidial border spines visibly behind the transverse level of the axial tip and that its pygidium is wider than long. Öpik also pointed out (ibid.) that *D. incertus* is confined to the Zone of *Ptychagnostus punctuosus* in Scandinavia, whereas *D. magister* is bi-zonal in Australia. Robison (1978, p. 7), moreover, added that the Australian specimens differ from those in Scandinavia in having a somewhat larger average size, tending to have a slightly shorter glabella, a pygidium with less constricted posterior axial furrow, slightly larger posterior-lateral border spines and a less curved posterior margin. He further stated that the Scandinavian specimens tend to lack a deltoid area. However, Robison tentatively concurred

with the synonymy proposed by Westergård. We have examined several specimens collected by Brøgger or Brøgger et al. and subsequently labelled as paratypes, and also additional topotypes. By far the greater number of the pygidia are distinctly wider than long, the location of the pygidial marginal spines, which are undeflected where preserved, vary from an anterior to a posterior position to the transverse level of the axial tip. Well preserved topotype cephalons also exhibit a deltoid area. The specimens from Finnmark have, as the Australian form, a slightly larger average size. The only morphological differences between Scandinavian and Australian specimens that we can find are that the Scandinavian pygidia have a more strongly curved posterior margin (also the specimens with the marginal spines situated far back), the axial node situated more posteriorly and slightly smaller marginal spines. We have not found any specimen, neither among the topotype nor the Finnmark material, with a posterior margin as gently curved as in those from Australia. It therefore may seem justified not to synonymize the two forms.

The specimens from the Baojing Formation in western Hunan, China, figured by Zhou et al. (1977, Pl. 36, figs. 20-21; also Yang 1978, Pl. 1, figs. 11-12) as *D. incertus* differ from Scandinavian specimens primarily in having a more quadratic pygidium with broader borders and a stouter, posteriorly less acute axis. Both the figured Chinese cephalon and pygidi-

um agree very well with those of *D. notalibrae* Öpik (1979, pp. 84-86, Pl. 19, figs. 1-4, Pl. 21, figs. 1-3) from the Undillan Zone of *Goniagnostus nathorsti* in Queensland, Australia, and belong most probably to that species.

Order Olenellida Resser, 1938
Family Olenellidae Vogdes, 1893
Subfamily Holmiinae Hupé, 1953

Genus *Kjerulfia* Kiær, 1917

Date of publication. — *Kjerulfia* and the type species, *K. lata*, were published by Johan Kiær in his paper "The Lower Cambrian *Holmia* fauna at Tømten in Norway". The year 1916 is given on the front page, but on p. 112 it says "Printed April 20th 1917". We consequently regard 1917 as the year of publication, as did Poulsen (p. O193) in the part on trilobite systematics in the "Treatise" (Moore, ed., 1959), but which is not reflected in its reference list. Some later authors have also given the year as 1917.

Type species. — *Kjerulfia lata* Kiær, 1917 by original designation.

Systematic position. — Until Kiær described *K. lata*, material of this form had been referred to *Holmia kjerulfi* (Linnarsson, 1871) (cf. Kiær 1917, p. 71). *Kjerulfia* has been assigned to various subfamilies, e.g. to the Holmiinae Hupé, 1953 by Hupé 1953(a) and Repina 1979, to the Callaviinae Poulsen, 1959 by Poulsen 1959 (in the "Treatise") and with doubt to the Neltneriinae Hupé, 1953 of the family Daguinaspidae Hupé, 1953 by Bergström 1973(c). In the two latter cases, *Holmia* was retained in the Holmiinae and Holmiidae, respectively. We are of the same opinion as Ahlberg and Bergström (in Ahlberg et al. 1986, p. 39), who assigned *Kjerulfia* to the subfamily Holmiinae (family Holmiidae). Thus, by comparing material of *Kjerulfia lata* and *Holmia kjerulfi*, which occur associated in Ringsaker, we can substantiate that *Kjerulfia* and *Holmia* are closely related and should be grouped together in the same subfamily. Among the many features in common, we especially mention the following: (1) L3 is distinctly wider (tr.) than LO, L1 and L2 and has its distal ends pointing in a postero-lateral direction, giving L3 a low (sag., ex-sag.) M-like shape. (2) L1 is less distinctly defined distally than the other glabellar lobes.

(3) The occipital ring has its node (spine) located very close to the posterior margin. (4) The presence of an anteriorly situated palpebro-ocular ridge. (5) The well-developed epipalpebral furrow. (6) The presence of both a postocular ridge and a metagenal ridge behind the palpebral lobe. The metagenal ridge is seen to end in a tiny spine in well-preserved specimens of *Holmia kjerulfi*. *Kjerulfia lata* has at least a slightly protruding angle of the posterior margin in the corresponding place. (7) The structure of the hypostome and its broad (tr.) and firm connection with the rostral plate. The hypostome of *Holmia kjerulfi* has four small, marginal spines posteriorly, as has also (new observation) *Kjerulfia lata*. (8) Lack of macropleurae. (9) Lack of obvious opisthothorax. (10) Presence of longer axial spines on the hindmost axial rings, and thus no single macrospine.

The combination of the above-mentioned features is not known in other olenellid genera. Thus, *Schmidtellus* Moberg, 1906 has longer (sag.) base of the axial spine of LO, and where the thorax is known, a macrospine and an opisthothorax. *Callavia* Matthew, 1897 differs i.a. in the shape of the glabella, in the lack of an epipalpebral furrow, and in the connection between hypostome and rostral plate. *Neltneria* Hupé, 1953 has i.a. a very different glabella. *Wanneria* Walcott, 1910 has a glabella that resembles those of *Holmia* and *Kjerulfia*, although L3 is not quite as dominating, but the hypostome is multispinose and the pygidium is bilobed. *Bondonella* Hupé, 1953 differs i.a. in having an almost parallel-sided glabella, and in not having an M-shaped L3.

***Kjerulfia lata* Kiær, 1917**

Figs. 3, 7:A-C

- 1917 *Kjerulfia lata* nov. gen. & sp. — Kiær, pp. 73-81, Pls. 9-13, 14, figs. 1-2 (descr. and figs. of all parts of the exoskeleton). With synonymy list to date.
- 1925 *Kjerulfia lata* Kjer [sic] — Warburg, p. 35, Text-figs. 11, 12a (remarks and copies of Kiær's reconstructions of genicranium in dorsal and ventral views).
- 1936 *Kjerulfia lata* Kiaer — Stubblefield, p. 422, Fig. 7 (copies of Kiær's reconstructions of genicranium in dorsal and ventral views).

- 1942 *Kjerulfia lata* Kiaer — Størmer, pp. 137-138, Pl. 2, fig. 1 (remarks and fig. of genicranium).
- 1953b *Kjerulfia lata* Kiaer — Hupé, Fig. 9A (reconstructions of genicranium in dorsal and ventral views).
- 1959 *Kjerulfia lata* Kiaer — Harrington, Fig. 28B (dorsal and ventral views of reconstructed genicranium).
- 1959 *Kjerulfia lata* Kiaer, 1917 [sic] — Poulsen, pp. 0193-0194, Fig. 137/1a-b (copies of Kiaer's reconstructions of dorsal exoskeleton and ventral view of genicranium).
- 1960 *Kjerulfia lata* Kiaer — Suvorova (in Tchernysheva), Fig. 37 (copy of Kiaer's reconstruction of dorsal exoskeleton).
- 1965 *Holmia* sp. — Reading, p. 175 (reported from Finnmark, determination by Henningsmoen).
- 1970 *Holmia* sp. — Banks, p. 21 (listed from Finnmark, determination by Henningsmoen).
- 1971 *Holmia* sp. — Henningsmoen, p. 90 (listed from Finnmark).
- 1973c *Kjerulfia lata* Kiaer, — 1916 Bergström, pp. 311-312 (remarks).
- 1974 *Holmia* sp. — Martinsson, p. 237 (listed from Finnmark).
- 1978 *Holmia* sp. — Bjørlykke, p. 49 (listed from Finnmark).
- 1980 *Holmia* cf. *mobergi* — Bergström, p. 12 (mentioned from Finnmark).
- 1981 *Holmia* cf. *mobergi* — Bergström, p. 22 (listed from Finnmark).
- 1984b *Kjerulfia lata* — Ahlberg, p. 19, Fig. 4 (listed).
- 1984b *Holmia* cf. *mobergi* — Ahlberg, pp. 20-21 (Fig. 5), 24 (listed from Finnmark).
- 1984 *Holmia* — Henningsmoen, pp. 23-24 (mentioned from Finnmark and fig. of genicranium).
- 1985 *Kjerulfia lata* Kiaer, 1917 — Ahlberg, p. 341, Fig. 2 (listed).
- 1985 *Holmia* cf. *mobergi* — Ahlberg, Fig. 3 (listed from Finnmark).
- 1986 *Kjerulfia lata* — Ahlberg & Bergström (in Ahlberg et al.), Fig. 1 (listed).
- 1986 *Holmia* cf. *mobergi* Bergström, 1973 — Ahlberg & Bergström (in Ahlberg et al.), p. 49, Figs. 1, 8 (remarks and figs. of genicrania from Finnmark).
- 1987 *Kjerulfia lata* Kiaer, 1917 — Nikolaisen, pp. 305-309, Fig. 1:F-G (remarks and figs. of genicranium).

Type specimen. — Lectotype (here selected) is the incomplete and slightly distorted genicranium, PMO 61376, figured by Kiaer 1917, Pl. 10, fig. 1, also: Størmer 1942, Pl. 2, fig. 1, from the Holmia Shale at Tømten Farm, Ringsaker, southern Norway.

Finnmark material. — One fragmentary right half of a genicranium (PMO 82712). Two very fragmentary external moulds of glabellae (PMO 98549, 98551) may be conspecific. Preserved in greenish-grey, micaceous siltstone (with flakes of greenish shale) from the middle part of the Lower Cambrian massive-bedded quartzite member (D2) of the Doublasgaissa Formation at locality 1.

Dimensions. — The genicranium is 33.5 mm long (genal spine excluded) and approximately 66.0 mm wide (twice the width of right half). The two additional glabellae (if conspecific) indicate individuals of approximately the same size.

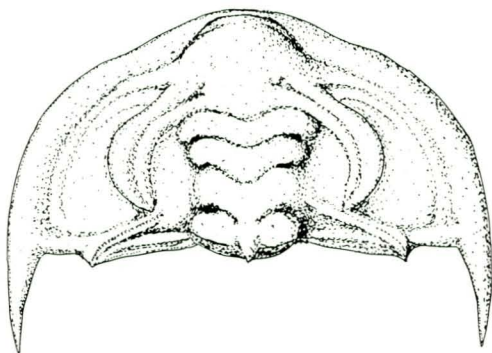


Fig. 3. Genicranium of *Kjerulfia lata* Kiaer, 1917. Reconstruction based on the incomplete specimens illustrated in Fig. 7:A-B. PMO 82712 and 98551. Natural size.

Description (based on PMO 82712). — *Genicranium* semicircular, twice as wide as long, and rather low. Cephalic border very narrow (sag.) anteriorly; antero-laterally and laterally rather broad and very low; posteriorly narrower and fairly convex (exsag.), and intersected by a metagenal ridge which is well delimited by distinct furrows running from SO and from posterior end of palpebral lobe. The metagenal ridge may well have ended in a metagenal spine (node). Genal spines fairly short, confluent with lateral cephalic border. Genal field posteriorly distinctly wider (tr.) than glabella.

A very shallow ridge curves outwards and backwards for some distance from the frontal glabellar lobe. *Glabella* laterally defined by weak axial furrow, practically missing at L1, anteriorly almost confluent with anterior margin of genicranium. L3 wider (tr.) than L1 and L2 and has the shape of a low M. S1 very deep and rather broad abaxially, weak adaxially and apparently not transglabellar; S2 fairly narrow, transglabellar but not reaching the periglabeular furrow; S3 narrow, well incised and transglabellar. *Palpebral lobes* reaching backwards to opposite occipital furrow. Anterior and posterior palpebro-ocular ridges divided by a strong epipalpebral furrow (only the proximal part of the palpebral lobe is preserved in the present material) that continues onto the frontal glabellar lobe to separate L3 and L4 (as defined by Bergström 1973b, pp. 209-210, Fig. 1). The epipalpebral furrow is clearly closer to palpebral area than to extraocular genal area.

Remarks. — The present material has been referred to as *Holmia* sp. in most previous reports, though none of these reports were founded on more than brief studies of it. The Finnmark material, however scarce and fragmentary, agrees in almost all details with the description given by Kiær (1917, pp. 73-81) of *Kjerulfia lata* from the *Holmia kjerulfi*-group zone at Tømten in Ringsaker, southern Norway. The most complete specimen at hand is slightly smaller than most of Kiær's specimens. That, together with the difference in preservation, may thus explain the very small differences which may be observed, e.g. the more rounded frontal glabellar lobe and the lower lateral border. The epipalpebral furrow continues distinctly onto the frontal glabellar lobe, but may have been exaggerated by dorso-ventral compression. A similar condition is, however, present in the smaller genicranium figured by Kiær (1917, Pl. 9, fig. 2).

