

A mid-Cambrian shelly fauna from Ritland, western Norway and its palaeogeographical implications

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A new mid-Cambrian shelly fauna from Ritland, western Norway, significantly extends the known development of the Andrarum limestone facies to the edge of the Baltic craton. The assemblage includes the trilobites *Axagnostus fallax* (Linnarsson), *Solenopleura bucculenta* Grönwall, *Anomocare* cf. *laeve* (Angelin) and abundant, etched specimens of the linguliformean brachiopod *Treptotreta? socialis* (von Seebach) together with *Dictyonina ornatella* (Linnarsson); the fauna indicates the presence of the *Jincella brachymetopa* Zone and also includes hyoliths, bradoriid crustaceans and sponge spicules. Elsewhere the trilobites and brachiopods have widespread distributions in amphicratonic settings during this part of the mid-Cambrian; the Scandinavian faunas signal the inshore migration of these more cosmopolitan elements, tracking the shallower-water development of calcareous facies of the Andrarum Limestone.

Key words: Trilobites, brachiopods, facies, Cambrian, Norway.

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Palaeogeographical maps for the Cambrian Period in Scandinavia are often terminated either at the Oslo Region or the Caledonian front (cf. Buchardt et al. 1997); more rarely areas west of these features are included but not specifically discussed (cf. Hagenfeldt 1989). This is not surprising since the Oslo Region has remained a standard reference area since the work of Kjerulf & Dahll (1857) and the later fundamental studies by Brøgger (1875, 1876, 1878 and 1882). To the west, proven Cambrian rocks in the Parautochthon and Lower Allochthon of southern Norway are mentioned in reviews by Martinsson (1974), Bergström (1980), Bergström & Gee (1985), while Bruton et al. (1989) provided faunal identifications for given sections from the thrust sheets of East Jotunheimen and the parautochthon of Hardangervidda (see also Bruton et al. 1985). They also figured selected specimens from the Cambrian of Rogaland, the subject of the present work. However, to date, these data have not contributed to palaeogeographic analyses of the region.

It was something of a sensation in 1949 when Bjørn Andersen (now Professor emeritus), discovered the first Cambrian fossils from the locality at Ritland in the district of Hjelmeland, Rogaland county. These were later described by Henningsmoen (1952), who

concluded that the fauna belonged to the lower Middle Cambrian *Paradoxides oelandicus* Stage. Rocks of this age are apparently lacking in the Oslo Region, Västergötland and Scania (see Martinsson 1974), and Henningsmoen envisaged a shallow-water marine embayment in the Rogaland area seaward of a landmass to the east.

In 1986, one of us (DLB), visited the area together with Mr Frank Nikolaisen and spent two days collecting from various exposures along the west-facing scarp of Austmannshovud, east of Ritland Farm (Fig. 1). We confirmed the presence of the *Acadoparadoxides* (*Baltoparadoxides*) *oelandicus* Stage from outcrops at the base of the slope and found a new, higher horizon, with limestone concretions, from which the fauna described here was recovered. This new fauna indicates the presence of the *Jincella brachymetopa* Zone of the younger *Paradoxides forchhammeri* Stage. The intervening *P. paradoxissimus* Stage has not been confirmed, but is possibly also present. The new data from Ritland significantly extend the facies and fauna of the Andrarum Limestone westwards.

The Ritland Locality

All figured material was collected from the west-facing scarp of Austmannshovud (MR 532692; Lyngsvatnet Series M 711. Sheet 1313 III), east of Ritland farm, not west as stated by Henningsmoen (1952, p. 14), in the Hjelmeland district, Josenfjord (Fig. 1). The locality is best reached by ferry from Stavanger to Tau and then by car on route 13 via Hjelmeland with parking at Kleivaland (MR 508695). Ritland farm lies in a broad alluvial-filled valley approximately 3 km ESE of Kleivaland and is reached on foot along a private forest track. The valley contains two adjoining lakes with tourist cabins on the east side and at the foot of Austmannshovud. Access to the latter is easiest along the southeast corner of the valley where erosion reveals a spectacular polymict, immature breccia with gneiss blocks measuring several metres across. This is not a typical basal conglomerate and Spjeldnæs (1985, p. 139) has suggested depositional processes involving rifting or faulting. From here northwards at least eight scree fans extend from the west slope of Austmannshovud and contain blocks of a dark arkose, black quartzite and black shales the latter yielding trace fossils, hyolithids, nonarticulated brachiopods, and sponge spicules. This is the fauna described by

