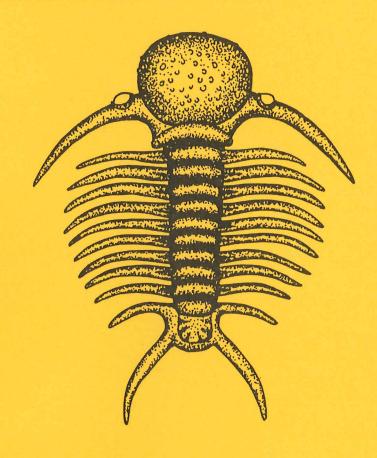
EXAMENSARBETE I GEOLOGI VID LUNDS UNIVERSITET

Historisk geologi och Paleontologi



Upper Cambrian trilobite faunas and biostratigraphy at Kakeled on Kinnekulle, Västergötland, Sweden

Fredrik Terfelt

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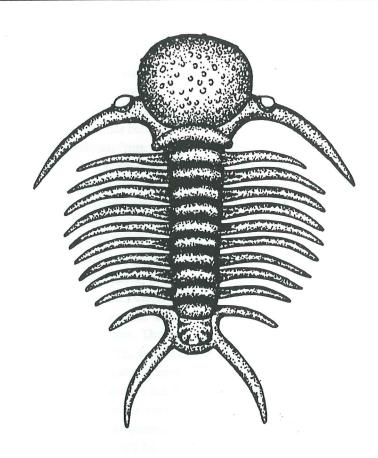
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Abstract: Upper Cambrian strata are well exposed in an old quarry at Kakeled on southwestern Kinnekulle, south-central Sweden. The exposures consist of fineley laminated alum shale with lenses and beds of dark grey limestone (stinkstone or orsten), and a few thin layers of sandstone. A 6.20 m thick section in the central part of the quarry has been measured and sampled in order to establish the succession of trilobite species. This section extends from the lower-middle part of the Agnostus pisiformis Zone into the Peltura scarabaeoides Zone. A 150 cm thick stinkstone bed ("The Great Stinkstone Bed") occurs in the Olenus/Homagnostus obesus Zone and in the upper part of the A. pisiformis Zone. It comprises a lower part measuring 30 cm and an upper part measuring 120 cm. These are separated by a thin (10 cm) bed of alum shale. Above "The Great Stinkstone Bed" nine additional stinkstone beds, with thicknesses varying from 10 to 55 cm, are present. Fossils are usually preserved only in the stinkstones, but in the A. pisiformis Zone trilobites can be found in both the shales and the stinkstones. The A. pisiformis Zone is dominated almost entirely by the zonal index, which occurs in abundance. A. pisiformis occurs throughout the A. pisiformis Zone and ranges up to the Olenus gibbosus Subzone. Nearly all specimens of A. pisiformis are disarticulated. The orientation of cephala and pygidia of A. pisiformis were measured on four shale surfaces and one stinkstone bedding plane. The majority of the shields were deposited with the convex side up and showed a preferred orientation, suggesting that their positions were affacted by currents. The orientation of the shields generally indicates a current direction roughly towards the present north. Above the A. pisiformis Zone the section comprises the Olenus/Homagnostus obesus Zone (30 cm), the upper part of the Parabolina spinulosa Zone (5 cm), the Peltura minor Zone (105 cm), and the Peltura scarabaeoides Zone (260 cm). The Leptoplastus and Protopeltura praecursor Zones are missing. The Olenus/H. obesus Zone is represented only by O. gibbosus and O. wahlenbergi Subzones, whereas the O. truncatus, O. attenuatus, O. dentatus, and O. scanicus Subzones are missing.

Keywords: Arthropoda, Trilobita, Brachiopoda, taxonomy, biostratigraphy, alum shale, Upper Cambrian, Kakeled, Kinnekulle, Västergötland, Sweden.

F. Terfelt, Department of Geology, Division of Historical Geology and Palaeontology, Lund University, Sölvegatan 13, SE-223 62 Lund, Sweden. E-mail: Fredrik.Terfelt@novell.geol.lu.se.

The Cambrian of Scandinavia is subdivided into three series, the Lower, Middle and the Upper Cambrian, also referred to as the Holmia, Paradoxides and Olenus Series. The Lower Cambrian is generally composed of light-coloured sandstones, siltstones and shales, whereas the Middle and Upper Cambrian is dominated by kerogen-rich black shales and mudstones known as alum shales, and lenses and beds of dark grey, organic-rich limestones referred to as stinkstones or orsten (anthraconite). The alum shale facies can be recognised from the very north of Norway to the southernmost parts of Sweden and varies in thickness from a few metres up to almost a hundred metres (Andersson et al. 1985; Thickpenny 1984, 1987). Throughout most of the Middle and Late Cambrian, Scandinavia was covered by an epicontinental sea. The influx of terrigenous material was generally extremely low (1-10 mm/1000 years) and basically restricted to reworking of eolic sediments and re-deposition of older strata (Buchardt et al. 1997). The general conception is that material forming black shales were deposited in anoxic to dysoxic environments and the alum shale is no exception. However, periods of anoxic conditions were apparently relatively few and short, and dysoxic conditions probably prevailed during deposition (Buchardt et al. 1997).

The term alum shale has for a long time been used for shales from which alum salt (potassium aluminium sulphate) can be extracted (Andersson et al. 1985). It has been quarried since the seventeenth century. Exploration and exploitation of alum shale have also been carried out because it is enriched in lead, uranium, sulphur and oil (e.g. Martinsson 1974). The formation of lenses and beds of stinkstones is not fully understood but is probably caused by chemical imbalance during an early diagenetic phase (e.g. Henningsmoen 1974; Dworatzek 1987). The change in chemistry was induced by the activity of bacteria in the pore water, leading to a rise in pH and precipitation of CaCO3 together with an input of bicarbonate as a result of dissolved shell material (Buchardt et al. 1997).

In Västergötland, Lower Palaeozoic sedimentary rocks are represented in four major areas: Billingen-Falbygden, Kinnekulle, Halle-Hunneberg and Lugnåsberget. With the exception of Lugnåsberget these hills or mountains are capped by dolerite intruded as sills during Permo-Carboniferous time (Andersson et al. 1985). The most complete Lower Palaeozoic successions are found on Kinnekulle and in the Billingen-Falbygden district (Fig. 1A) where the strata are more or less horizontal and tectonically undisturbed, comprising the Cambrian, the

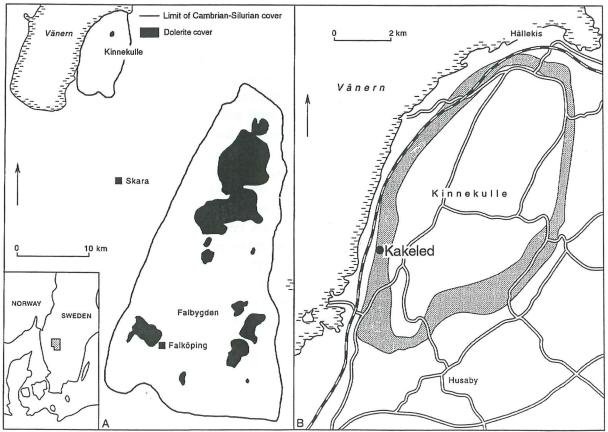


Fig. 1. A. Map of central Västergötland showing the extent of Cambrian-Silurian rocks and Permo-Carboniferous dolerites. B. Map of Kinnekulle showing the location of the Kakeled quarry and the distribution of Middle-Upper Cambrian deposits (shaded). Adopted from Ahlberg & Ahlgren (1996, Fig. 1)

Ordovician and the Lower Silurian. The Lower Cambrian in Västergötland is represented by the Mickwitzia Sandstone and the Lingulid Sandstone. The former has a thickness of about 10 metres and the latter measures about 25 metres (Martinsson 1974). The Middle Cambrian is divided into three stages, in ascending order: the *Acadoparadoxides oelandicus*, the *Paradoxides paradoxissimus* and the *Paradoxides forchhammeri* Stages. The *A. oelandicus* stage is missing in Västergötland, where the thickness of the Middle Cambrian is approximately 11 metres (Westergård 1946). The Upper Cambrian (the Olenid Series) of Västergötland has a thickness between 12 and 16 metres. It is well exposed on Kinnekulle and in the Billingen-Falbygden area.