The Finnmark material has more recently been referred to as a form possibly conspecific with or close to *Holmia mobergi* Bergström (1973c, pp. 288-292, Figs. 3-6) i.e. by Bergström 1980 (p.12), 1981 (p. 22), Ahlberg 1984b (pp. 20-21, 24) and 1985 (p. 343) and by Ahlberg & Bergström (in Ahlberg et al. 1986, Fig. 8, p. 49). According to Ahlberg & Bergström (1983, p. 245) *H. mobergi* belongs to an earlier species group of *Holmia* than does *H. kjerulfi*. The Finnmark form differs from *H. mober-*

gi in having a clearly wider genicranium, wider (tr.) genal areas, a less obtuse angle between frontal glabellar lobe and anterior palpebro-ocular ridge, and a less convex (tr.) lateral border.

In addition to the genotype, *Kjerulfia* includes only *K. selandica* Poulsen (1969, pp. 13-16, Pl. unnumbered, figs. 1-2) from a borehole near Slagelse, western Zealand, Denmark, *K. orcina* Orłowski (1974, pp. 13-15, Pl. 3, figs. 4-5, Pl. 4, figs. 1-8, Pl. 5, figs. 1-5; also 1985a, p. 234, text-fig. 2, Pl. 1, figs. 5-6) from the *Holmia* Zone in Gór Świętokrzyskie (Holy Cross Mts.), Poland, *K. schwarzbachi* Ahlberg & Bergström (1986, pp. 51-52, Figs. 10-11) from *Lusiatops*-Schiefer, Niederludwigshof, Görlitz, eastern Germany, and *K. palpebra* Ahlberg (1984a, pp. 257-259, Figs. 6-7) from the *Holmia kjerulfi*-group Zone in the upper part of the Grammajukku Formation at Delliknäs, Leisvall area, central Swedish Lapland. *K. lata* differs from the Danish form in having much broader (tr.) lateral borders, and from the Polish and the northern Swedish form in having a much wider genal field and lower lateral borders.

An epipalpebral furrow that continues onto the frontal glabellar lobe is distinctly present in many olenellid species; from southern Scandinavia for instance *Wanneria? lundgreni* (Moberg, 1892; see Moberg 1899, Pl. 14, fig. 2; also Bergström 1973c, Fig. 17), *H. sulcata* Bergström (1973c, pp. 292-294, Figs. 7-8) and *H. grandis* Kiær (1917, pp. 70-71, Pl. 6, fig. 12). However, *K. lata* seems to differ from them all in that the epipalpebral furrow is very close to S3.

Order Redlichiida Richter, 1933

Suborder Redlichiina Richter, 1933

Superfamily Ellipsocephalacea Matthew, 1888

Date of publication. — The family name Ellipsocephalidæ was introduced by Matthew in his article "Illustrations of the Fauna of the St. John Group. No. IV". The year 1887 is printed on the first page of the article and has since been attributed to the author's name for the family and its super- and subfamily derivatives. However, on the front page of the complete volume, the year of printing for the proceedings and transactions for the year 1887 is 1888. For that reason we believe that it is

correct to substitute "Matthew, 1887" with "Matthew, 1888".

Family Ellipsocephalidae Matthew, 1888
Subfamily Ellipsocephalinae Matthew, 1888

Genus *Ellipsocephalus* Zenker, 1833

Synonym. — ?*Strenuella* (*Ellipsostrenua*) Kautsky, 1945 (type species by original designation: *S. (E.) gripi* Kautsky, 1945), according to Ahlberg & Bergström 1978, pp. 12, 17.

Type species. — *Ellipsocephalus ambiguus* Zenker, 1833 (= subjective junior synonym of *Trilobites Hoffii* Schlotheim, 1823) by monotypy.

***Ellipsocephalus* cf. *hoffii* (Schlotheim, 1823)**

Fig. 4, Fig. 7:D—I

- cf. 1958 *Ellipsocephalus hoffii* (Schlotheim, 1823) — Šnajdr, pp. 88-92, Pl. 7, figs. 1-8, Pl. 8, figs. 1-7, ?8 (descr. and figs. of topotype dorsal exoskeletons). With synonymy list to date.
- 1961 An ellipsocephalid — Henningsmoen, p. 94 (recorded from Finnmark).
- 1965 *Ellipsocephalus* sp. — Reading, p. 175 (listed from Finnmark).
- 1970 *Ellipsocephalus hoffii* (Schlotheim, 1823) — Horný & Bastl, pp. 166-167, Pl. 2, fig. 1 (type specimens listed and fig. of neotype).
- 1971 Ellipsocephalid — Henningsmoen, p. 90 (reported from Finnmark).
- 1974 *Ellipsocephalus* sp. — Martinsson, p. 237 (reported from Finnmark).
- 1984 *Ellipsocephalus* — Henningsmoen, pp. 23-24 (reported from Finnmark and fig. of incomplete dorsal exoskeleton with shedded librigenae).
- cf. 1985b *Ellipsocephalus hoffii* Schlotheim, 1823 — Orłowski, pp. 252-253, Pl. 1, figs. 1-8 (short descr. and figs. of dorsal exoskeleton and cranidia).

Type specimen. — Neotype is the practically complete dorsal exoskeleton with shedded librigenae preserved in Národního Museum in Prague, cat. no. Br-185, from the Zone of *Hydrocephalus lyelli* (subzone of *Ellipsocephalus hoffii*), Jince Formation, at Jince, Český (Bohemia), Czechoslovakia, selected and figu-

red by Šnajdr 1958, Pl. 7, fig. 6 (also: Horný & Bastl 1970, Pl. 2, fig. 1).

Finnmark material. — One incomplete cranidium articulated with eleven thoracic segments with counterpiece (PMO 72350, 72351), one very fragmentary dorsal exoskeleton with shedded librigenae with counterpiece (PMO 72349, 72348), about twenty-five more or less fragmentary cranidia of which most are internal moulds or counterparts of such and three incomplete thoraces, preserved in mudstone and impure quartzite from the lower Middle Cambrian quartzite and shale member (K1) of the Kistedal Formation at locality 4.

Dimensions. — The cranidium articulated with eleven thoracic tergites is 35.5 mm long (the posteriormost part of thorax and the pygidium is lacking). The cranidium is 15.5 mm long and 25.0 mm wide (twice the width of left half). The largest cranidium (internal mould) has an 18 mm long glabella (excluding the occipital ring) which suggests a cranidium fully 23 mm long and 37 mm wide.

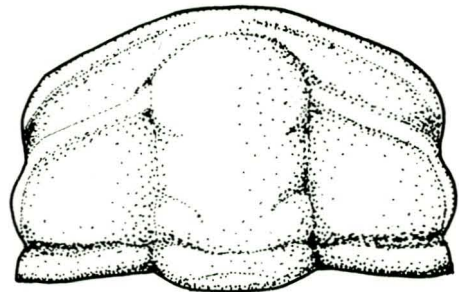


Fig. 4. Cranidium of *Ellipsocephalus* cf. *hoffii* (Schlotheim, 1823). Reconstruction based on that of the specimen in Fig. 7:D. PMO 72350. Approximately x 2 1/2.

Description. — *Cranidium* about two-thirds as long as wide, sub-trapezoidal, but with bluntly pointed, mesially somewhat truncated, anterior margin. Preglabellar field short, about as long (sag.) as occipital ring (small specimens have a relatively somewhat longer preglabellar field). *Glabella* with subparallel sides, slightly widened at base of eye ridges and rounded in front (but bluntly pointed on internal moulds). Occipital furrow shallow but fairly well pronounced. Occipital ring with a small, low median

node. Lateral glabellar furrows not visible, except for a weakly developed, oblique S1 in larger cranidia. Periglabbellar furrow well defined posteriorly, progressively effaced forwards. *Fixigenae* about as wide as glabella, with faintly developed, narrow and oblique eye ridges, and with shallow but distinct posterior border furrows. *Facial sutures* rounding off antero-lateral corners, subparallel in front of eye lobes, slightly convex and gently diverging behind these. *Palpebral lobes* poorly delimited from palpebral area of *fixigenae*, about one-quarter as long as cranium, situated about mid-way between anterior and posterior corners of the cranium. Surface of cranium appears smooth. *Librigenae*, *doublure* and *hypostome* unknown. *Thorax* incompletely known; one specimen shows twelve tergites. Pleurae wider than axis (more so rearwards), and with oblique, moderately broad (exsag.) pleural furrows. Fulcra slightly further from axial furrow than from pleural tips. Anterior pleural band raised into a convex (exsag.) ridge along the anterior margin of pleura. Pleural ends apparently non-spinose but rather bluntly pointed and bent gently down. *Pygidium* poorly known, but apparently small and short.

Remarks. — The present exoskeletal parts agree, in as far as the state of preservation allows comparison, rather well with corresponding parts in the topotype material (see also Orłowski 1985b, fig. 1) of the presumably younger type species, *E. hoffii*, as described and figured by Šnajdr (1958, pp. 88-92, Pl. 7, figs. 1-8, Pl. 8, figs. 1-7, ?8) from the Zone of *Hydrocephalus lyelli* (subzone of *E. hoffii*), Jince Formation at Konicek, Vystrkov and Jince in Český (Bohemia), as well as with topotype material preserved in the Paleontologisk Museum in Oslo. *E. hoffii* is also recorded and briefly described from both the Zone of *Paradoxides insularis*, the Zone of *P. pinus* and the Zone of *P. polonicus* in the Gór Świętokrzyskie (Holy Cross Mts.), Poland by Orłowski (1985b, pp. 252-253, Pl. 1, figs. 1-8). However, the present form seems to differ from Bohemian material of *E. hoffii* in having slightly wider (tr.) *fixigenae* and correspondingly wider (tr.) pleurae, and in having a slightly more pronounced occipital furrow. It differs from the Polish material, which is preserved more like most of the Finnmark material, in having a shorter (sag.) preglabellar field and wider (tr.) *fixigenae*.

Another Bohemian form similar to the present is the presumably more concurrent *E. vetustus* Pompeckj (1896, p. 552, Pl. 17, fig. 3; see Šnajdr 1958, pp. 92-94, Pl. 6, figs. 21-22, Pl. 8, fig. 9, Pl. 9, figs. 1-11) from the Skryje Beds (Zone of *Eccaparadoxides pusillus*), Jince Formation, but which differs in having cranidia with a broader (sag.) preglabellar area.

The cranidia from Finnmark differ from those of the southern Scandinavian *Ellipsocephalus polytomus* Linnarsson (1877, pp. 12-15, Pl. 2, fig. 1; see Westergård 1936, pp. 56-58, Pl. 11, figs. 5-7) from the Zone of *Eccaparadoxides oelandicus* in having a wider (tr.) palpebral area of *fixigena*, a less curved anterior margin and wider (tr.) pleural areas, and from the younger *Ellipsocephalus lejostracus* (Angelin, 1852, p. 24, Pl. 19, fig. 3; see Westergård 1950, pp. 11-13, Pl. 2, figs. 7-14) from the Zone of *Ptychagnostus gibbus*, which has a very similar cranium, in having non-spinose pleural ends.

A complete dorsal exoskeleton from *Eccaparadoxides oelandicus* beds in a bore-core from Bödahamn, northernmost Öland, Sweden, figured by Wærn (1952, Pl. 1, fig. 3) has only twelve thoracic tergites. It differs from the Finnmark form in having much shorter (tr.) pleurae. Otherwise its cranium equals that of *Ellipsocephalus polytomus*.

A number of both named and unnamed forms from widely scattered areas in central and southwestern Europe have been assigned to *Ellipsocephalus* (e.g. Orłowski 1959b, 1964, 1965, 1971, 1975a, 1975b, 1985b; Samsonowicz 1959, 1962; Lendzion 1972; Lendzion in Arén & Lendzion 1978; Sdzuy 1958, 1961, 1966, 1968; Liñán Guizarro 1978). The state of preservation of most of these, as well as that of the present material, renders comparison with the Finnmark form rather difficult and speculative, not least due to the fact that ellipsocephalines have effaced cranial features and that intraspecific variation is common (Sdzuy 1961, p. 575). However, some forms have cranidia quite similar to those present: *E. guerichi* Orłowski (1959b, pp. 516-517, Pl. 1, figs. 6-10; also 1964, p. 82, Pl. 4, figs. 4-9; 1965, p. 137, Pl. 1, fig. 6; 1985b, p. 254, Pl. 2, figs. 9-15) from the *Eccaparadoxides oelandicus* Zone of the eastern part of the Gór Świętokrzyskie (Holy Cross Mts.) in central Poland differs in having a wider (sag.) preglabellar area and narrower (tr.) thoracic pleural

areas; *Ellipsocephalus puschi* Orłowski (1959b, p. 517, Pl. 2, figs. 1a-c; also 1964, p. 82, Pl. 4, figs. 1-3; 1985b, p. 253, Pl. 2, figs. 5-8) from the same horizon and area differs in having a wider (sag.) preglabellar area; *E. leonicus* Sdzuy (1958, p. 238, Pl. 1, fig. 5; also 1961, pp. 575-577 [293-295], Pl. 8, fig. 1, Pl. 34, fig. 3) from "Trilobite beds", Los Barrios de Luna, Spain, differs in having a wider (sag.) preglabellar area and slightly narrower (tr.) fixigenae.