Henningsmoen (1952), and belongs to the *Acadoparadoxides* (*Baltoparadoxides*) *oelandicus* Stage (Fig. 2). We estimate the thickness of shale to be at least 120 m and these are capped by a pale weathering (autochthonous?) quartzite. Shales in the topmost 20 m, exposed in the vertical cliff below the quartzite, contain pale limestone concretions and loose blocks of these yield coquinas of trilobites including *Axagnostus fallax* (Linnarsson, 1869), *Solenopleura bucculenta* Grönwall, 1902, *Anomocare* cf. *laeve* (Angelin, 1852) and abundant etched specimens of the nonarticulated brachiopod *Treptotreta? socialis* (von Seebach, 1865) together with *Dictyonina ornatella* (Linnarson, 1876), indicative of the *Jincella brachymetopa* Zone of the *Paradoxides forchammeri* Stage.

In total, five micromorphic species of brachiopod were retrieved by acid etching from blocks of limestone collected at the Ritland locality. Four of the species, *Obolus? sp.*, *Lingulella sp.*, *Treptotreta? socialis* and *Acrothele granulata* are chitinophosphatic lingulates whilst the other, *Dictyonina ornatella* is a chitinophosphatic paterinate. *T? socialis* overwhelmingly dominates the assemblage with several hundred specimens available for study, in contrast to the few individuals retrieved of the other genera. Elsewhere in the sequence at Ritland, Henningsmoen (1952) illustrated