On Kinnekulle Upper Cambrian strata are exposed in a number of old quarries. One of these quarries is situated at Kakeled on the southwestern slope of Kinnekulle (Fig. 1B). It has only been briefly described in the literature, and the aim of this paper is to describe the biostratigraphy and the succession of trilobite species in the Kakeled quarry. The orientation of agnostid shields and the depositional environment is also briefly discussed.

Description of the quarry

Kakeled is situated 14 km northeast of Lidköping and about 1 km west of Västerplana Church (Fig. 1B). It is an old quarry where the local farmers used to burn shale together with limestone in a big field oven to produce lime for agricultural purposes (Fig. 2). The measured section is located in the eastern part of the quarry. It is 6.2 m thick and can be followed for about 30 m. The most complete succession is found in the central part of the quarry. The section extends from the lower-middle part of the Agnostus pisiformis Zone into the Peltura scarabaeoides Zone. It consists of finely laminated alum shale with lenses and beds of dark grey limestone (stinkstone or orsten), and a few thin layers of sandstone. In the Agnostus pisiformis and Olenus/ Agnostus obesus Zones there is a 150 cm thick stinkstone bed referred to as "The Great Stinkstone Bed". It comprises a lower part measuring 30 cm and a upper part measuring 120 cm. These are separated by a thin (10 cm) bed of alum shale. Nine other stinkstone beds with varying thicknesses between 10 and 55 cm (Fig. 4), are present above "The Great Stinkstone Bed". The alum shale is more or less uniform throughout the section but can differ somewhat in the degree of lamination. Due to weathering, the preservation of the shale in the uppermost parts (above "The Great

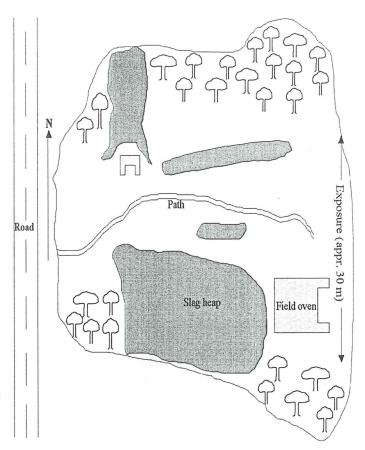


Fig. 2. Sketch-map of the Kakeled quarry.

Stinkstone Bed") is not so good as in the lower parts. Fossils are usually preserved only in the stinkstone beds, but in the *Agnostus pisiformis* Zone trilobites can be found in both the shales and the stinkstones. The succession at Kakeled was briefly described by Ahlberg & Ahlgren (*in* Ahlberg 1998, p. 41) and Eklöf et al. (1999).

Upper Cambrian biostratigraphy of Scandinavia

The succession of trilobites and other faunal elements in the Upper Cambrian of Scandinavia has been studied since the second half of the nineteenth century (e.g. Linnarsson 1868; Nathorst 1869, 1877; Tullberg 1882). The most comprehensive study is that by Westergård (1922), who thoroughly investigated a great number of sections in Sweden and subdivided the Upper Cambrian into six biozones. In ascending order these are the *Agnostus pisiformis* Zone, the *Olenus* Zone, the *Parabolina spinulosa* and *Orusia lenticularis* Zone, the *Leptoplastus* and *Eurycare* Zone, the *Peltura*, *Sphaerophthalmus* and *Ctenopyge* Zone (subdivided into four subzones), and the

Zones		Subzones
Acerocare		Acerocare ecorne
		Westergaardia
		Peltura costata
		Peltura transiens
Peltura Zones	Peltura scarabaeoides	Peltura megalops
		Parabolina lobata
		Ctenopyge linnarssoni
		Ctenopyge bisulcata
	Peltura minor	Ctenopyge affinis
		Ctenopyge tumida
		Ctenopyge spectabilis
		Ctenopyge similis
	Protopeltura praecursor	Ctenopyge flagellifera
		Ctenopyge postcurrens
		Leptoplastus neglectus
Leptoplastus		Leptoplastus stenotus
		Leptoplastus angustatus
		Leptoplastus ovatus
		Leptoplastus raphidophorus
		Leptoplastus paucisegmentatus
Parabolina spinulosa		Parabolina spinulosa
		Parabolina brevispina
Olenus Zones	Homagnostus obesus	Olenus scanicus
		Olenus dentatus
		Olenus attenuatus
		Olenus wahlenbergi
		Olenus truncatus
		Olenus gibbosus
-	Agnostus pisiformis	

Fig. 3. Zonation of the upper Cambrian of Scandinavia. Modified from Martinsson (1974), following Nielsen & Schovsbo (1999).

Acerocare, Cyclognathus and Parabolina Zone (subdivided into four subzones).

The zonation was subsequently refined by Westergård (1947). In that paper the Upper Cambrian was subdivided into six zones and 24 subzones. Henningsmoen (1957) monographed the olenid trilobites and introduced an even more refined zonation of the upper Cambrian of Scandinavia by subdividing it further, into eight zones and 32 subzones. In this zonation Henningsmoen (1957) split the Peltura Zone into three zones, the Protopeltura praecursor Zone, the Peltura minor Zone and the Peltura scarabaeoides Zone, the last two formerly treated as subzones by Westergård (1947). The Leptoplastus/ Eurycare Zone was subdivided into five subzones by Westergård (1947), and in ascending order these are the Leptoplastus paucisegmentatus, L. raphidophorus, L. ovatus and Eurycare latum, E. angustatum, and L. stenotus zones. A sixth subzone, L. crassicorne, was added by Henningsmoen (1957) between the L. raphidophorus Subzone and the *L. ovatus* Subzone. He also inserted two new subzones in the lowermost part of the *Peltura* zone, the Protopeltura broeggeri Subzone and the P. holtedahli Subzone. Recently, however, Nielsen & Schovsbo (1999)

showed that these three subzones should be abandoned, and a revised zonation is shown in Fig. 3.

Lithologic succession and biostratigraphy

The exposed succession is 6.2 m thick and ranges from the *Agnostus pisiformis* Zone into the *Peltura scarabaeoides* Zone. The base of "the Great Stinkstone Bed" was selected as reference level (0 cm). Seventeen species of trilobites and one brachiopod (*Orusia lenticularis*) have been identified, and these can be used for a biostratigraphical subdivision of the succession. Their ranges are shown in Fig. 4.