Finally, it must be noted that the fairly wide (tr.) pleurae of the present form are strongly reminiscent of those of *Germaropyge germari* (Barrande, 1852; see e.g. Horný & Bastl 1970, Pl. 2, fig. 2) and *G. sanctacrucensis* Samsonowicz (1959, pp. 527, 529, Pl. 2, figs. 4-12; see also Orłowski 1975a, pp. 371-372, Pls. 1-4), the former from the Bohemian lowermost Middle Cambrian and the latter from the Lower Cambrian Protolenus Zone of Gór Świętokrzyskie (Holy Cross Mts.), Poland. Because the librigenae of the Finnmark form are unknown, it cannot fully be compared with species of *Germaropyge*.

Superfamily Paradoxidacea Hawle & Corda, 1847 (nom. transl. Poulsen 1959, ex Paradoxides Hawle & Corda, 1847)

Family Paradoxididae Hawle & Corda, 1847
Subfamily Paradoxidinae Hawle & Corda, 1847

Remarks. — The nominate genus was revised by Šnajdr in a preliminary report (1957) and rather thoroughly soon after (1958). He erected two new genera for species with the rostral plate and hypostome not ankylosed, *Eccaparadoxides* and *Acadoparadoxides*, and awoke Barrande's sleeping taxon *Hydrocephalus* for a group of species with a rather characteristic ontogenetic development. Additional information on *Paradoxides* and *Hydrocephalus* was given also later by the same author (1987). These taxa have been somewhat differently considered by subsequent authors. Some have accepted them as genera (Courtessole 1967; Bergström & Levi-Setti 1978), some as subgenera (Sdzuy 1968; Repina 1969; Solovyev 1969; Jegorova & Shabanov 1972; Courtessole 1973; Liñán Guijarro 1978; Medrano 1982; Gil Cid 1984) and some have excluded or rejected them (Orłowski 1959a; 1964; 1965; 1985b; Sdzuy 1961; Rushton 1966; Jegorova & Savitskij 1969; Jegorova 1976). None of these have

discussed the matter more than briefly, except for Solovyev (1969). He regarded all the genera above as subgenera and gave amended diagnostic concepts. Furthermore, he erected a new subgenus, *Eoparadoxides*, for the stratigraphically low and large species with a flat and broad (sag., exsag.), sagittally close to anterior border often depressed, anterior cranial border, transglabellar S1 and S2, narrow (tr.) and small fixigenae, librigenae with a very broad doublure and a small genal notch, thorax of 17-18 tergites, and a small rounded pygidium. However, it is beyond the scope of this paper to deal closely with the systematic classification of *Paradoxides* s.l. Thus, the Finnmark material will be treated under generic names in accordance with Šnajdr (1957; 1958), but accepting the general view that *Acadoparadoxides* and most probably also *Eoparadoxides* are subjective junior synonyms of *Eccaparadoxides*.

Genus *Eccaparadoxides* Šnajdr, 1957

Synonyms. — *Phanoptes* Hawle & Corda, 1847 [until ICZN third edition regarded as *nom. obl.*] (type species by monotypy: *Phanoptes pulcher* Hawle & Corda, 1847 = subjective synonym of *Eccaparadoxides pusillus*); *Acadoparadoxides* Šnajdr, 1957 (type species by original designation: *Paradoxides Sacheri* Barrande, 1852); ?*Paradoxides* (*Eoparadoxides*) Solovyev, 1969 (type species by original designation: *Paradoxides Harlani* Green, 1834).

Type species. — *Paradoxides pusillus* Barrande, 1846 by original designation.

Eccaparadoxides cf. *pusillus* (Barrande, 1846)

Fig. 8:F

cf. 1958 *Eccaparadoxides pusillus* (Barrande, 1846) — Šnajdr, pp. 116-128, Pl. 20, figs. 1-46, Pl. 21, figs. 1-19, Pl. 22, figs. 1-15 (descr., ontogeny and figs. of ontogenetic stages and all parts of the holaspis exoskeleton). With synonymy list to date. non 1962 *Paradoxides* cf. *rugulosus* Corda — Hutchinson, pp. 115-116, Pl. 23, figs. 1-3 (remarks and figs. of cranidia).

- cf. 1969 *Paradoxides* (*Eccaparadoxides*) *pusillus* (Barrande, 1846) — Solovyev, Pl. 5, figs. 2-3 (reconstructions of meraspid and holaspid dorsal exoskeleton).
- cf. 1970 *Eccaparadoxides pusillus* (Barrande, 1846) — Horný & Bastl, pp. 257-258, Pl. 3, fig. 3 (list of type specimens and fig. of almost complete dorsal exoskeleton fig. by Šnajdr 1958, Pl. 22, fig. 3) [for synonymous taxa, see Horný & Bastl *ibid.* index p. 343].
- cf. 1978 *Eccaparadoxides pusillus* (Barrande) — Šnajdr, p. 21, Pl. 6, fig. 4 (remarks and fig. of teratological pygidium).
- cf. 1978 *Paradoxides* (*Eccaparadoxides*) cf. *pusillus* (Barrande 1846) — Liñán Guijarro, pp. 179-180, Pl. 9, figs. 1-4 (remarks and figs. of cranidia).
- cf. 1984 *Paradoxides* (*Eccaparadoxides*) *pusillus* [sic.] (Barr. 1846) — Gil Cid, pp. 309, 311, ?312 (listed, recorded).
- cf. 1984 *Eccaparadoxides pusillus* (Barrande, 1846) — Šnajdr, p. 183 (remarks on lectotype of *Phanoptes pulcher* Hawle & Corda, 1847, Pl. 1, fig. 2).
- cf. 1984 *Eccaparadoxides pusillus* (Barrande, 1846) — Šnajdr, p. 189, Pl. 14, fig. 2 (remarks on lectotype of *Paradoxides rugulosus* Hawle & Corda, 1847, p. 32).

Type specimen. — Lectotype (selected by Šnajdr 1958) is the complete meraspid dorsal exoskeleton, SBNM coll. Barrande CC 321 No. 1244, figured by Barrande 1872, Pl. 9, figs. 22-23 (also: Šnajdr 1958, Pl. 20, fig. 43) from the zone with *Eccaparadoxides pusillus*, Skryje Beds, Jince Formation, lower Middle Cambrian at the "Podhruškou" locality, near Týřovice, Český (Bohemia).

Finmark material. — One incomplete and poorly preserved cranidium (PMO 86583) from locality 2, preserved in impure quartzite from the lower Middle Cambrian quartzite and shale member (K1) of the Kistedal Formation. Three incomplete hypostomes (PMO 86229, 86235, 86540) from locality 4 may belong to this form or to *Hydrocephalus* cf. *carens* and are described under the latter.

Dimensions. — The cranidium is 12 mm long and approximately 13 mm wide at eye-line (twice the width of the left half).

Remarks. — The present cranidium, however very poorly preserved, agrees quite well with equal-sized cranidia of the presumably stratigraphically concurrent *E. pusillus* as described and illustrated by Šnajdr (1958, pp. 116-129, Pls. 21-22). Nevertheless, it cannot unequivocally be included in that species until better and more complete material is available, and is therefore described under open nomenclature.

The Finmark form differs from the likewise lowermost Middle Cambrian *E. insularis* (Westergård, 1936, pp. 39-40, Pl. 7, figs. 19) from Öland, Sweden (also recorded from central Poland; Orłowski 1959a; Bednarczyk 1984, and from Rogaland, western Norway; Henningsmoen 1952, Pl. 1, figs. 3-4) in having a less pyriform glabella and a broader (exsag.) antero-lateral cranidial border which is more pointed sagittally.

The present cranidium is also similar to that of *E. immanis* Solovyev (1969, pp. 15-16, Pl. 2, figs. 1-4) from the lower Middle Cambrian Zone of *Oryctocephalops frischenfeldi-Schistocephalus* at Olenek, Anabara in northern Yakutsk, northern Siberia, but the latter has a less pointed anterior margin and less pronounced antero-lateral borders.

Two other, geographically widely separated species very similar to *E. pusillus* are the highly variable *E. etemincus* (Matthew, 1883; see Hutchinson 1962, pp. 114-115, Pl. 19, figs. 3-9, also Martin & Dean 1988, p. 18, Pl. 1, figs. 1-7, 11-12, 15) from the "P. bennettii Zone" (i.e. the Chamberlain Brooks Formation; see Martin & Dean 1988) of southeastern Newfoundland and *E. asturianus* (Sdzuy, 1968, pp. 91-93, Pl. 2, figs. 1-5, ?6, ?13-17) from the lower Middle Cambrian of Sebares, eastern Asturias, Spain. *E. etemincus* seems to differ from *E. pusillus* in having a somewhat narrower (sag.) anterior border and a slightly more pyriform glabella, whereas *E. asturianus* is hardly distinguishable. As it stands, it is quite possible that these three forms, together with some of the other contemporaneous and less well documented species, are conspecific and that the minor differences between them do not even reflect subspecific features but only intraspecific variation.

Genus *Hydrocephalus* Barrande, 1846

Synonym. — *Phlysiacium* Hawle & Corda, 1847 (type species by monotypy: *Phlysiacium para-*

doxum Hawle & Corda, 1847 = subjective junior synonym of *Hydrocephalus carens*); *Plutonia* Hicks, 1868 [*non* Stabile 1864] (type species by monotypy: *Plutonia Sedgwickii* Hicks, 1869); *Plutonides* Hicks, 1895 (= neonym of *Plutonia* Hicks, 1868).

Type species. — *Hydrocephalus Carens* Barrande, 1846 by subsequent designation by Šnajdr 1958.

***Hydrocephalus cf. carens* Barrande, 1846**

Fig. 8:A-E

- cf. 1958 *Hydrocephalus carens* Barrande, 1846, nov. emend. — Šnajdr, pp. 130-139, Pl. 24, figs. 1-38, Pl. 25, figs. 1-21, Pl. 26, figs. 1-11, Pl. 27, figs. 1-10, Pl. 28, figs. 1 (*non*fig. 2 [cf. Šnajdr 1987, p. 101]), Pl. 29, fig. 1, Pl. 42, figs. 1-3, 5, 7-8 (descr., ontogeny, figs. of ontogenetic stages and all parts of the holaspid exoskeleton). With synonymy list to date.
- 1961 *Paradoxides* [partim.] — Henningsmoen, p. 93 (recorded from Finnmark).
- 1965 *Paradoxides* sp. — Reading, p. 175 (listed from Finnmark).
- cf. 1969 *Paradoxides (Hydrocephalus) carens* (Barrande, 1846) — Solovyev, Pl. 5, figs. 4-5 (reconstr. of meraspid and holaspid dorsal exoskeleton).
- cf. 1970 *Hydrocephalus carens* Barrande, 1846 — Horný & Bastl, pp. 94-97, Pl. 2, figs. 3 (list of type specimens and fig. of Hawle & Corda's holotype of *Paradoxides dormitzeri*) [for synonymous taxa, see Horný & Bastl *ibid.* index, p. 345].
- 1971 *Paradoxides* sp. — Henningsmoen, p. 90 (reported from Finnmark).
- 1974 *Paradoxides* sp. [partim.] — Martinsson, p. 237 (reported from Finnmark).
- cf. 1978 *Hydrocephalus carens* Barrande — Šnajdr, pp. 10, 15-18, 21, Pl. 1, figs. 8-9, Pl. 4, fig. 1, Pl. 6, figs. 5-8, Pl. 7, figs. 7-9, Pl. 8, figs. 1-5 (remarks and figs. of anomalous parts of the dorsal exoskeleton).
- 1984 *Eccaparadoxides* — Henningsmoen, p. 24 (mentioned from Finnmark).
- cf. 1984 *Hydrocephalus carens* Barrande, 1846 — Šnajdr, pp. 151-152 (selection of lectotype of *Paradoxides dormitzeri* Hawle & Corda, 1847).

cf. 1984 *Hydrocephalus carens* Barrande, 1846 — Šnajdr, p. 164 (remarks on lectotype of *Paradoxides inflatus* Hawle & Corda, 1846).

cf. 1984 *Hydrocephalus carens* Barrande, 1846 — Šnajdr, p. 178, Pl. 14, fig. 3 (remarks on lectotype of *Phlysiacium paradoxum* Hawle & Corda, 1847).

cf. 1987 *Hydrocephalus carens* Barrande, 1846 — Šnajdr, pp. 101-102.