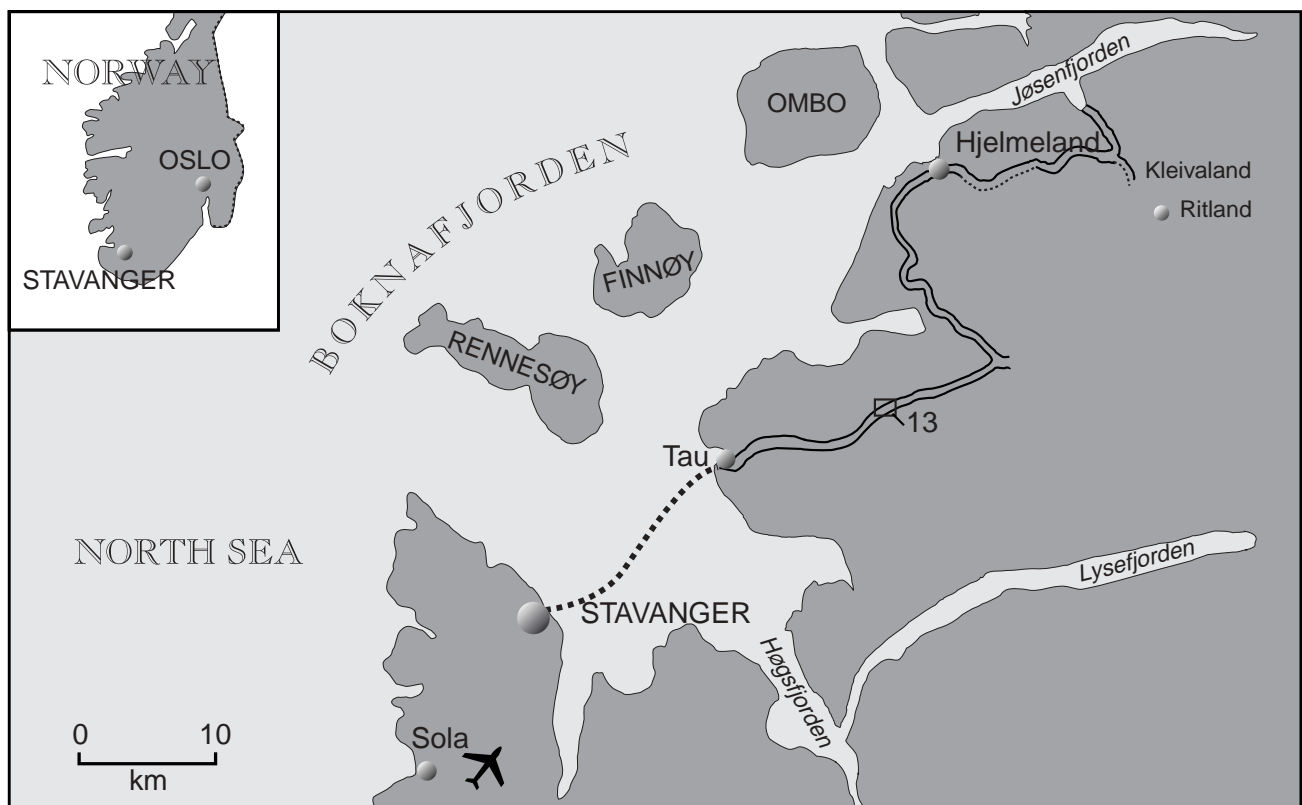


Fig. 1. Locality map and route to Ritland from Stavanger, west Norway.

Fig. 2. Schematic lithostratigraphical section at Ritland with fossiliferous concretions assigned to the *Jincella brachymetopa* Zone. Zonal system for Middle Cambrian based on Shergold (1997, p. 310). Lithological symbols: triangles – polymict breccia; horizontal lines – shales; limestone ornament – carbonate concretions; stippled ornament – quartzite.

	STAGES	ZONES	LITHOSTRAT.	
MIDDLE CAMBRIAN	<i>Paradoxides forchhammeri</i>	<i>Lejopyge laevigata</i>	Stippled ornament with a question mark	
		<i>Jincella brachymetopa</i>	Limestone ornament with circular patterns	
	<i>Paradoxides paradoxissimus</i>	<i>Ptychagnostus punctuosus</i>	Horizontal lines	
		<i>Hypagnostus parvifrons</i>	Horizontal lines with a question mark	
		<i>Tomagnostus fissus</i> <i>Acidusus atavus</i>	Horizontal lines	
		<i>Triplagnostus gibbus</i>	Horizontal lines	
	<i>Acadoparadoxides oelandicus</i>	<i>Acadoparadoxides pinus</i>	Horizontal lines	
		<i>Acadoparadoxides insularis</i>	Horizontal lines	
			?	Triangles

and noted the lingulates *Lingulella* sp., *Acrothele granulata* (Linnarsson, 1876) and *Treptotreta? socialis* from lower in the *Paradoxides oelandicus* Zone.

Martinsson (1974) listed Middle Cambrian brachiopods from the Baltoscandian successions, noting that the taxonomy of the long-ranging nonarticulates has yet to be revised to modern terms. As a whole the assemblage is most similar to the nonarticulated brachiopod fauna of the Swedish Andrarum Limestone (Berg-Madsen 1985a, b), currently under revision (M.G. Bassett, pers. comm.). Here *T? socialis* and *D. ornatella* are common elements together with other acrotretids, acrothelids and lingulides.

The Ritland fauna and its significance

Compared with Middle Cambrian faunas from elsewhere in Norway (cf. Brøgger 1878, Strand 1929, 1948, Spjeldnæs 1955, 1962), the fauna from Ritland is very

diverse containing trilobites, nonarticulated brachiopods and large quantities of cystoid stem columnals that can be closely compared with those described and listed by Berg-Madsen (1985b, 1986) from the Andrarum Limestone of Bornholm (cf. Martinsson 1974, p. 205). We therefore assign the fauna from Ritland to the *Jincella brachymetopa* Zone and show (Fig. 3) the distribution of the limestone facies at this time.