-120 cm to 100 cm: Agnostus pisiformis Zone

The lower 120 cm consists of black alum shale with a few fine-grained, grey to light grey stinkstone lenses. The alum shale is unweathered and finely laminated. The only fossil found is the zonal index, *A. pisiformis*, which occurs in vast numbers on some bedding surfaces. The fossils are generally poorly preserved in the shale although a few surfaces show a fairly good preservation. Three complete specimens were collected. The preservation in the stinkstone lenses is excellent but no complete specimens were found. The shields occur either along the outer parts of the lenses or as thin, horizontal bands within the limestone concretions.

The upper 100 cm of the *A. pisiformis* Zone forms part of "the Great Stinkstone Bed". The colour ranges from white or yellow to dark grey. The shields of *A. pisiformis* are preserved in thick, irregular to horizontal bands. 30 cm above the reference level there is a 10 cm thick alum shale bed. Two thin sandstone wedges are present near the top of the *A. pisiformis* Zone. No fossils were found in the shale or in the sandstone.

100 cm to 130 cm: Olenus and Homagnostus obesus Zone

The lower 20 cm belongs to the *Olenus gibbosus* Subzone. The subzonal index fossil *O. gibbosus* is very common and it occurs together with *Homagnostus obesus*, *A. pisiformis* and *O. transversus* (rare). The stinkstones sometimes consist exclusively of fragmentary pieces of the index fossil. The upper 10 cm belongs to the *Olenus wahlenbergi* Subzone. Trilobites found here are *O. wahlenbergi* and *H. obesus*.

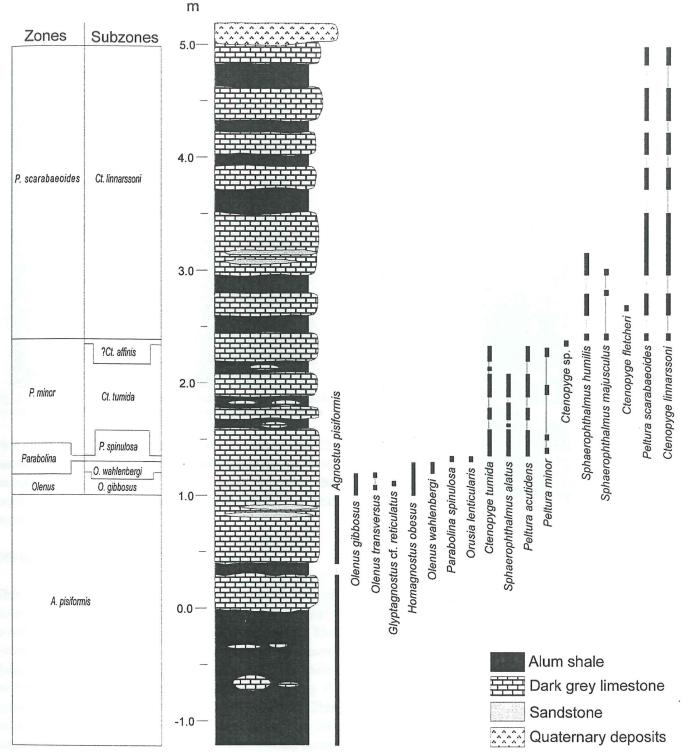


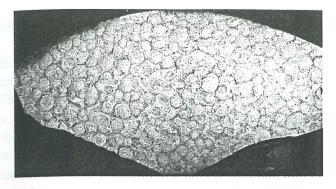
Fig. 4. Lithologic succession, biostratigraphic zonation, and ranges of trilobite and brachiopod taxa in the Upper Cambrian at Kakeled, Kinnekulle, Västergötland.

130 cm to 135 cm: Parabolina spinulosa and Orusia lenticularis Zone

This zone occurs directly above the *Olenus wahlenbergi* Subzone. Three pygidia of *Parabolina spinulosa* were found on bedding planes otherwise completely covered by the brachiopod *Orusia lenticularis*.

135 cm to 240 cm: Peltura minor Zone

The lower 25 cm forms the top of "the Great Stinkstone Bed". The remaining 80 cm consists of three stinkstone beds and three beds of alum shale. All three alum shale beds contain stinkstone lenses. The major part of the zone belongs to the *Ctenopyge tumida* Subzone. The most common trilobites are *Sphaerophthalmus alatus* and



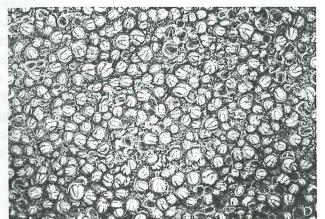


Fig. 5. Example of an alum shale surface (A) and a stinkstone surface (B) with densely packed shields of *Agnostus pisiformis*.

Peltura acutidens. Less common are P. minor and Ct. tumida. Two specimens assigned to Ctenopyge sp. were found in the uppermost part of this zone, indicating the presence of the Ctenopyge affinis Subzone (see the section on systematic palaeontology).

240 cm to 500 cm: Peltura scarabaeoides Zone

This interval comprises six stinkstone beds and six beds of alum shale. The alum shale beds are generally strongly weathered and do not contain any stinkstone lenses. The entire interval belongs to the *Ctenopyge linnarssoni* Subzone. The lowermost 15 cm consists of alum shale, overlain by a 20 cm thick stinkstone bed containing *P. scarabaeoides*, *Sph. humilis* and *Ct. linnarssoni*. This stinkstone bed is overlain by a 15 cm thick alum shale bed succeeded by a 55 cm thick stinkstone bed. Fossils found in the stinkstone bed are *P. scarabaeoides*, *Ct. linnarssoni*, *Sph. humilis*, *Sph. majusculus* and *Ct. fletcheri*. The four stinkstone beds in the upper part of the zone have yielded *P. scarabaeoides* and *Ct. linnarssoni*.

As a result of quarrying, the top of the succession has been removed. The top surface has subsequently been covered, at least partly, by Quaternary deposits from the adjacent cultivated field.

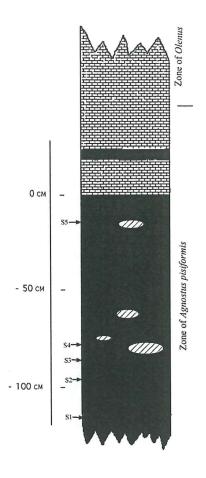


Fig. 6. Sample levels for surfaces 1 to 5 in the Kakeled quarry.

Remarks. - The succession of trilobite species shows that there are several gaps in the sequence. Thus, there is no evidence for the presence of the O. truncatus, O. attenuatus, O. dentatus and O. scanicus Subzones in the Olenus! Homagnostus obesus Zone. Furthermore, the lower subzone of the Parabolina spinulosa Zone, the Parabolina brevispina Subzone, is missing. It is also obvious that the Leptoplastus and Protopeltura praecursor Zones are missing. In the P. minor Zone, the Ct. similis Subzone and the Ct. spectabilis Subzone (the two lowermost subzones) are lacking. In the P. scarabaeoides Zone, there is only evidence for the presence of the Ct. linnarssoni Subzone, whereas the Ct. bisulcata Subzone, the Parabolina lobata Subzone and the Peltura megalops Subzone are missing. There are no fossils indicative of the Acerocare Zone.