Type specimen. — Lectotype is the almost complete internal mould of a meraspid dorsal exoskeleton, NM L 16579, from the zone with *Eccaparadoxides pusillus*, Skryje Beds, Jince Formation, "Podhruškou" locality, near Týřovice, Český (Bohemia), figured by Barrande 1852, Pl. 49, figs. 9a-b, selected and also figured by Šnajdr 1958, p. 131, Pl. 24, fig. 32.

Finnmark material. — One incomplete cranidium (PMO 72403), one smaller and very poorly preserved cranidium (PMO 86235), three librigenae PMO 86227, 86229, 86231), three incomplete but not too poorly preserved hypostomes tentatively assigned to this form (PMO 86235, 86540, 86229), one fragmentary and very poorly preserved thorax (PMO 86584), one well preserved pleura (PMO 86231) and some smaller fragments, preserved in shale or impure quartzite from the lower Middle Cambrian quartzite and shale member (K1) of the Kistedal Formation at locality 4.

Dimensions. — The larger cranidium (PMO 72403) is 39 mm long and about 52 mm wide at eye-line (estimated by doubling the width of left half). The largest hypostome (PMO 86235) is 13.8 mm wide.

Description. *Cranidium* with anterior margin well rounded. Anterior border narrow and close to sagittal line, but slightly widening towards the facial sutures. *Glabella* pyriform, with occipital ring, L1 and L2 of about equal length (exsag.). Occipital furrow rather straight. Lateral glabellar furrows shallowest at mesial part; S1 transglabellar and curved slightly inwards and rearwards, S2 gently arched forwards and connected across glabella in a gentle rearwards arch. Internal mould of a smaller cranidium present shows oblique, strong but short (tr.) S3, whereas the larger cranidium does not show S3 but faint traces of S4. The post-S2 part of the glabella widens but slightly forwards and is about three-quar-

ters as long as the anterior part, which widens distinctly forwards to mid-length and is well rounded in front. Palpebral area of *fixigena* about one-third as wide (tr.) as occipital ring, posterior area not preserved in the present material. *Palpebral lobes* distinct, gently curved, diverging rearwards, with base almost as far forward as on level with greatest width of glabella, and with posterior tips reaching as far back as opposite occipital furrow. *Librigenae* (excluding genal spine) about twice as long as palpebral lobe. Lateral and posterior borders distinct, well defined by sharply incised border furrows. Librigenal field nowhere as narrow as border. Genal spine long, curved, at its very point more so slightly inwards. Inner spine angle very slightly obtuse. Posterior branch of *facial suture* shorter than anterior branch; both branches being shorter than the ocular suture. Flip right-angled. *Hypos-tome*, tentatively assigned to this form, with large middle body that tapers quite rapidly backwards, with strong maculae situated far back, and with prosoxon made of fine raised lines forming a pattern of subparallel inverted U's (cf. below). The quite small *thorax* present is effaced and fragmentary, but a well preserved pleura shows a strongly defined, slightly sigmoidal pleural furrow that mid-way is as broad (exsag.) as each of the two pleural bands. The pleura extends into a confluent, curved spine of moderate length pointing obliquely out- and rearwards. *Terrace lines* distinct on the doublure of the librigenae, elsewhere the surface of the dorsal exoskeleton appears smooth (the larger cranium is, however, slightly weathered).

Remarks. — The two incomplete and partly poorly preserved cranidia of the Finnmark form do not allow a very close comparison with established species, but the librigenae and well preserved pleura present agree fairly well with equivalent parts of *H. carens* as illustrated by Šnajdr (1958, Pl. 27, figs. 5, 9, 11-12, Pl. 28, figs. 1-2, Pl. 29, fig. 1, Pl. 30, fig. 1) as well as of topotype material preserved in the Paleontologisk Museum in Oslo. On the other hand, the three hypostomes associated with the Finnmark material above are apparently somewhat less quadratic in outline than those of *H. carens* illustrated by Šnajdr (ibid., Pl. 26, figs. 1-9). Thus, they are slightly more similar to those of *E. pusillus* (see ibid., Pl. 21, figs. 16-18, also; Šnajdr 1987, Pl. 2, fig.

6). The difference is, however, trifling and the three hypostomes are tentatively included here, because so far only *H. cf. carens* has been found at that locality. Further collecting at the Digermul peninsula may of course reveal that *H. cf. carens* and *E. cf. pusillus* occur together as they do in Bohemia, and that the three hypostomes belong to the latter form.

Hydrocephalus is represented in the middle Middle Cambrian deposits at Andrarum, Scania in Sweden and at Øleå, Bornholm in Denmark. Two forms have been recorded; *H. hicksii palpebrosus* (Linnarsson, 1879, pp. 9-11, Pl. 1, figs. 5-11; see Grønwall 1902; also Berg-Madsen 1985, p. 370) and *H. hicksii hicksii* (Salter, 1865; see Linnarsson 1883, pp. 14-15, Pl. 3, figs. 1-5; also Grønwall 1902, Berg-Madsen 1985, p. 360), the latter being the slightly younger. Both differ from the present form in having a less rounded anterior margin of the glabella and quite strong S3 and S4. The same characters separate the Finnmark form from the British and Newfoundland species included in *Hydrocephalus* by Solovyev (1969, p. 16), i.e. *H. aurora* (Salter, 1869; see Lake 1935, pp. 212-214, Pl. 30, figs. 1-6), *H. illingi* (Lake, 1935, pp. 202-203, Pl. 30, fig. 7 [? = *H. aurora*]), *H. parvoculus* (Howell, 1925, p. 89, Pl. 3, figs. 12-13) and of course *H. h. hicksii* (Salter, 1865; see Lake 1934-1935, pp. 196-200, Pl. 25, figs. 4-9, Pl. 26, fig. 1-2; also Martin & Dean 1988, p. 19, Pl. 3, figs. 4, 7).

A form worthy to be mentioned here is that from the northern Siberian Platform described and figured by Solovyev (1969, p. 14, Pl. 2, figs. 5-10; see also Jegorova 1976, pp. 71-72, Pl. 50, figs. 1-2) as *Paradoxides (Acadoparadoxides) sacheri jakutica* [sic.], which differs in having a wider palpebral area of fixigenae. The Siberian form may, particularly when the larvae or the thorax is found, prove to belong to *Hydrocephalus*.

Genus *Paradoxides* Brongniart, 1822

Synonym. — *Vinicella* Šnajdr, 1957 (type species by original designation: *Trilobites desideratus* Barrande, 1846 = subjective junior synonym of *Trilobites gracilis* Boeck, 1828; see Šnajdr 1978, pp. 24-25).

Type species. — *Entomostracites paradoxissimus* Wahlenberg, 1818 (= objective senior

synonym of *Paradoxides Tessini* Brongniart, 1822) by subsequent designation by Barrande 1852.

***Paradoxides davidis* Salter, 1863 (s.l.)**

Figs. 8:G-I, 9:A-G, 10:A-F

- 1961 *Paradoxides* (including *P. paradoxissimus*) — Henningsmoen, p. 39 (recorded from Finnmark).
- 1965 *Paradoxides* spp. — Reading, p. 176 (listed from Finnmark).
- 1971 *Paradoxides paradoxissimus* — Henningsmoen, p. 90 (reported from Finnmark).
- 1971 *Paradoxides* cf. *davidis* — Henningsmoen, p. 90 (reported from Finnmark).
- 1974 *Paradoxides* sp. — Martinsson, p. 237 (reported from Finnmark).
- 1978 *Paradoxides* — Bjørlykke, p. 49 (listed from Finnmark).
- 1978 *Paradoxides davidis* Salter, 1863 — Bergström & Levi-Setti, pp. 6-12, Pls. 2-7, Pl. 8, figs. 1, 3-4, 7-8, Pl. 9, figs. 1-3, 5, Pl. 10, figs. 1-7 (descr. of phenotypic variation and figs. of holotype and topotype material of all parts of the exoskeleton). With synonymy list to date.
- 1984 to arter av [two species of] *Paradoxides* — Henningsmoen, pp. 23-24 (mentioned and fig. of early holaspid dorsal exoskeleton from Finnmark).
- 1984 *Paradoxides davidis* Salter, 1863 — Whittington, pp. 586-588, Pl. 53, figs. 1-3, 8 (remarks and figs. of hypostome).
- 1985 *Paradoxides (Paradoxides) davidis davidis* Salter, 1863 — Morris & Fortey, p. 110, Pl. 7, fig. 3, Pl. 8, fig. 4 (figs. of holotype).
- 1988 *Paradoxides (Paradoxides) davidis davidis* Salter, 1863 — Martin & Dean, p. 18, Pl. 4, figs. 4, 11-17 (remarks and figs. of cranidium and pygidia).
- 1988 *Paradoxides davidis* Salter, 1863 — Whittington, pp. 586-588, Pl. 53, figs. 1-3, 8, text-fig. 8 (description and figs. of hypostomes).

Type specimen. — Holotype is the external mould of an almost complete but distorted dorsal exoskeleton (BM 45083 and counterpart BM 45084) from Menevian Beds at Porth-y-rhaw, St. Davids, Pembrokeshire, South

Wales, selected by Bergström & Levi-Setti (1978) who figured a cast (ibid., Pl. 2, fig. 1).

Finnmark material. — One cephalon articulated with a nearly complete thorax (PMO 72396), one nearly complete young holaspid dorsal exoskeleton (PMO 111.608 with counterpiece PMO 111.609), one thorax (PMO 72358) and fragments of others, about sixty cranidia, more than twenty larger parts of librigenae, over twenty hypostomes and five pygidia. All preserved in greenish-grey, shaly mudstone from the Middle Cambrian sandstone and shale member (K2) of the Kistedal Formation at localities 5 and 7-13.

Dimensions. — The specimen consisting of a cephalon articulated with twenty tergites, is 86 mm long. Fragments of the dorsal exoskeleton indicate individuals of approximately 2.5 times the size of this. The younger holaspid dorsal exoskeleton is approximately 15 mm long (estimated because the anterior of the cephalon is missing). The smallest cranidium (PMO 72429) is 4.3 mm long and 6.9 mm wide at eye-line. The largest pygidium present (PMO 72392) is 10 mm long.

Remarks. — *P. davidis* has recently been thoroughly revised by Bergström & Levi-Setti (1978) on basis of material from Newfoundland and from the type locality in South Wales. Including the nominate subspecies, they were able to recognise four different subspecies founded on variations in the pygidial morphology and, for one of them, on an aberrant number of thoracic tergites. Their three new subspecies, occurring at separate horizons in Newfoundland, were thought to have been derived by allopatric geographic speciation from a stable stock of the nominate subspecies. A similarly detailed stratigraphical collection is not as yet available from Finnmark. However, the few pygidia at hand indicate that different subspecies occur. The pygidium of the younger holaspid dorsal exoskeleton (Fig. 8:H-I) is rather similar to those of *P. davidis davidis*, another isolated pygidium articulated with the last thoracic tergite (Fig. 10:F) strongly recalls that of *P. d. trapezopyge*, whereas the largest one present (Fig. 10:E) does not quite agree with any of those figured by Bergström & Levi-Setti. The granulation on several fragments, especially such from larger individuals, agrees well with that found in *P. d. davidis* and *P.*

d. trapezopyge. The earlier reports of both *P. paradoxissimus* and *P. cf. davidis* from Finnmark must be viewed in the light of the then unpublished demonstration of the wide range of morphological variation in *P. davidis* as well as lack of more complete and better preserved material as collected later from Finnmark by Prof. B.-D. Erdtmann and his students. Furthermore, the Scandinavian species of *Paradoxides* are not yet well enough known, partly because of the scarcity of complete dorsal exoskeletons. It is, for instance, possible that material assigned to *P. paradoxissimus* may include more than one form. Thus, Strand (1929, p. 349) points out that there are different morphs of the pygidium. As to the cephalon, the Finnmark specimens agree very well with that of *P. davidis* although the palpebral lobes seem to extend further back than in the material figured by Bergström & Levi-Setti (1978), which, however, shows some variation (cf. their Pl. 5, figs. 3 and 6).