Both the trilobite (Conway Morris & Rushton 1988) and brachiopod (Engelbretson 1996) faunas apparently belong to a biofacies with a widespread distribution during the mid-Cambrian. It is possible that the carbonate facies of the Andrarum limestone encouraged the inshore migrations of many elements, previously recorded from older rocks, of an otherwise deeper-water, oceanic fauna along the margins of Baltica during a regressive, oxic event within the *Jincella brachymetopa* Zone. In their review of Cambrian faunas in the Caledonides, Conway Morris & Rushton (1988, pp. 100–102) pointed to regressions and transgressions to explain faunal turnovers along cratonic margins during the Mid-Cambrian. Thus

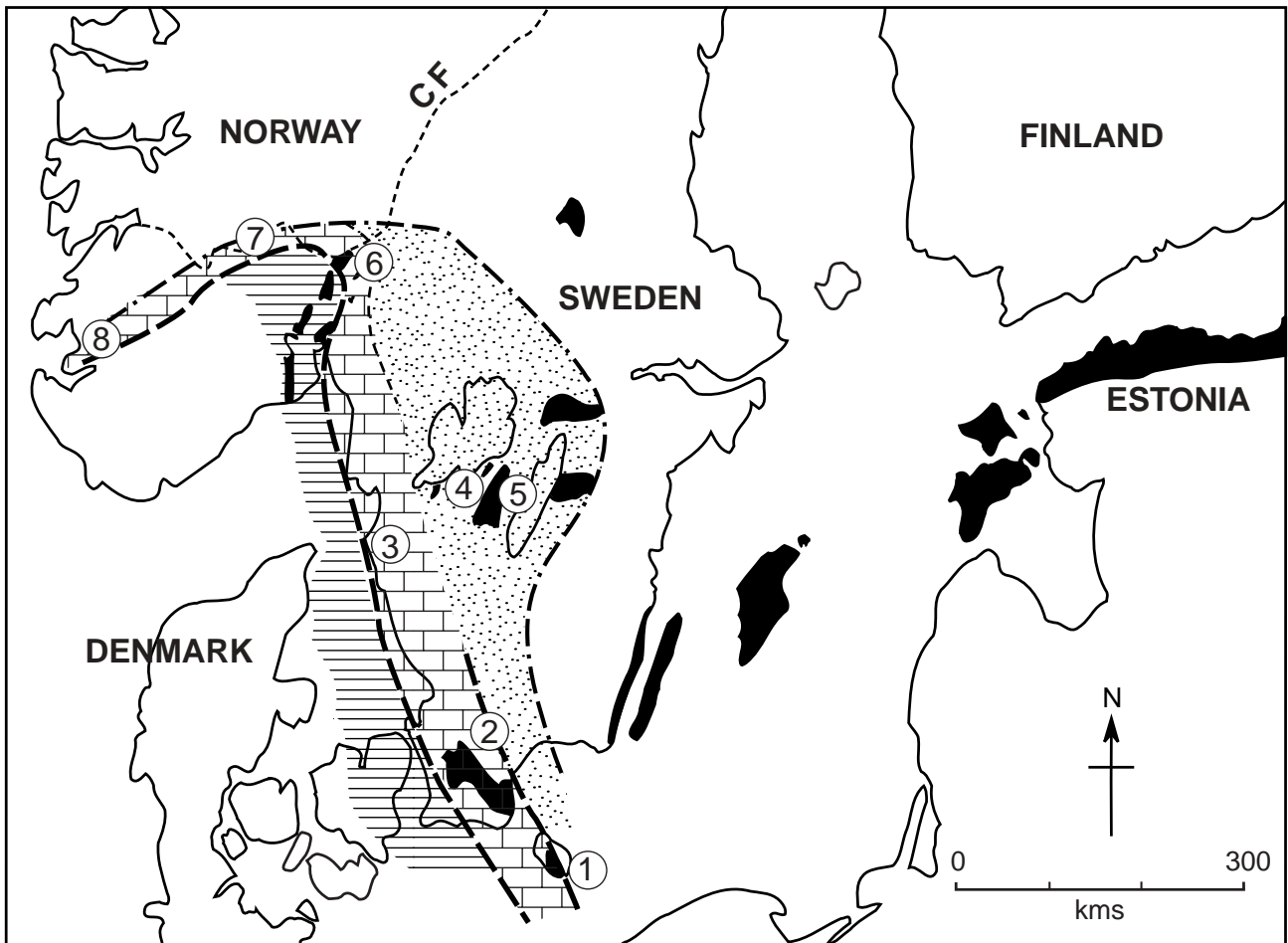


Fig. 3. Map of the Baltoscandian area showing major outcrops of Lower Palaeozoic rocks in black and proposed facies belts during the Middle Cambrian *Jincella brachymetopa* Zone interval. Horizontal shading - deeper water Alum Shale facies; limestone symbol - shallower water Andrarum Limestone facies; dotted symbol - nearshore facies including glauconitic sandstone and conglomerates. Information for Andrarum Limestone facies based on following localities: 1. Bornholm; 2. Scania; 3. Bohus; 4. Halleberg and Hunneberg; 5. Falbygden and Billingen; 6. Mjøsa; 7. Valdres; 8. Ritland. (For details of other facies see Martinsson 1974, Buchardt et al. 1997).

transgressions promoted the migration of cooler-water faunas with associated deepening and a regressive period, such as that represented by the Andrarum Limestone, encouraged the incursion of trilobite families such as the Anomocaridae known from Siberia (Egorova et al. 1982) and China (Chang 1998) and the Dolichometopidae from China (Chang 1998) and Australia (Öpik 1961, 1982). In correlating the upper Middle Cambrian of Queensland with the Andrarum Limestone, Öpik (1961, pp. 37–38) noted that the latter must be extremely condensed and Niels Schovsbo (pers. comm. to Harper 16–08–1999), suggested that the unit is a condensed multiple event horizon, bypassed by clastic sediment but recording both transgressions and regressions.