Orientation of agnostid shields

In the Agnostus pisiformis Zone at Kakeled, trilobites are preserved both in the alum shales and in the stinkstones. The only fossil encountered in this zone is the zonal index, A. pisiformis. Shields of this species occur in abundance and several surfaces are completely covered by them (Fig. 5). In the shale, the preservation is generally poor and the specimens are almost exclusively disarticulated (only three complete specimens were found). The latter is also true for the specimens in the stinkstone, but their preservation is generally excellent. The disarticulation may indicate transport before deposition (Öpik 1979). This is in contrast to the traditional conception of the depositional pattern where the alum shale is believed to have been deposited during anoxic-dysoxic conditions in fairly deep, stagnant waters (Dworatzek 1987; Bergström & Gee 1985). In such environments one would expect the shields to sink to the

bottom with the convex side down and with their polar angle randomly oriented. In the case of horizontal water movement the shields would flip over and rest with the convex side up. With only one prevailing current direction (unimodal water current) the shields would be oriented with their articulating margin downcurrent (Nagle 1967; Eklöf et al. 1999). A bi-directional water current (waves or tides) would orient the shields with their longitudinal axis perpendicular to the current directions (Nagle 1967; Eklöf et al. 1999).

To clarify whether the alum shale was deposited during calm conditions in deep, stagnant water or in an environment affected by water movements, four alum shale slabs and one stinkstone lens were collected for further investigation and measuring (Fig. 6). On each surface the polar angle was measured for the cephala and pygidia and the distribution of convex up and convex down was counted

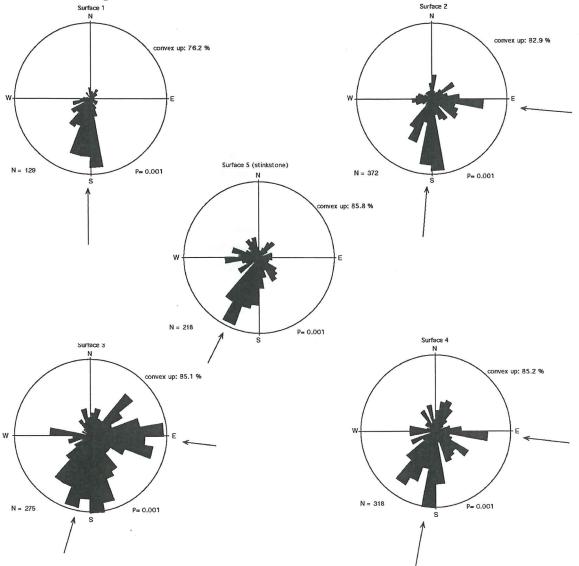


Fig. 7. Polar angle distribution of *Agnostus pisiformis* shields in four alum shale surfaces and one stinkstone surface in the Kakeled quarry. Also shown is the percentage of shields with their convex side up, the number of measured shields and the significance level (P). Arrows denote inferred current directions.

for the shields. The polar angles for the convex down were not measured as they give a result close to random (Eklöf et al. 1999).

On all five surfaces the majority of the shields were deposited with the convex side up (in average 84.2%), thus indicating deposition in non-stagnant water, and were showing a preferred distribution of the shields towards the south (Fig. 7). The shields deposited with their convex side down can be explained as a result of irregularities in the bottom sediment where shields can rest unaffected by water movements (Eklöf et al. 1999). In two of the surfaces (S1 and S5) a significantly unipolar distribution was detected, in S1 the orientation was to the south and in S5 to the south-southwest. The remaining three surfaces (S2-S4) show bimodal distributions with orientation towards the south and towards the east.

The unimodal orientation towards the south detected in surface 1 and 5 probably indicate a southern wind driven current, as wave and tidal currents are considered to give bimodal distribution patterns. Winddriven currents rarely reach below a depth of 100 m (Skinner & Porter 1987, p.380), thus indicating a fairly shallow water environment. Surfaces 2, 3 and 4 show a more complex pattern with bimodal distributions towards the south and east, respectively, possibly indicating a two current system with one current component acting from the south and another current component acting from east. However, it is difficult to get unambiguous interpretations concerning the current directions in this material but it is quite clear that the orientations of the shields were caused by water currents, strongly indicating deposition in a shallow environment affected by currents.

Systematic palaeontology

Terminology. - The morphological terms used are those advocated by Whittington (*in* Kaesler 1997). For the olenid trilobites, some of Henningsmoen's (1957, figs. 1-2) terms are adopted. The suprageneric classification follows Fortey (*in* Kaesler 1997).

Repository. - Discussed and illustrated specimens are housed at the Department of Geology, University of Lund.

Class Trilobita Walch, 1771

Order Agnostida Salter, 1864

Family Agnostidae M'Coy, 1849

Genus Agnostus Brongniart, 1822

Agnostus pisiformis (Wahlenberg, 1818)

Fig. 8A-B

Material. - Several hundred specimens in varying sizes from both shale and stinkstone. Three complete specimens are known from the shale. The remainder of the specimens are disarticulated.

Remarks. - Agnostus pisiformis is probably the best known fossil arthropod in Scandinavia. The species was thoroughly described and discussed by Müller & Walossek (1987), mainly on the basis of isolated and extremely well preserved specimens from Västergötland.

The specimens from Kakeled are strongly flattened and generally poorly preserved in the shale, whereas they are well preserved in the stinkstone beds (Fig. 5).

Occurrence. - In the Kakeled quarry the species is very abundant in the Agnostus pisiformis Zone. It ranges upwards into the Olenus gibbosus Subzone. A. pisiformis has been described from Scandinavia (Sweden, Norway, Denmark), the Outwoods Shales in the English Midlands, east maritime Canada, Siberia and Queensland, Australia (Rushton 1978).

Genus Homagnostus Howell, 1935

Homagnostus obesus (Belt, 1867)

Fig. 8C-E

Material. - Numerous complete or nearly complete cephala and pygidia.

Remarks. - Scandinavian material of *H. obesus* was discussed by Westergård (1922, p. 116, pl. 1, figs. 4 a, b; 1947, pp. 3-4) and Ahlberg & Ahlgren (1996, p. 131, fig. 3A-G). Westergård (1947) pointed out that the median preglabellar furrow commonly reaches the marginal