The cephalic parts of the Finnmark material of *P. davidis* are also very similar to corresponding parts of the Bohemian *P. paradoxissimus gracilis* (Boeck 1828). However, the pattern of raised lines on the ventral side of the rostri-hypostomal plate agrees with that of *P. davidis*. Thus, the lateral lines of the hypostome reach the rostral plate more or less at a right angle, whereas they tend to curve more or less forwards and inwards near the junction in *P. paradoxissimus gracilis*. Furthermore, *P. p. gracilis* differs in normally having a quite narrow (tr.) pygidium where the posterior margin is uplifted and slightly pointed, but other morphological types do not seem to be uncommon (cf. Šnajdr 1958, Pl. 13, figs. 8, 11; 1978a, Pl. 5, figs. 2-5, Pl. 6, figs. 1-2). Noteworthy is that the tendency to develop a postero-lateral spine can be seen in the largest of the Finnmark pygidia — a spine that is fully developed in some Bohemian specimens (cf. Šnajdr 1958, Pl. 11, fig. 1 [*Vinicella desiderata* is according to Šnajdr 1978, pp. 24-25, synonymous with *P. p. gracilis*]; Horný & Bastl 1970, Pl. 3, fig. 4; Šnajdr 1978, Pl. 5, figs. 3-4, Pl. 6, fig. 1). Thus, it is possible that *P. p. gracilis* may occur in Finnmark, but further material, especially of complete dorsal exoskeletons, is needed to verify this.

Order Ptychopariida Swinnerton, 1915
Suborder Ptychopariina Richter, 1933
Superfamily Ptychopariacea Matthew, 1888
Family Ptychopariidae Matthew, 1888
Subfamily Nassoviinae Howell, 1937

Genus *Nassovia* Howell, 1937

Type species. — *Liostracus globiceps* Grönwall, 1902 by original designation.

Nassovia? *mjollnir* n. sp.

Figs. 5a-b, 10:H-J

- 1961 an undetermined trilobite — Henningsmoen, p. 94 (recorded from Finnmark).
 1971 *Groenwallia?* n.sp. — Henningsmoen, p. 90 (listed from Finnmark).
 1984 en ukjent trilobitt [an unknown trilobite] — Henningsmoen, p. 24 (mentioned from Finnmark).

Derivation of name. — From the name of the Old Norse God Thor's hammer, Mjöllnir, alluding to the likeness of the cranium to ancient stylised illustrations of the hammer.

Type specimen. — Holotype (PMO 72388) is a flattened, slightly longitudinally compressed but fairly complete cephalon with five articulated thoracic tergites from the Middle Cambrian sandstone and shale member (K2) of the Kistedal Formation at locality 13.

Additional material. — One topotype incomplete librigena (PMO 72389), and one fragmentary, most probably conspecific pygidium (PMO 86143) from locality 16.

Dimensions. — The holotype cephalon is 14 mm long and 32 mm wide across occipital furrow (restored).

Diagnosis. — A *Nassovia?* species with both anterior and posterior branches of facial sutures strongly diverging, preglabellar area very nearly half as broad (sag.) as length of glabella, lateral glabellar furrows weakly impressed, and posterior area of fixigena as wide (tr.) as occipital ring.

Description. — *Cephalon* subsemicircular, more than twice as wide as long (genal spines

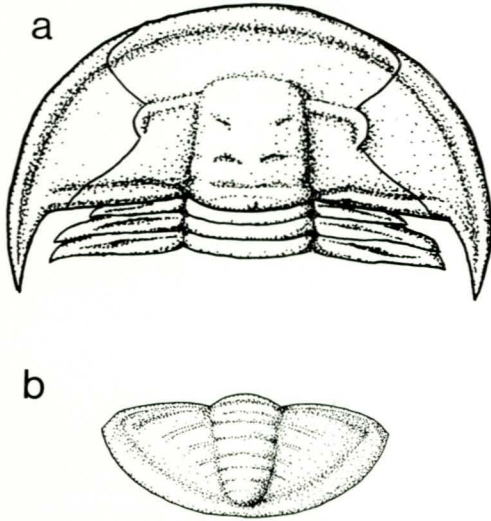


Fig. 5. *Nassovia? mjollnir* n.sp. a. Reconstruction of the cephalon with anterior three thoracic tergites based on the holotype illustrated in Fig. 10:J, PMO 72388. x 2. b. Reconstruction of the pygidium based on the specimen illustrated in Fig. 10:I, PMO 86143. x 3.

excluded), most probably fairly low, but with very deep and broad anterior and lateral border furrows. *Cranidium* hour-glass-shaped, slightly less than half as long as wide and being widest posteriorly. Preglabellar field very nearly one-third as long (sag.) as glabella. Anterior border strong, apparently rather convex (sag.), and only slightly shorter (sag.) than preglabellar field. *Glabella* gently coniform but markedly truncate (bluntly rounded) anteriorly, distinctly defined by narrow but shallow periglabbellar furrow, and slightly longer than wide. Lateral glabellar furrows rather shallow and only two pairs are discernible in the only cranidium present. Occipital furrow shallow and, like lateral glabellar furrows, not reaching the periglabbellar furrow. Occipital ring one-sixth as long (sag.) as glabella, with a faint band furrow and apparently with a very low median node. *Palpebral* area of *fixigena* about half as wide (tr.) as width of glabella at eye-line, posterior area about as wide as occipital ring. Posterior border furrow (exsag.) but deep and almost straight. Posterior border narrow (exsag.). Eye ridges prominent, directed slightly obliquely outwards and backwards. *Palpebral lobes* fairly short (exsag.), situated slightly behind S2. Anterior branches of *facial sutures* strongly diverging forwards (almost 90°) but

converging across anterior border to create rounded antero-lateral cranidial corners (best seen in the facial suture of the associated *librigena*), posterior branches strongly diverging slightly sigmoidally backwards (approximately 115°) and cutting the posterior border rather close to the genal spine. A faint impression on the glabella appears to show the outline of the hypostome. *Doublure* as wide as border. *Librigena* with a medium-sized and very broad-based genal spine. The isolated *librigena* shows part of the terrace-bearing *doublure*. The adaxial limitation of it appears to be natural rather than broken, and as it is too short to reach the axial line of the cephalon, there appears to have been a rostral plate present. The *librigena* furthermore shows a very fine radiation of caecal lines from the eye. The surface of the holotype is less well preserved, but traces of such lines are seen on the preglabellar field. *Thoracic tergites* narrow (sag., exsag.), with axial rings apparently without median nodes, pleurae distinctly wider (tr.) than axial ring, except in first tergite where much shorter, and with fulcra closer to axial furrow than to distal ends. Whether pleural ends are pointed or blunt cannot be seen in the present material. *Pygidium*, provided the present specimen is conspecific, triangular in outline and slightly more than twice as wide as long. Axis broad (tr.) and composed of five rings and a terminal axial piece. *Doublure* fairly broad.

Remarks. *Nassovia? mjollnir* n.sp. seems to occupy an intermediate position between the monospecific *Nassovia* and *Groenwallia* as represented by *G. microphthalmia* (Angelin, 1852, p. 22, Pl. 18, fig. 4; see Westergård 1953, pp. 32-34, Pl. 7, figs. 13-17; also Bruton 1985, pp. 322-323, Fig. 5:G-I, K-L). The new species differs from *N. globiceps* (Grönwall, 1902, pp. 145-146, Pl. 4, figs. 12a-b) from the Zone of *Ptychagnostus punctuosus* at Øleå, Bornholm in Denmark, in having the anterior branches of facial sutures strongly divergent forwards, glabella less coniform and palpebral lobes closer to the glabella, and from *G. microphthalmia* from the slightly younger *Paradoxides forchhammeri* Series of southern Scandinavia in having a shorter preglabellar area, more anteriorly situated palpebral lobes, more triangular posterior area of *fixigenae*, more transverse eye ridges and a stronger, much less coniform glabella.

The pygidium differs from that of *Andrarina costata* (Angelin, 1854; see Bruton 1985, pp. 322-323, Fig. 5:A-D) in having a shorter axis with fewer rings, and from that of *G. micropht-halma* in being more triangular.

The gross morphology of the new species seems to agree best with that of *N. globiceps* although close comparison is difficult due to sparse material of both forms and difference in preservation. For that reason we have included it in *Nassovia* but with considerable doubt. The exact stratigraphical level of the holotype of *N.?* *mjollnir* is uncertain, but beds yielding a large number of trilobites at other localities on the Digermul peninsula, including the pygidium assigned here, agree stratigraphically with that of *N. globiceps* in Bornholm.

The librigena of *N.?* *mjollnir* has anterior prolongations of the doublure similar to that found in olenids and in *Andrarina* (see Bruton 1985, p. 323, Fig. 5:J). However, the new species differs markedly from *Andrarina* in having a much larger preglabellar area, palpebral lobes situated more posteriorly and closer to the glabella, and larger, much more broad-based genal spines (as in North American members of *Nassoviinae*). We agree with Bruton (1985) in that *Groenwallia* probably should be excluded from the *Andrarinidae*, but too little is known of the *Nassoviinae* to include it there with confidence.

Ptychopariine genus & species indet.

Fig. 10:G

Remarks. — A single, 3 mm long, poorly preserved and fragmentary external mould of a cranidium occurs associated with *Paradoxides davidis*, *Peronopsis ferox sallesi*, *Doryagnostus incertus* and the pygidium here assigned to *Nassovia?* *mjollnir* in greenish-grey, shaly mudstone in the sandstone and shale member (K2) of the Kistedal Formation at locality 16. It shows a glabella that tapers strongly forwards and has a very markedly truncate front, a moderately broad (sag.) preglabellar field and a quite narrow anterior border. Hence the present cranidium resembles that of *Ullaspis conifrons* Westergård (1948, p. 22, pl. 4, figs. 14-16) from presumably the Zone of *Lejopyge laevigata* at Ullavi in Närke, Sweden, but differs in having a broader (sag.) preglabellar field and eyelobes located further from the glabella.

Superfamily Anomocaracea Poulsen, 1927 (*nom. transl.* Poulsen, 1959, *ex Anomocari- dae* Poulsen, 1927)

Family Anomocaridae Poulsen, 1927

Genus *Anomocarina* Lermontova, 1940

Type species. — *Proetus? excavatus* Angelin, 1852, by original designation.

Anomocarina? sp.

Fig. 10:K-L

Material. — One external mould of a large, incomplete pygidium (PMO 72375) and an external mould of a fragment of a slightly larger pygidium (PMO 72371), both from the Middle Cambrian sandstone and shale (K2) of the Kistedal Formation, the former preserved in micaceous shale from a loose block at locality 17, the latter preserved in impure mudstone from locality 14.

Dimensions. — The incomplete pygidium (PMO 72375) has an axial length of approximately 19 mm of which the axis occupies about 15 mm. The width is unmeasurable due to fragmentation, but was possibly about twice the width.

Description. — Pygidial axis tapering slightly backwards, composed of six rings carrying strong band furrows and a large, elevated terminal axial piece with a poorly defined, strongly backwardly tapering projection. Pleural furrows broad (exsag.). Pleural ribs flat, which gives rise to distinct anterior and posterior edges. Doublure wide, giving rise to a distinct paradoublural line that is pointed backwards sagittally. Middle part of posterior margin gently emarginate.

Remarks. — The present pygidia are far too fragmentary to allow any close comparison with established species. The shape and number of the axis and its rings together with 'double-edged' pleural ribs may indicate that they belong to *Anomocarina*, as exemplified by *A. extornata* (Westergård, 1930, p. 17, Pl. 4, fig. 23; 1950, Pl. 3, figs. 12, 15-18, Pl. 4, figs. 3-5) from the Andrarum Limestone at Andrarum in Scania, Sweden, *A. sibirica* (Westergård, 1930, Pl. 2, figs. 15, 17-18, Pl. 3, figs. 1, ?2) from the upper Middle Cambrian Ben-

nett Island, New Siberian islands in the Laptev Sea north of Siberia, and *A. splendens* Lermontova (1940, Pl. 48, figs. 2-2a) from the upper Middle Cambrian of the Anabarsk and Lena-Aldansk districts in northern Siberia. Especially noteworthy is that one of Westergård's figured pygidia (1950, Pl. 4, fig. 4) shows a pointed paradoublural line as in the present form.

However, at least two other species should also be considered as possibly related; *Metanomocare petaloides* Lermontova (1940, p. 156, Pl. 47, figs. 5-5a) from the upper Middle Cambrian of Lena, northern Siberia, and *Chondranomocare irbinica* Repina (1960, pp. 209-210, Pl. 16, figs. 8-9; see Repina et al. 1975, p. 150, Pl. 22, figs. 13-16) from the lower Middle Cambrian of eastern and western Sajan, Kuznetskij Alatau, northern Siberian Platform. *M. petaloides* differs from the Finnmark form in having a well developed postaxial ridge and the paradoublural line closer to the axis, whereas *C. irbinica* differs in having a longer pygidium with a wider doublure.

Finally, 'double-edged' pleural ribs are also present in pygidia of *Anomocarioides*, but pygidia of that genus differ from that of the Finnmark form in having a long axis with many more rings.

Stratigraphic occurrence of Lower and Middle Cambrian fossils from the Digermul peninsula

The occurrence in the stratigraphic units is given for both trilobites and other fossils. Some fossils have not yet been described, e.g. hyolithids and several brachiopods.