Clearly the Andrarum Limestone represents a shallow-water facies with an associated short-lived fauna.

The identification of this fauna at Ritland extends its distribution significantly westwards and allows a revision of facies patterns across the southern parts of Baltoscandia during the *Jincella brachymetopa* interval. In addition to its type section in Scania and southern Bornholm and an outcrop in a crevice at Bohus (Martinsson 1974), this facies fauna is known from Halleberg and Hunneberg together with Billingen and Falbygden in Sweden, within the Lower Allochthon at Valdres (Brøgger 1876) and from the northern part of the Mjøsa area, Norway (Strand 1929). The Andrarum Limestone and related facies thus formed an arcuate belt extending from Ritland through the northern parts of the Oslo Region to Scania and Bornholm (Fig. 3). Landward, to the north and east in Närke and in Östergötland and parts of Västergötland, a range of more nearshore facies including glauconitic

sandstones and conglomerates were developed. Seaward, to the south and west, the more typical Alum shales were deposited.

Material and methods

All trilobites and larger brachiopods figured have been prepared from shale or limestone and photographed using a ring light illumination. Specimens were coloured with a black opaque (Perfex Corp., P.O. Box 7, Ocean City, N.J., USA) and then coated with ammonium chloride before photographing. The smaller nonarticulated brachiopods and other phosphatic fossils were etched from limestones using acetic acid, mounted on stubs and coated with gold palladium before photographing using a Jeol JSM-35C apparatus. All material is deposited in the collections of the Paleontological Museum, University of Oslo (PMO) and figured material catalogued accordingly.