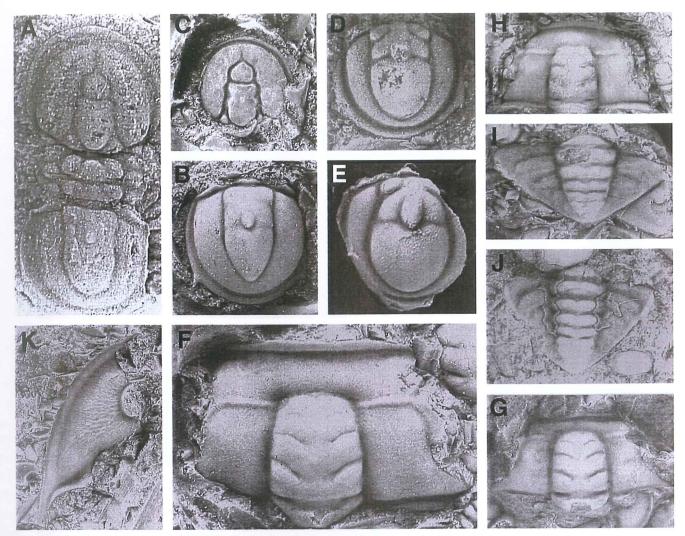


Fig. 8. A-B. *Agnostus pisiformis* (Wahlenberg, 1818), *A. pisiformis* Zone in the Kakeled quarry. A, complete specimen; ×22. B, pygidium; × 8.5. C-E. *Homagnostus obesus* (Belt, 1867), *Olenus/H. obesus* Zone in the Kakeled quarry. C, cephalon; ×8. D, pygidium; ×6. E, pygidium; ×9. F-K. *Olenus gibbosus* (Wahlenberg 1818), *O. gibbosus* Subzone in the Kakeled quarry. F, cranidium; ×6. G, cranidium; ×5. H, cranidium; ×4. I, wide pygidium; ×5. J, narrow pygidium; ×4.5. K, librigena; ×6.

furrow. However, in the Kakeled material the median furrow generally fades out before reaching the marginal furrow.

Occurrence. - If Pratt's (1992) wide concept of *H. obesus* is applied, the species has a nearly world-wide distribution. In Scandinavia, the species is present throughout the Olenus/Homagnostus Zone, except in the Olenus scanicus Subzone (Westergård 1947). At Gum on Kinnekulle the species ranges upwards into the lower part of the Parabolina spinulosa Zone (Ahlberg & Ahlgren 1996, p. 131). At Kakeled the upper three subzones and the O. truncatus Subzone of the H. obesus and Olenus Zone are absent. H. obesus is fairly common in the O. gibbosus and the O. wahlenbergi Subzones.

Genus Glyptagnostus Whitehouse, 1936

Glyptagnostus reticulatus (Angelin, 1851)

Fig. 9K-L

Material. - One fragmentary shield.

Remarks. - G. reticulatus from Scandinavia was discussed by, e.g., Westergård (1947, pp. 5-7 pl. 1, figs. 1-6) and Ahlberg & Ahlgren (1996, pp. 135-136, fig 4. I-P). The specimen found in the Kakeled quarry belongs either to G. reticulatus reticulatus or G. reticulatus nodulosus Westergård, 1947. According to Westergård (1947), G. reticulatus reticulatus is present in the two lowermost subzones in the Olenus/Homagnostus obesus Zone, whereas G. reticulatus nodulosus occurs in the Subzones of O. truncatus and O. wahlenbergi. As the fragmentary

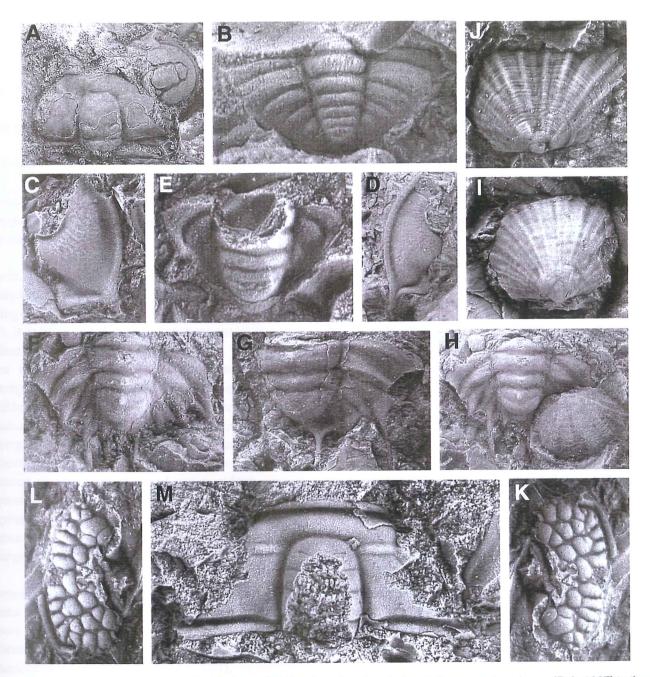


Fig. 9. A. Cranidium of *Olenus gibbosus* (Wahlenberg, 1818) to the left and cephalon of *Homagnostus obesus* (Belt, 1867) to the right; ×6; *O. gibbosus* Subzone in the Kakeled quarry. B, M. *Olenus transversus* (Westergård, 1922), *O. gibbosus* Subzone in the Kakeled quarry. B, Pygidium; ×15. M, cranidium; ×7. C-E. *Olenus wahlenbergi* (Westergård, 1922), *O. wahlenbergi* Subzone in the Kakeled quarry. C, librigena; ×9. D, librigena; ×8. E, pygidium; ×13. F-H. *Parabolina spinulosa* (Wahlenberg 1818), *P. spinulosa* Subzone in the Kakeled quarry. F, pygidium; ×7.5. G, Pygidium; ×9. H, Pygidium together with the brachiopod *Orusia lenticularis*; ×7. I-J. *Orusia lenticularis* (Wahlenberg, 1818), *P. spinulosa* Subzone in the Kakeled quarry. I, pedicle valve; ×11.5. J, brachial valve; ×11.5. K-L *Glyptagnostus reticulatus* (Angelin 1851), *O. gibbosus* Subzone in the Kakeled quarry. K, fragment of pygidium or cephalon; ×11.5. L, mirror image of the same specimen.

specimen from Kakeled occurs in the *O. gibbosus* Subzone (the lowermost subzone), it seems likely that it belongs to *G. reticulatus reticulatus*.

Occurrence. - G. reticulatus is a cosmopolitan species which is widely used for global correlations (e.g. Palmer 1962; Robison et al. 1977).

Order Ptychopariida Swinnerton, 1915

Family Olenidae Burmeister, 1843

Genus Olenus Dalman, 1827

Olenus gibbosus (Wahlenberg, 1818)

Fig. 8F-K

Material. - Several complete or nearly complete cranidia and pygidia, four more or less complete librigenae, and innumerable fragments.

Remarks. -The species was discussed at length by Westergård (1922, pp. 124-125, pl. 5, figs.1-10) and Henningsmoen (1957, pp. 105-106, pl. 1, fig. 1, pl. 3, pl. 9, fig. 7). It is represented by two varieties, one with a wide pygidium, and one with a narrow pygidium. The latter has one or two pygidial segments more than the former (Westergård 1922). At Kakeled both varieties are present. O. gibbosus is closely related to O. transversus, O. truncatus, O. wahlenbergi, O. attenuatus and O. dentatus (Westergård 1922), and they form a natural group. Discrimination between these species is generally difficult and based on, e.g., the shape of the pygidium and the librigenae. The pygidium of O. gibbosus has a pronounced triangular outline with one or two pairs of spines and the librigena has an obtuse inner spine angle (see Henningsmoen 1957, fig. 1).

Occurrence. - Olenus and H. obesus Zone, O. gibbosus Subzone, in the Kakeled quarry. The species is found in vast numbers together with H. obesus (common). The species has been identified in Scandinavia (Sweden, Norway, Denmark) and Wales (Henningsmoen 1957).

Olenus transversus Westergård, 1922

Fig. 9B, M

Material. - One complete pygidium and one nearly complete cranidium.