Stratigraphic table.

Mainly from Reading (1965), Føyn (1967), Banks (1970), Banks et al. (1971) and Welsch (1986).

Digermul Group (pars)

Kistedal Formation (pars):

K4 Black shale member. 200m. Upper Cambrian.

K3 Black quartzite member. 10-35m. Middle(?) Cambrian.

K2 Sandstone and shale member. 200m. Middle Cambrian.

K1 Quartzite and shale member. 100m. Middle Cambrian.

Vestertana Group

Duolbasgaissa Formation (Lower Cambrian):

D2 Upper Duolbasgaissa member (massive-bedded quartzite). 300m.

D1 Lower Duolbasgaissa member (thin-bedded quartzite). 200-220m.

Breivik Formation (Lower Cambrian):

B2 Upper Breivik member (green siltstones). 300-400m.

B1 Lower Breivik member (green siltstones and quartzites). 220-225m.

Stappogiedde Formation:

S3 Manndrapereelv member (red quartzitic sandstone). 180m (With Vendian/Lower Cambrian boundary?).

S2 Innerelv member (blue-green and red-violet slate). 220-255m.

S1 Lillevatn member (quartzitic sandstone). 40m.

Early Cambrian fossils from the Breivik (B) and Duolbasgaissa (D) Formations.

Trilobita:

Kjerulfia lata Kiær, 1917 (D2)

Foraminiferida [cf. Glaessner 1963, 1978]:

Platysolenites antiquissimus Eichwald, 1860 (B1)

Ichnofossils:

Phycodes pedum Seilacher, 1955 (B1), *P. palmatum* Hall, 1852 (B2), *P. sp.* (B1), *Rusophycus* (B1, D1, D2), *Cruziana* (D1, D2), *Dimorphichnus* (D1, D2), *Diplichnites* (D2), *Cochlichnus* (B1), *Plagiomus* (D1, D2), *Rhizocorallium* (D2), *Teichichnus* (B2), *Syringomorpha*, determined here as *S. nilssoni* (Torell, 1868) (D2), *Diplocraterion* (D1, D2), *Skolithos* (D2) and various other trace fossils. To the above list, mainly from Banks (1970), should be added *Bergaeria* (D2) (cf. below), *Rusophycus dispar* (Linnarsson, 1871) (D), recorded by Bergström 1981, and the following recorded by Welsch 1983: *Planolites* (B1), *Palaeophycus* (B1) and *Taphrhelminthopsis*. Trace fossils have been recorded as far down as in the middle

member (S2) of the Stappogiedde Formation by Reading (1965) and Banks (1970).

Remarks. — As pointed out by Føyn & Glaessner (1979, p. 27), transitional beds spanning the Precambrian-Cambrian boundary should be present on the Digermul peninsula, possibly represented by a part of the Manndraperelv member (S3) of the Stappogiedde Formation, as discussed by them (l.c., pp. 29, 45; cf. also Føyn 1985, p. 237). Although an international agreement on the base of the Cambrian has as yet not been reached, the Cambrian age of *Platysolenites antiquissimus* generally is accepted. The species occurs at several localities in northern Scandinavia. Thus, it was found by S. Føyn in the Breivik Formation east of the Digermul peninsula (Føyn 1967; Hamar 1967) and later by N.L. Banks in the same formation on the peninsula itself (Banks 1970, p. 21, Banks 1973), 150m above the top of the Stappogiedde Formation. *P. antiquissimus* further occurs in southern Scandinavia and on the East-European Platform. The species is indicative of the Zone of *Platysolenites antiquissimus* and occurs possibly also in the overlying Zone of *Schmidtellus mickwitzi* as discussed by Ahlberg & Bergström (1978), Vidal (1981a, 1981b, p. 192 and 1981c, p. 40) and Ahlberg (1984, p. 4). The occurrence of *P. antiquissimus* on the Digermul peninsula, some 600-700m below the occurrence of *Kjerulfia lata*, might well indicate the lower part of the *Platysolenites* range zone as advocated by Føyn & Glaessner (1979, p. 43) and as suggested by Ahlberg (1984, p. 5) at least the upper part of the Zone of *P. antiquissimus*. The identification of the olenellid from the middle of the upper member (D2) of the Duolbasgaissa Formation as *Kjerulfia lata* strongly indicates the Zone of *Holmia kjerulfi* or the overlying Zone of *Proampyx linnarssoni*. Thus, *Kjerulfia lata* is elsewhere known only from these two uppermost-Lower Cambrian zones in Ringsaker, one of the Mjøsa districts in southern Norway, where its occurrence in the Zone of *Proampyx linnarssoni* recently has been ascertained (Nikolaisen 1987). The presence of *K. lata* shows that the Duolbasgaissa Formation ranges markedly higher up than in the correlation charts given by Bergström 1981 (Fig. 1) and Ahlberg 1984 (Fig. 1) and which was based on an identification of the olenellid as *Holmia cf. mobergi* Bergström, 1973.

The trace fossil *Syringomorpha nilssoni* (Torell, 1868) is previously known only from Lower Cambrian beds in southern Sweden (and in erratic blocks also in Germany). It occurs in great numbers in some beds of quartzite in the upper member (D2) of the Duolbasgaissa Formation.

A large slab with several large specimens of *Bergaueria* Prantl, 1946 was collected from the same member (D2) by the Oxford Expedition to Finnmark 1961 (leader Dr. D.R. Berry). The slab was left at the camp site in Hånsvikdalen, but two of the specimens were brought back. A photograph of the slab and one specimen (PMO 72854) with a diameter around 7cm and vertically sectioned was sent to the senior author by Mr. M.F. Tuke. The name of the ichnofossil was erroneously given as *Baueria* in the list of fossils by Henningsmoen in Reading 1965, Fig. 4 (and in later quotations of the list).

Early Cambrian and Late Precambrian fossils are known from various localities in northern Norway and northern Sweden (cf. Føyn & Glaessner 1979). Some Early Cambrian and Late Precambrian acritarchs were reported from Finnmark by Vidal 1981. No Early Cambrian (or younger) trilobites have been found in Finnmark outside the Digermul peninsula. From the eastern part of the adjoining Troms county, Vogt (1967) recorded *Strenuella (Ariouella) primaeva* (Brøgger, 1879) from two localities. The material was assigned to *Strenuaeva inflata* Ahlberg & Bergström, 1978 and to *S. inflata?* by Ahlberg 1980. From a third locality in eastern Troms, Vogt (1967, p. 22) reported *Ellipsocephalus* sp. (= *Ellipsocephalus?* sp. Ahlberg 1980). In northernmost Sweden, *Strenuaeva inflata*, *Comluella? lapponica* Ahlberg, 1979, *Proampyx triangularis* Ahlberg & Bergström, 1978 and *Ellipsocephalus cf. gripi* (Kautsky, 1945) have been described from northern Lapland, across the state border from eastern Troms. The fauna indicates a late Early Cambrian age (cf. Ahlberg 1985).

Middle Cambrian fossils from K1 of the Kistedal Formation

Trilobita:

Ellipsocephalus cf. *hoffii* (Schlotheim, 1923)
Eccaparadoxides cf. *pusillus* (Barrande, 1846)
Hydrocephalus cf. *carens* Barrande, 1846

Phyllocarida:
Undescribed form

Brachiopoda:
Dictyonina? sp. (Recorded here, PMO 86240)
Lingulepis? sp.

Acritarcha (Described by Welsch 1986 from upper part of K1 to 1m above the K1/K2 boundary):

Aranidium granulatum Welsch, 1985
Cristallinium cambriense (Slavikova, 1968)
C. ovillense (Cramer & Diez, 1972)
Eliasum cf. *E. llaniscum* Fombella, 1977
Micrhystridium *M. breviacanthum* Slavikova, 1968?
M. brevicornum Jankaukas, 1976
M. dissimulare Volkova, 1969
M. lanatum Volkova, 1969
M. lubomlense Kirjanov, 1974
M. obscurum Volkova, 1969
M. semiapertum Welsch, 1986
M. shinetonense Downie, 1958
M. spinosum Volkova, 1969
M. stellatum Deflandre, 1945
M. tornatum Volkova, 1968
Multiplicisp haeridium martae Cramer & Diez, 1972

Ichnofossils (Horizontal and vertical burrows recorded by Reading 1965)

Remarks. — The trilobites occur near the base of K1 (Reading 1965, p. 181). The trilobite fauna in K1 resembles lower Middle Cambrian faunas in Czechoslovakia and Poland rather than in Scandinavia. The two paradoxidid species suggest the lowermost Middle Cambrian zone in the Barrandian area in Czechoslovakia, i.e. the Zone of *Eccaparadoxides pusillus*, probably corresponding to the Zone of *Eccaparadoxides insularis* of the zonal group of *Eccaparadoxides oelandicus* in Scandinavia. *Ellipsocephalus hoffii* occurs in Bohemia in the middle of the Middle Cambrian, but is recorded in Poland also from the lower Middle Cambrian Zones of *E. insularis* and *E. pinus* (cf. Orłowski 1985b).

Middle Cambrian fossils from K2 of the Kistedal Formation

Trilobita:
Peronopsis ferox (Tullberg, 1880) *salsesi* (Bergeron, 1889)

Doryagnostus incertus (Brøgger, 1878)
Paradoxides davidis Salter, 1863 s.l.
Nassovia? *mjollnir* n. sp.
Ptychopariinae gen. et sp. indet.
Anomocarina? sp.

Brachiopoda (Two species described and figured by Strand 1935):

Lingulepis sp. Strand 1925: *Lingulella* (*Lingulepis*) cf. *roberti* Matthew, 1895
Other inarticulates
Billingsella sp. Strand 1935: *B. cf. retroflexa* (Matthew, 1896). Figured also by Erdtmann 1983, p. 20.

Hyalolithida (Material not yet described. One specimen figured by Erdtmann 1983, p. 21).

Varia:
Hyalolithellus? sp.
Problematicum

Acritarcha (Described by Welsch 1986 from middle part of K2):

Cristallium cambriense (Slavikova, 1968)
C. ovillense (Cramer & Diez, 1972)
Eliasum cf. *E. llaniscum* Fombella, 1977
Micrhystridium aff. *M. breviacanthum* Slavikova, 1968?
M. obscurum Volkova, 1969
M. stellatum Deflandre, 1945
Timofeevia lancarae (Cramer & Diez, 1972)
T. cf. T. microretis Martin, 1981
T. pentagonalis (Vanguetaine, 1974)?
T. phosphoritica Vanguetaine, 1978

Ichnofossils (Horizontal burrows recorded by Reading 1965.)

Remarks. — As far as there is stratigraphical control, the trilobites collected from K2 come from the lower half of the member. The upper part of K2 has yielded non-trilobite fossils, predominantly brachiopods. According to Strand (1935), the two brachiopod species that he described suggest the zonal group of *Paradoxides forchhammeri*. However, the Middle Cambrian brachiopod faunas from the Kistedal Formation are in need of a revision now that so much more material has been collected.

The trilobite fauna known from K2 may safely be assigned to the Zone of *Ptychagnostus punctuosus* in the zonal group of *Paradoxides paradoxissimus*. Thus, *Doryagnostus incertus*

and *Paradoxides davidis* are recorded elsewhere in Scandinavia only from the Zone of *P. punctuosus*. The symbol of this zone is 1c δ , in Norway and B4 in Sweden. *Doryagnostus incertus* is known with certainty only from Scandinavia. *Paradoxides davidis* occurs both in Scandinavia, Britain, Newfoundland, Nova Scotia and possibly in Spain. In Britain and Newfoundland it occurs in horizons corresponding to B4 and the underlying Zone of *Hypagnostus parvifrons* (1c γ , B3) (Bergström & Levi-Setti 1978, p. 15), but for Britain restricted to the zone of *P. punctuosus* only by Thomas et al. (1984, p. 11). *Peronopsis ferox sallesi*, not earlier recorded from Scandinavia, occurs in middle Middle Cambrian horizons in France and Spain. Berg-Madsen (1985, 1986) has given good reasons for including the Scandinavian Zone of *Ptychagnostus lundgreni* – *P. nathorsti* (1c δ , C1) in the Zone of *P. punctuosus* (1c δ , B4). Whereas the former zone was earlier referred to the zonal group of *Paradoxides forchhammeri* in Sweden (cf. e.g. Westergård 1946, p. 8), it had already been assigned to the underlying zonal group of *P. paradoxissimus* in Norway (Henningsmoen 1956). Berg-Madsen's concept of the Zone of *P. punctuosus* (now 1c δ , B4-C1) in Scandinavia allows correlation with the North American *P. punctuosus* Interval-zone, established by Robison (1984, p. 5).