Remarks. - The species was described by Westergård (1922, p. 125, pl. 3, figs. 11-17; pl. 5, figs 16, 17) and Henningsmoen (1957, p. 108, pl. 3). O. transversus is easily distinguished from O. gibbosus by the morphological differences in the pygidium. The pygidium of O.

transversus lacks pleural spines, the shape is more rounded and the pleural field is considerably wider than the rachis. Three to four axial rings are present in the rachis, but Westergård (1922) noted a form with five axial rings and a narrow rachis. The pygidium from Kakeled seems to agree well with the latter variant.

Occurrence. - O. gibbosus and H. obesus Zone, O. gibbosus Subzone, in the Kakeled quarry. O. transversus is very rare and occurs together with O. gibbosus and H. obesus in the upper part of the subzone. The species has been described from Skåne, Östergötland, Västergötland, Jämtland and Närke (Westergård 1922), and Norway (Henningsmoen 1957).

Olenus wahlenbergi Westergård, 1922

Fig. 9C-E

Material. - Five more or less complete librigenae, several cranidia and a few pygidia.

Remarks. - The species was described in detail by Westergård (1922, p.128, pl. 5, fig. 5-14) and Henningsmoen (1957, pp. 110-111, pl. 3). O. wahlenbergi probably evolved from O. truncatus since they share many morphological features and intermediate forms exist (Henningsmoen 1957). The assignment to O. wahlenbergi is here based on the librigenae. The librigenae of O. wahlenbergi is rather characteristic with a large flip, a large eye aperture and a librigenal spine that deviates from the course of the lateral rim.

Occurrence. - Olenus and H. obesus Zone, O. wahlenbergi Subzone, in the Kakeled quarry. It is here associated with H. obesus, and occurs immediately above the O. gibbosus Subzone (the O. truncatus Subzone is either very thin or missing at Kakeled). O. wahlenbergi has been identified in Sweden, Norway, Denmark (Henningsmoen 1957) and England (Rushton 1974).

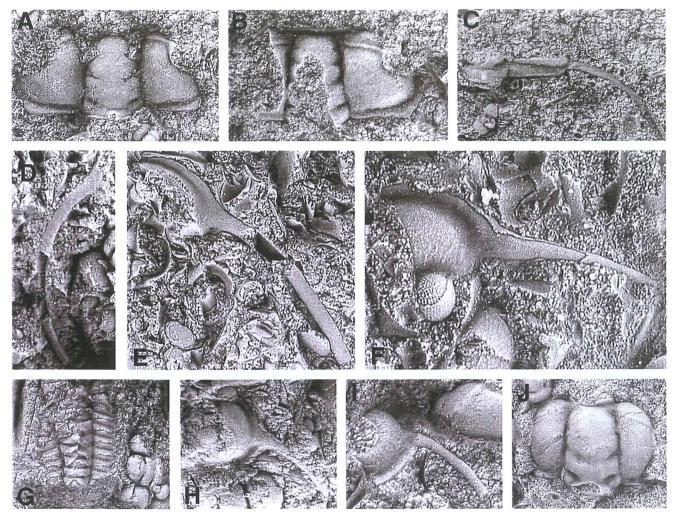


Fig. 10. A-E. *Ctenopyge tumida* Westergård, 1922; *Ct. tumida* Subzone in the Kakeled quarry. A, cranidium; × 10.5. B, cranidium; × 9. C, thoracic segment with spine; × 7. D, librigena; × 11. E, librigena; × 11. F-J. *Sphaerophthalmus alatus* (Boeck, 1888), *Peltura minor* Zone in the Kakeled quarry. F, librigena with eye; × 21.5. G, incomplete thorax probably belonging to the species; × 6. H, librigena; × 15. I, librigena probably belonging to the species; × 13. J, cranidium; × 8.

Genus Parabolina Salter, 1849

Parabolina spinulosa (Wahlenberg, 1818)

Fig. 9F-H

Material. - Three nearly complete pygidia and several fragmentary pygidia. One incomplete cephalon is tentatively assigned to the species.

Remarks. - The species was described and discussed by Westergård (1922, pp. 134-135, pl. 6, figs. 14-20), Henningsmoen (1957, pp. 126-128, pl. 1, fig. 2, text-fig. 12) and Clarkson et al. (1997). The pygidium is very characteristic and can not be confused with any other species.

Occurrence. - P. spinulosa occurs together with the brachiopod Orusia lenticularis in the Parabolina spinulosa

and *Orusia lenticularis* Subzone in the Kakeled quarry. This subzone occurs directly above the *O. wahlenbergi* Subzone. The species has been described from Sweden, Norway, Denmark, England, Wales and Eastern Canada (Henningsmoen 1957).

Genus Ctenopyge Linnarsson, 1880

Ctenopyge tumida Westergård, 1922

Fig. 10A-E

Material. -Ten more or less complete cephala, two nearly complete librigenae and one thoracic segment with a spine.

Remarks. - Ct. tumida was described and discussed by Westergård (1922, pp. 155-156, pl. 11, figs. 13-20) and

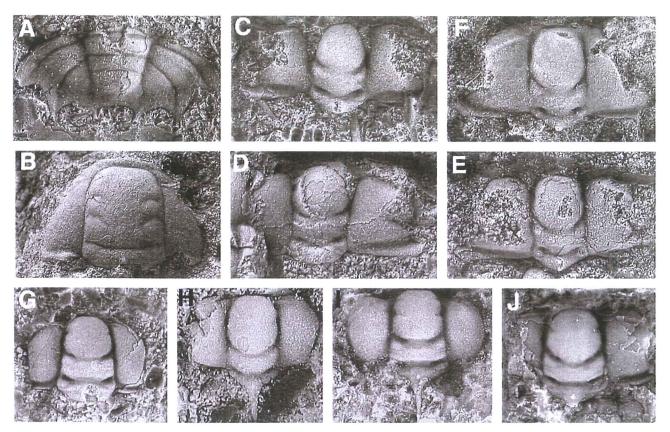


Fig. 11. A. *Peltura acutidens* Brögger, 1882; *Ct. tumida* Subzone in the Kakeled quarry, pygidium ×11. B. *Peltura minor* (Brögger, 1882), *P. minor* Zone in the Kakeled quarry, cranidium; ×5. C-F. *Ctenopyge* sp. Probably the *Ct. affinis* Subzone in the Kakeled quarry. C, cranidium; ×13. D, cranidium; ×13. E, cranidium; ×13.5. F, cranidium; ×12.5. G-J. *Sphaerophthalmus humilis* (Phillips, 1848), *Peltura scarabaeoides* Zone in the Kakeled quarry. G, cranidium; ×7.5. H, cranidium; ×10. I, cranidium; ×13. J, cranidium; ×8.

Henningsmoen (1957, pp. 198-199, pl. 5, pl. 20, fig. 16). Westergård (1922) included two different forms in this species. The major difference concerns the postocular facial suture. In one of the forms the suture is transverse, while it in the other runs obliquely backwards. Henningsmoen (1957) treated the two forms as two different species, the former as *Ct. tumida* and the latter as a new species, *Ct. tumidoides*. The material from Kakeled only includes forms with a transverse postocular facial suture, and the specimens are assigned to *Ct. tumida*.

Occurrence. - Peltura minor Zone, Ctenopyge tumida Subzone, in the Kakeled quarry. Ct. tumida is associated with Peltura minor, Peltura acutidens, and Sphaerophthalmus alatus. The species has been described from Sweden, Denmark and Norway (Henningsmoen, 1957).

Ctenopyge fletcheri (Matthew, 1901)

Material. - One incomplete librigena.

Remarks. - The librigena of this species is very characteristic with a very wide, flattened spine longitudinal ribs on both sides. It was first described by Linnarsson (1880) as Ctenopyge? sp. ind. Forms with the same type of librigena were assigned to Ct. teretifrons by Westergård (1922), but Poulsen (1923) showed that the librigenae that had been referred to Ct. teretifrons instead belonged to Ct. directa Westergård 1922. Westergård (1944) erected a new species, Ct. laticornis, for specimens with the characters mentioned above. Similar librigenae were, however, already assigned to a new species, Sph. fletcheri, by Matthew (1901). Thus, Ct. laticornis Westergård, 1944 is a junior subjective synonym of Ct. fletcheri (Matthew, 1901). Westergård (1947) compared the librigenae of Ct. laticornis and Ct. fletcheri and found a slight difference in the position of the eye aperture. However, Henningsmoen (1957) found this difference insignificant and he regarded specimens assigned to Ct. laticornis and Sph. fletcheri as conspecific (see Henningsmoen 1957, p. 206 for more details).

Occurrence. - P. scarabaeoides Zone, Ct. linnarssoni Subzone, in the Kakeled quarry. It occurs together with P. scarabaeoides, Sph. humilis, Sph. majusculus and Ct. *linnarssoni*. The species has been described from Sweden, Norway, Denmark and Canada (Henningsmoen 1957).

Ctenopyge linnarssoni Westergård, 1922

Fig. 12H-I

Material. - Ten incomplete librigenae, several fragmentary librigenae and one poorly preserved cranidium.

Remarks. - The species has been described by Westergård (1922, pp. 162-163, pl. 13, figs. 3-5) and Henningsmoen (1957, p. 207, pl. 5, pl. 22, fig. 8). In all the specimens from Kakeled, the librigenal spine is attached to the librigena in a more or less perpendicular mode.

Occurrence. - P. scarabaeoides Zone, Ct. linnarssoni Subzone, in the Kakeled quarry. It is associated with Sph. humilis, Sph. majusculus, Ct. fletcheri and P. scarabaeoides.

Ctenopyge sp.

Fig. 11C-F

Material. - Four fairly complete cranidia.

Remarks. - The specimens clearly belong to the genus Ctenopyge since they have a lot of features in common with other Ctenopyge species. The cranidia resemble those of Ct. affinis gracilis Henningsmoen, 1957, but have wider and more convex fixigenae with a longer posterior border. The specimens occur in the same limestone bed as Ct. tumida, but not on the same surface. No specimens of Ct. tumida are present above Ctenopyge sp., and Ct. affinis gracilis was probably recovered from a level within the Ct. affinis Subzone.

Occurrence. - Upper part of the Peltura minor Zone, probably the Ct. affinis affinis Subzone, in the Kakeled quarry.

Genus Sphaerophthalmus Angelin, 1854

Sphaerophthalmus alatus (Boeck, 1838)

Fig. 10F-J

Material. - Hundreds of complete cranidia, several more or less complete librigenae and a thorax. No pygidia have been found.

Remarks. - The species was described as Ct. major by Westergård (1922, pp. 163-165, pl. 13, figs. 9-18). A great deal of confusion has surrounded this species, but Henningsmoen (1957, pp. 212-215) clarified the problems. After restudying the lectotype he came to the conclusion that Boeck's (1838) species is distinct from the species referred to as Spaerophthalmus alatus by all authors after Boeck (except Kjerulf and Störmer). Thus, the species called Sph. alatus by Westergård (1922) actually belongs to Sph. humilis and the species he referred to as Sph. major belongs to Sph. alatus. Regarding Sph. major, as described by Lake (1913), there are lots of uncertainties concerning the taxonomic affinity (Henningsmoen 1957).

Occurrence. - Common in the Peltura minor Zone, Ctenopyge tumida Subzone, and rare in the Peltura scarabaeoides Zone, Ctenopyge bisulcata Subzone, in the Kakeled quarry. The species is also present in the Ct. affinis Subzone. Sph. alatus has been recorded from Sweden, Norway, Denmark (Bornholm), Poland and possibly from Canada (Henningsmoen 1957; Orlowski 1968).

Sphaerophthalmus humilis (Phillips, 1848)

Fig. 11G-J

Material. - Several cranidia and five pygidia.

Remarks. - The species was described as Sph. alatus by Westergård (1922, pp. 165-166, pl. 8, figs. 20-29), and comprehensively discussed by Henningsmoen (1957, pp. 215-217, pl. 5, pl. 22, figs. 7, 11-15). As noted above, Sph. humilis was formerly believed to be a synonym of Sph. alatus (Boeck, 1838) until Henningsmoen (1957) proved otherwise. The spine on the occipital ring is preserved in two cranidia from Kakeled. The cranidial surface shows a faint granulation.

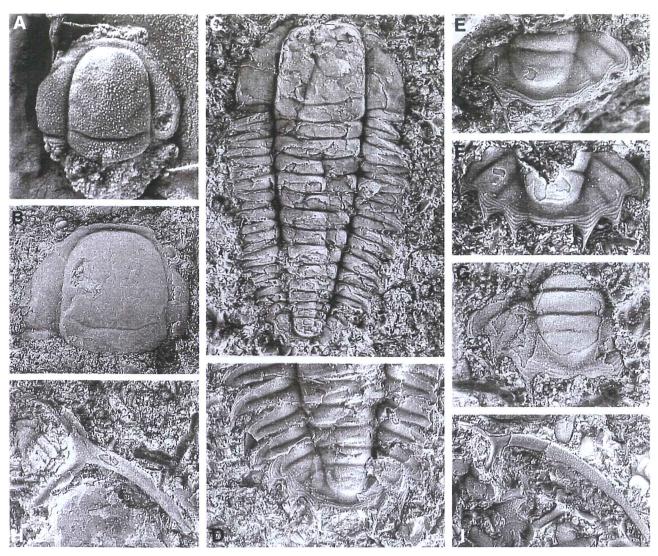


Fig. 12. A-G. *Peltura scarabaeoides* (Wahlenberg, 1818), *P. scarabaeoides* Zone in the Kakeled quarry. A, juvenile cranidium; ×10. B, adult cranidium; ×4.5. C, Complete specimen; ×5.5. D, pygidium and part of the thorax; ×7.5. E, pygidium; ×7. F, pygidium; ×9.5. G, pygidium; ×9. H-I. *Ctenopyge linnarssoni* Westergård, 1922; *Ct. linnarssoni* Subzone in the Kakeled quarry. H, librigena; ×5.5.

Occurrence.- Lower part of the *P. scarabaeoides* Zone in the Kakeled quarry. The two lowermost subzones in the *P. scarabaeoides* Zone have almost identical faunas except for species of *Ctenopyge*. Since the *Ctenopyge* species defining the lowermost subzone are absent, the separation of subzones in the lower part of the *P. scarabaeoides* Zone in the Kakeled quarry is impossible. *Sph. humilis* occurs together with *P. scarabaeoides*, *Sph. majusculus*, *Ct. fletcheri*, *Ct. linnarssoni* and *Sph. alatus* (only one specimen). The species has been described from Sweden, Norway, Denmark, Poland, England, Wales and Eastern Canada (Henningsmoen 1957).