Middle(?) Cambrian Member of the Kistedal Formation K3

Only trace fossils (*Cruziana*) have been found in the black quartzite member (K3) of the Kistedal Formation. The size of the specimens of *Cruziana* (almost 3 cm wide) suggests a Middle Cambrian age, since the known Upper Cambrian trilobites are small in this area.

Trilobite zones

The trilobite faunas found in the Lower and Middle Cambrian beds on the Digermul peninsula indicate the following zones.

Middle Cambrian

Zone of *Ptychagnostus punctuosus* (within the lower part of K2)

Zone of *Eccaparadoxides pusillus*/ *E. insularis* (near the base of K1).

Lower Cambrian

Zone of *Holmia kjerulfi* or, possibly, the overlying Zone of *Proampyx linnarssoni* (in the middle of D2).

The number of zones is small as compared to the standard succession of southern Scandinavia. This may not necessarily be due to gaps, since the fossils are mainly concentrated in the argillaceous horizons in a predominantly arenaceous succession. Furthermore, in some shales no fossils have been found, in others only non-trilobite fossils. The lack of calcareous concretions or beds on the Digermul peninsula is in contrast to the alum shale sequence in southern Scandinavia, where fossils generally are well preserved in the limestones, but in many localities are missing or rare in the shale (Andersson, Dahlman, Gee & Snäll 1985, p. 35).

Affinites of the trilobite faunas

Lower Cambrian

The Early Cambrian trilobite found, *Kjerulfia lata*, is elsewhere known only from southern Norway. It may be added that the characteristic trace fossil *Syringomorpha nilssoni* is elsewhere known in situ only in southern Sweden.

Lower Middle Cambrian

The trilobites in the lower member (K1) of the Kistedal Formation belong to genera which occur elsewhere in Scandinavia, but the species are different and are all compared to species in Czechoslovakia and Poland (p. 77).

Middle Middle Cambrian

The trilobite species in the second member (K2) of the Kistedal Formation are likewise assigned to genera known elsewhere in Scandinavia. *Doryagnostus incertus* is known with certainty only from Scandinavia, whereas *Paradoxides davidis* occurs in Scandinavia, Britain, Newfoundland, Nova Scotia and possibly in Spain. One species, *Nassovia? mjollnir* is new, and the subspecies *Peronopsis ferox sallesi* has only been recorded from Spain and France.

The Middle Cambrian trilobite faunas in K1 and K2 appear more meagre than in contemporaneous faunas in southern Scandinavia. This may partly be due to the long research history in the numerous outcrops in southern Scandinavia and also to the lack of calcareous sediments in K1 and K2. However, this does not explain the occurrence in the K1- and K2-

faunas of trilobites not known from the Alum Shale Formation in southern Scandinavia. A corresponding situation continues in the Upper Cambrian and Lower Tremadoc trilobite (ole-nid) faunas of the Digermul peninsula, as noted by Nikolaisen & Henningsmoen (1985), who suggested that the differences in faunas might be due to the severe bottom conditions prevailing in the 'Alum Shale' sea in southern Scandinavia.

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Fig. 6.

All specimens figured in dorsal view.

A-G. *Peronopsis ferox* (Tullberg, 1880) *sallei* (Bergeron, 1889). Lower trilobite horizon in the middle Middle Cambrian sandstone and shale member (K2) of the Kistedal Formation. Locality 12. Collection M.-L. Windolph & M. Welsch 1981.

A. Fairly complete but slightly distorted and exfoliated cephalon. PMO 111.589. x 9.

B. Latex cast of external mould of incomplete but only slightly distorted cephalon. PMO 111.593. x 10.

C. Small but undistorted cephalon. PMO 111.603. x 18.

D. Nearly complete and very slightly, transversely compressed internal mould of pygidium. PMO 111.599. x 12.

E. Latex cast of external mould of exfoliated pygidium with second tergite attached. PMO 111.598. x 10.

F. Latex cast of external mould of incomplete but only slightly distorted and flattened pygidium. PMO 111.588. x 9.

G. Latex cast of external mould of slightly crushed pygidium with very poorly preserved thorax attached. PMO 111.600. x 9.

H-M. *Doryagnostus incertus* (Brøgger, 1878). Middle Middle Cambrian sandstone and shale member (K2) of the Kistedal Formation.

H. Fragmentary cephalon. PMO 86437. Locality 7. Collection H.G. Reading 1959. x 9.

I. Fairly complete but sagittally compressed pygidium. PMO 72382. Locality 7. Collection as for H. x 9.

J. Latex cast of external mould of small pygidium with attached but poorly preserved thorax and posterior part of cephalon. PMO 86292. Locality 10. Collection as for H. x 12.

K. Latex cast of external mould of fragmentary pygidium. PMO 72378. Locality 7. Collection as for H. x 8.

L. Large, almost complete but poorly preserved internal mould of pygidium. PMO 111.605. Upper trilobite horizon at locality 12. Collection M.-L. Windolph & M. Welsch 1981. x 7.

M. Latex cast of external mould of nearly complete but slightly distorted pygidium. PMO 86480. Locality 11. Collection as for H. x 7.

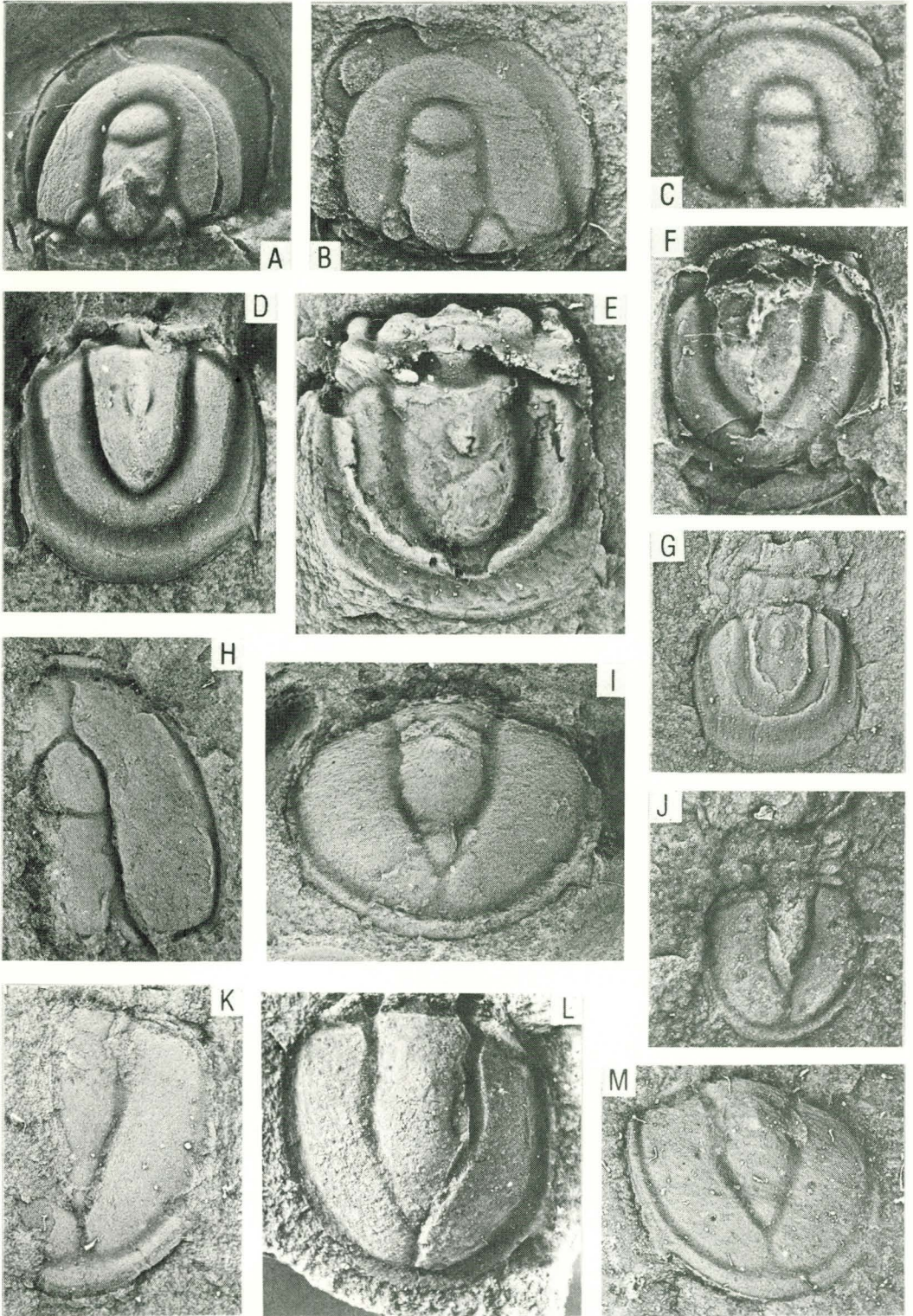


Fig. 7.

A-C. *Kjerulfia lata* Kiær, 1917. Lower Cambrian massive-bedded quartzite member (D2) of the Doulbassgaissa Formation. Scree at the outcrops on the northwestern slope of Bardeviktind.

A. Dorsal view of fragmentary specimen showing right half of genicranium lacking palpebral lobe. PMO 82712. Original of Henningsmoen 1984, p. 23, fig. A and Ahlberg & Bergström 1986, Figs. 1, 8. Collection G. Henningsmoen 1963. x 1 1/2.

B. Dorsal view of latex cast of very fragmentary genicranium. PMO 98551. Collection K.E. Henningsmoen 1963. x 1 1/2.

C. Dorsal view of latex cast of fragmentary glabella. PMO 98549. Collection F. Nikolaisen 1963. x 1 1/2.

D-I. *Ellipsocephalus* cf. *hoffii* (Schlotheim, 1823). Middle Cambrian quartzite and shale member (K1) of the Kistedal Formation. Northeastern slope in Kistedal (Gistovagge).

D. Dorsal view of fragmentary anterior part of incomplete axial shield. PMO 72350. Collection G. Henningsmoen & F. Nikolaisen 1960. x 2.

E. Dorsal view of fairly complete but internal mould of cranidium. PMO 72355. Collection as for D. x 4.

F. Dorsal view of fragmentary axial shield. Anterior part of specimen figured is a cast made of silicon rubber from the counterpiece. PMO 72348 and 72349. Collection H.G. Reading 1959 x 2

G. Dorsal view of internal mould of fragmentary cranidium. PMO 72356. Collection as for D. x 2.

H. Dorsal view of internal mould of fragmentary cranidium. PMO 72354. Collection as for D. x 2.

I. Dorsal view of internal mould of fragmentary cranidium. PMO 72345. Collection as for F. x 2.

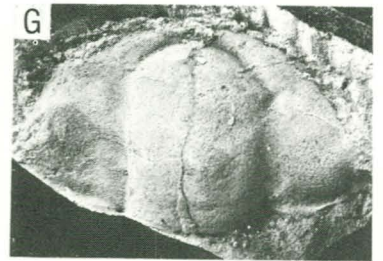
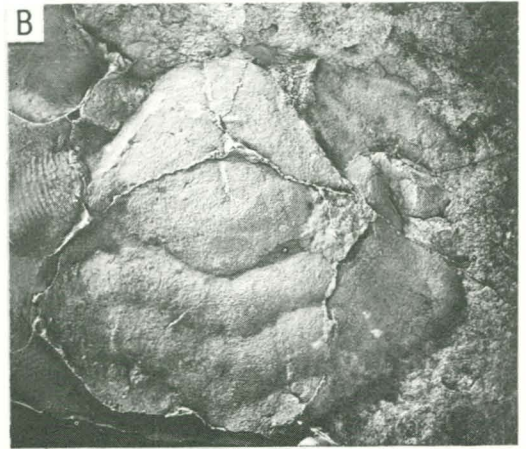
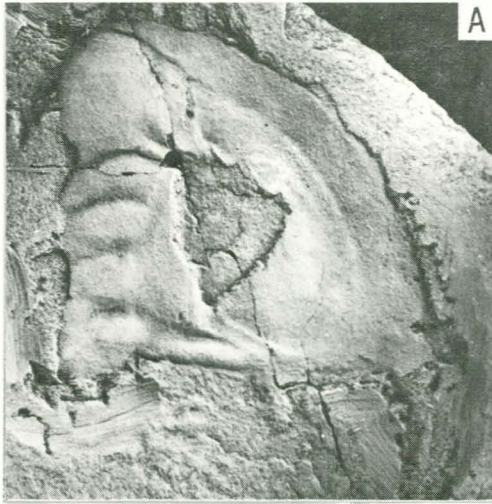


Fig. 8.

A-E. *Hydrocephalus cf. carens* Barrande, 1846. Lower Middle Cambrian quartzite and shale member (K1) of the Kistedal Formation.