Sphaerophthalmus majusculus Linnarsson, 1880

Material. - Three incomplete cranidia.

Remarks. - The species was described and discussed by Henningsmoen (1957, pp. 218-219, pl. 5, pl. 22, figs. 16-17) and Westergård (1922, pp. 166-167, pl. 13, figs. 30-35).

Occurrence. - Lower part of the *P. scarabaeoides* Zone in the Kakeled quarry. It occurs together with *Sph. humilis, P. scarabaeoides* and *Ct. fletcheri. Sph. majusculus* has been recorded from Sweden, Norway and possibly from England (Westergård 1922; Henningsmoen 1957).

Genus Peltura Milne Edwards, 1840

Peltura acutidens Brögger, 1882

Fig. 11A

Material. - Several pygidia and cranidia.

Remarks. - Peltura acutidens is easily distinguished from other species of Peltura by the features of the pygidium, namely three axial rings and three pairs of well developed pleural spines. The pygidium resembles that of Peltura scarabaeoides westergaardi Henningsmoen, 1957, but differs in having a shorter distance between the posterior pairs of spines. The species has been described in detail by Westergård (1922, p. 175, pl. 15, figs. 14-17) and Henningsmoen (1957, pp. 233-234, pl. 6, pl. 25, figs. 1, 3, 4, 7, 9, 11).

Occurrence. - P. minor Zone, Ct. tumida Subzone, in the Kakeled quarry, where it is associated with P. minor, Ct. tumida and Sph. alatus. The species has been recorded from Sweden and Norway (Henningsmoen 1957).

Peltura minor (Brögger, 1882)

Fig. 11B

Material. - Three complete cranidia, and internal moulds of four cranidia.

Remarks. - The species has been described by Westergård (1922, p. 175, pl. 15, figs. 3-11) and Henningsmoen (1957, pp. 235-236, pl. 6; pl. 25, figs. 2, 5). The cranidium resembles that of *P. acutidens*, but the glabella is more rectangular in outline. The pygidium lacks marginal spines.

Occurrence. - Peltura minor Zone, Ct. tumida Subzone, in the Kakeled quarry. It is associated with Ct. tumida, Sph. alatus and P. acutidens. P. minor has been recorded from Sweden and Norway (Henningsmoen 1957).

Peltura scarabaeoides scarabaeoides (Wahlenberg, 1818)

Fig. 12A-G

Material. - Several pygidia, cranidia, librigenae, and thoracic segments.

Remarks. - The species was described and discussed by. e.g., Westergård (1922, pp. 173-174, pl. 15, figs. 12, 13, 18), Henningsmoen (1957, pp. 237-239, pl. 2, fig 1, pl. 6, pl. 25, figs. 6, 13-14, pl. 26, figs. 1-2) and Clarkson (1973, pp. 746-748, fig. 4 a, c). Henningsmoen (1957) described a subspecies of P. scarabaeoides scarabaeoides called P. s. westergaardi. It differs from P. scarabaeoides scarabaeoides in having longer and straighter pygidial spines, and a shorter distance between the posterior pair of spines. The two posterior pairs of spines are not bent down in P. s. westergaardi. Henningsmoen (1957, p. 239) noted that P. s. westergaardi has a greater distance between the posterior pair of the pygidial spines, but this is not correct as the distance between the spines in P. s. westergaardi is smaller than in P. scarabaeoides (compare Henningsmoen 1957, pl. 25, figs. 14-15).

In the Kakeled material no pygidia were found that fully agrees with the description of *P. scarabaeoides westergaardi*. However, pygidia with very long spines (like those in *P. scarabaeoides westergaardi*) with the posterior pair of spines far apart (like those in *P. scarabaeoides scarabaeoides*) have been recorded. Furthermore, one pygidium with a short distance between the posterior pair of spines (like those in *P. scarabaeoides westergaardi*), but with short, bent down spines (like those in *P. scarabaeoides scarabaeoides*), was found. These intermediate forms are common and associated with *P. scarabaeoides scarabaeoides* in the Kakeled quarry.

Occurrence. - P. scarabaeoides Zone, Ct. linnarssoni Subzone, in the Kakeled quarry. It is associated with Sph. humilis, Sph. majusculus and Ct. linnarssoni. The species has been recorded from Scandinavia, Poland, Great Britain and Canada (Henningsmoen 1957; Orlowski 1968).

Class Articulata Huxley, 1869

Order Orthida Schuchert & Cooper, 1932

Family Finkelnburgiidae Schuchert & Cooper, 1931

Genus Orusia Walcott, 1905

Orusia lenticularis (Wahlenberg, 1818)

Fig. 9I-J

Material. - Hundreds of disarticulated specimens.

Remarks. - This species is normally associated with the trilobite Parabolina spinulosa. This is also the case in the Kakeled quarry. Generally, O. lenticularis occurs in abundance and its valves are densely packed and cover the bedding planes almost completely. In some of the specimens the ornamentation is less distinct due to the preservation.

Occurrence. - Parabolina spinulosa and Orusia lenticularis Zone in the Kakeled quarry. The species has been recorded from Sweden, Norway, Denmark (Bornholm), Canada, Great Britain and Poland (Orlowski 1968).

Concluding remarks

Upper Cambrian strata are well exposed in a number of old quarries on Kinnekulle (Westergård 1922, 1943). Drillings show thicknesses of 14.2 and 14.8 m (Westergård 1943). The Agnostus pisiformis Zone is between 2 and 3.5 m thick, and represented by alum shale and scattered stinkstone lenses (Westergård 1943). The Olenus/Homagnostus obesus Zone varies in thickness between 0.6 and 2 m (Westergård 1943). Generally it is about 1 m thick. The Peltura minor Zone and the P. scarabaeoides Zone combined measures about 9 m in thickness (Westergård 1943). The Parabolina spinulosa, the Leptoplastus and the Protopeltura praecursor Zones are generally thin or missing (Westergård 1947). The Acerocare Zone is missing or represented by the Parabolina heres (= Peltura transiens) Subzone (Westergård 1947).

The section at Kakeled is representative for the Upper Cambrian of Kinnekulle. In terms of stratigraphic completeness it is comparable to other sections in the area. The *Agnostus pisiformis* Zone is 2.2 m thick at Kakeled and probably only the lowermost part is unexposed. The *Olenus/H. obesus* Zone is remarkably thin (0.3 m) in the Kakeled section. As in most other localities on Kinnekulle the *Parabolina spinulosa* Zone is very thin. The *Leptoplastus* Zone is generally present, but very thin on Kinnekulle (Westergård 1922). This zone has not been recorded at Kakeled. At Kakeled, the *Peltura* beds (the *P. minor* and *P. scarabaeoides* Zones) are represented by 3.65 m and it is obvious that the upper part is missing.

The percentage of stinkstones appears to be much higher at Kakeled than in most other sections on Kinnekulle. At Kakeled the stinkstones comprise about 70% of the succession. On northern and eastern Kinnekulle the Upper Cambrian generally consists of less than 40% stinkstones, increasing to 50% or more to the southwest.

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