- A. Dorsal view of fragmentary cranidium. PMO 72403. Locality 4. Collection F. Nikolaisen 1960. x 1.
- B. Dorso-lateral view of latex cast of external mould of almost complete right librigena. PMO 86231. Locality 4. Collection G. Henningsmoen & F. Nikolaisen 1960. x 2.
- C. Ventral view of incomplete hypostome. PMO 86235. Locality 4. Collection as for B. x 3 1/2.
- D. Dorsal view of nearly complete right thoracic pleura. PMO 86231. Locality 4. Collection as for B. x 2.
- E. Dorsal view of very incomplete and very poorly preserved thorax. PMO 86584. Locality 3. Collection M.F. Tuke 1961. x 1 1/2.

F. *Eccaparadoxides cf. pusillus* (Barrande, 1846). Dorsal view of fragmentary and very poorly preserved cranidium and two axial rings. PMO 86583. Most probably lowermost part of the lower Middle Cambrian quartzite and shale member (K1) of the Kistedal Formation. Locality 2. Collection M.F. Tuke 1961. x 3 1/2.

G-I. *Paradoxides davidis* Salter, 1863. Middle Middle Cambrian sandstone and shale member (K2) of the Kistedal Formation.

- G. Dorso-lateral view of almost complete left librigena. PMO 72390. Locality 10. Collection H.G. Reading et al. 1959. x 2.
- H. Dorsal view of small and slightly incomplete dorsal exoskeleton. PMO 111.608. "Upper trilobite sequence" at locality 12. Collection M.-L. Windolph & M. Welsch 1981. x 6.
- I. Dorsal view of latex cast of the external mould of the dorsal exoskeleton in H. PMO 111.609. Same locality and collectors. x 6.

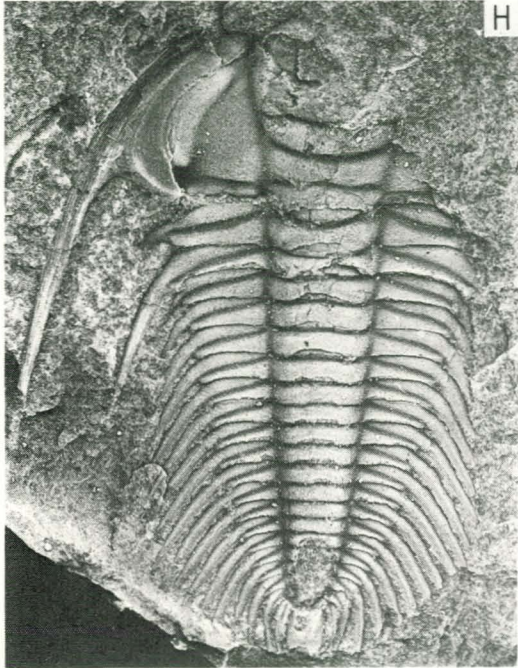
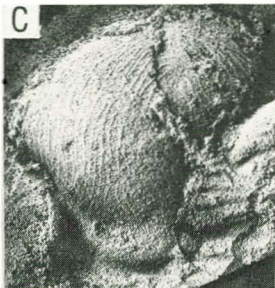
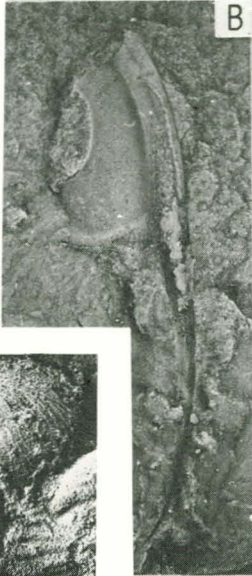
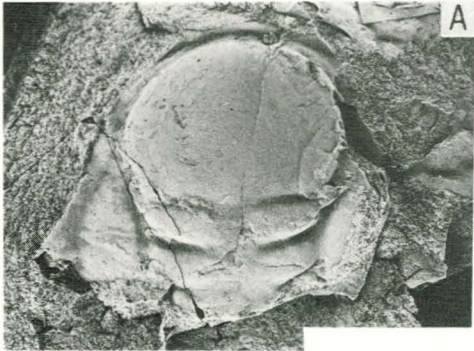


Fig. 9.

A-G. *Paradoxides davidis* Salter, 1863. Middle Middle Cambrian sandstone and shale member (K2) of the Kistedal Formation.

- A. Dorsal view of almost complete but fairly small and sagittally slightly compressed cranidium. PMO 111.596. 'Lower trilobite sequence' at locality 12. Collection M.-L. Windolph & M. Welsch 1981. x 6.
- B. Dorsal view of latex cast of external mould of almost complete but small cranidium. Note difference in size between the two palpebral lobes. PMO 111.609. Locality and collectors as in A. x 6.
- C. Ventral view of almost complete but slightly sagittally compressed rostri-hypostomal plate. PMO 111.586. Locality and collectors as in A. x 6.
- D. Dorsal view of fragmentary and slightly distorted cranidium. PMO 111.601. Locality and collectors as in A. x 6.
- E. Dorsal view of incomplete and strongly flattened cranidium. PMO 72391. Locality and collectors as in E. x 2.
- F. Dorsal view of incomplete cephalothorax. PMO 72396. Locality 10. Collection H.G. Reading et al. 1959. x 1.
- G. Ventral view of slightly incomplete and somewhat distorted rostri-hypostomal plate. PMO 72379. Locality 7. Collection H.G. Reading et al. 1959. x 5.

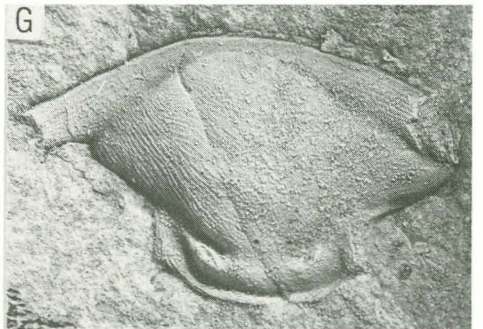
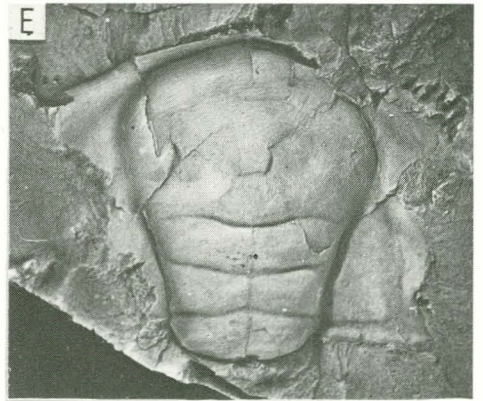
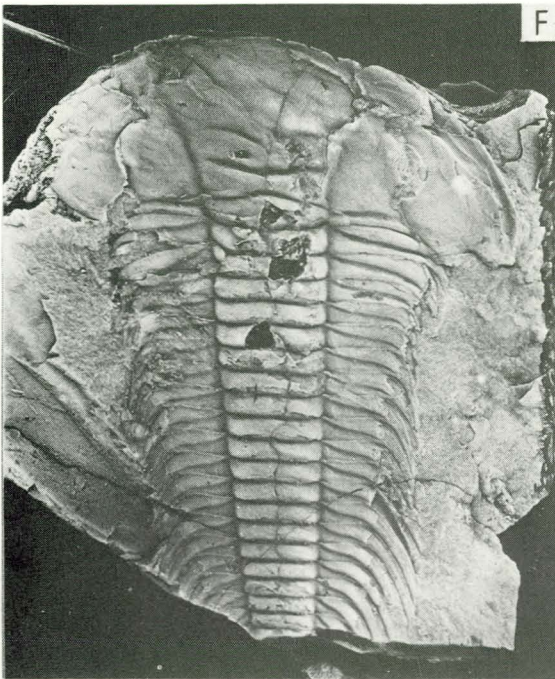
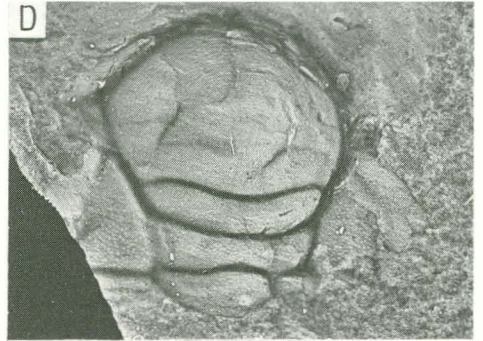
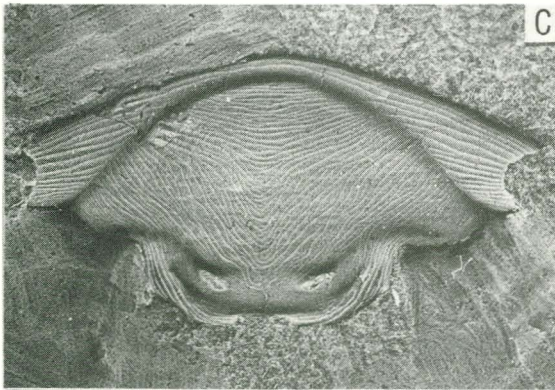
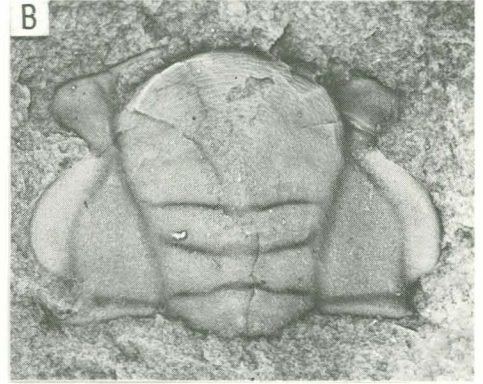
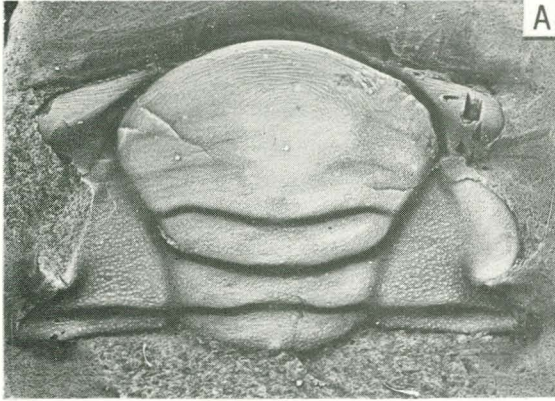


Fig. 10.

A-F. *Paradoxides davidis* Salter, 1863. Middle Middle Cambrian sandstone and shale member (K2) of the Kistedal Formation.

- A. Dorsal view of small and slightly distorted but almost complete cranidium. PMO 111.587. 'Lower trilobite sequence' at locality 12. Collection M.-L. Windolph & M. Welsch 1981. x 8 1/2.
- B. Dorsal view of incomplete and distorted cranidium showing long postocular facial suture. PMO 72445. Locality 16. Collection G. Henningsmoen 1960. x 1 1/2.
- C. Dorsal view of latex cast of five thoracic tergites from the posterior part of the thorax. PMO 72393. Locality 10. Collection H.G. Reading 1959 et al. 1959. x 4.
- D. Dorsal view of almost complete cranidium and anterior part of thorax, most probably representing a moult assemblage. PMO 86283. Locality 7. Collection as for C. x 2.
- E. Dorsal view of latex cast of large pygidium. PMO 72394. Locality and collection as for C. x 3.
- F. Dorsal view of latex cast of external mould of complete but slightly sagittally compressed pygidium with ankylosed incomplete thoracic tergite. PMO 111.602. Locality and collectors as for A. x 5.
- G. Ptychopariine gen. & sp. indet. Dorsal view of latex cast of external mould of small and poorly preserved cranidium. PMO 72453. Middle Middle Cambrian sandstone and shale member (K2) of the Kistedal Formation. Locality 16. Collection G. Henningsmoen 1960. x 6.

H-J. *Nassovia? mjollnir* n. sp. Middle Middle Cambrian sandstone and shale member of the Kistedal Formation.

- H. Dorsal view of paratype left, incomplete librigena showing long anterior doublure. PMO 72389. Locality 13. Collection H.G. Reading et al. 1959. x 2.
- I. Dorsal view of fragmentary pygidium most probably belonging to this species. PMO 86143. Locality 16. Collection F. Nikolaisen 1963. x 4.
- J. Dorsal view of holotype, flattened but almost complete cephalon with anterior part of the thorax attached. PMO 72388. Locality and collectors as for H. x 2.

K-L. *Anomocarina?* sp. Middle Middle Cambrian sandstone and shale member (K2) of the Kistedal Formation.

- K. Dorsal view of latex cast of incomplete and poorly preserved pygidium. PMO 72375. Loose block at locality 17. Collection G. Henningsmoen 1960. x 2.
- L. Dorsal view of latex cast of external mould of small fragment of pygidium. PMO 72371. Locality 14. Collection H.G. Reading et al. 1959. x 1 1/2.