Systematic Palaeontology Trilobites (DLB)

Superfamily Agnostoidea M'Coy, 1849
Family Diplagnostidae Whitehouse, 1936
Subfamily Diplagnostinae Whitehouse, 1936
Genus *Axagnostus* Laurie, 1990

Type species. – By original designation, *Aagnostus fallax* Linnarsson, 1869.

Axagnostus fallax (Linnarsson, 1869)
Figs 4H, J-P

1989 *Peronopsis* cf. *quadrata* (Linnarsson, 1869); Bruton et al., fig. 3: 10,14,15.

For synonymy and discussion see Laurie (1990).

Discussion. – Laurie (1990) has recently treated the history and systematics of this species, selected a lectotype (see also Shergold & Laurie, 1997, fig. 230b) and refigured material illustrated by Westergård (1946). The present material adds nothing new but study of this and additional specimens of related species, not available to Laurie, adds to the discussion. Laurie (1990, p. 318), clearly distinguished *Axagnostus* from *Peronopsis* (Hawle & Corda 1847; see Robison 1978, 1982; Rushton 1979), characterised in having a bipartite glabella with simple basal lobes, absence of a preglabellar median furrow and pygidia in which

the transverse rachial furrows are absent or weakly developed. The present material clearly belongs to the *fallax* species-group in which border furrows are broad and pygidia have border spines and a lanceolate rachis with node. Study of Norwegian and Swedish specimens of *Axagnostus fallax* show that they are different from *Acadagnostus* (see Shergold & Laurie 1997, p. 362), said to be the senior synonym, and there is a continuous sequence of forms from *Axagnostus fallax* (upper *Triplagnostus* (*T.*) *gibbus* - *Hypagnostus parvifrons* zones), through morphs previously identified as *Peronopsis ferox* (Tullberg, 1880) and *P. minor* (Brøgger, 1878), both recorded from the *Ptychagnostus punctosus* Zone in Norway and Sweden and extending together with *Peronopsis quadrata* (Tullberg) into the *Jincella brachymetopa* Zone in Scania and on Bornholm (Berg-Madsen 1985, Table 1).

All these forms differ from each other in the amount of character-change shown to take place during the ontogeny of *Axagnostus fallax* (see Robison 1982, p.18), thus making diagnosis of individual species difficult. In addition, Robison (1982), has shown that small morphological changes occur both geographically and stratigraphically in Scandinavia and the western United States of America where *Axagnostus ferox* consistently appears above *A. fallax* from which it differs in having a shorter, more rounded rachis. One of the pygidia figured here (Fig. 4L), is like the lectotype of *A. ferox* (see Westergård 1946, pl. 2, figs. 27a,b), whilst the remainder, together with the cranidia, are identical to specimens of *A. fallax* figured by Laurie (1990).

The pygidia (Figs 4M-P), have a well defined lanceolate rachis which does not reach the border furrow, a prominent node and a weak furrow marking the first rachial ring. The pleural field is strongly convex, a change in slope separating it from the border furrow and margin. The latter broadens postero-laterally with a pair of short spines. The border is widest inside the spine, a feature present in small holaspide pygidia but not in large holaspides of *A. fallax* (cf. Robison 1982, pl. 6, fig. 8a,b and pl. 6, fig. 6a,b). It is also present in pygidia of *A. minor* and *A. quadrata* figured by Westergård (1946, pl. 3).

Brøgger (1878, table opposite, p. 34) listed the name *minor* for morphs from the Middle Cambrian of Norway that Westergård (1946, pl. 3, figs 3–7), later identified as *Peronopsis fallax minor*. The Norwegian material has never been figured and topotype material in collections of the Palaeontological Museum, University of Oslo, is flattened in shale unsuitable for defining the species. Moreover, as noted by Laurie (1990, p. 322), Westergård's specimens probably include more than one species and a revision is needed in order to redefine the taxon. In Bruton et al. 1989 (fig. 3: 10, 15), a pygidium (Fig. 4N) was mistakenly identi-

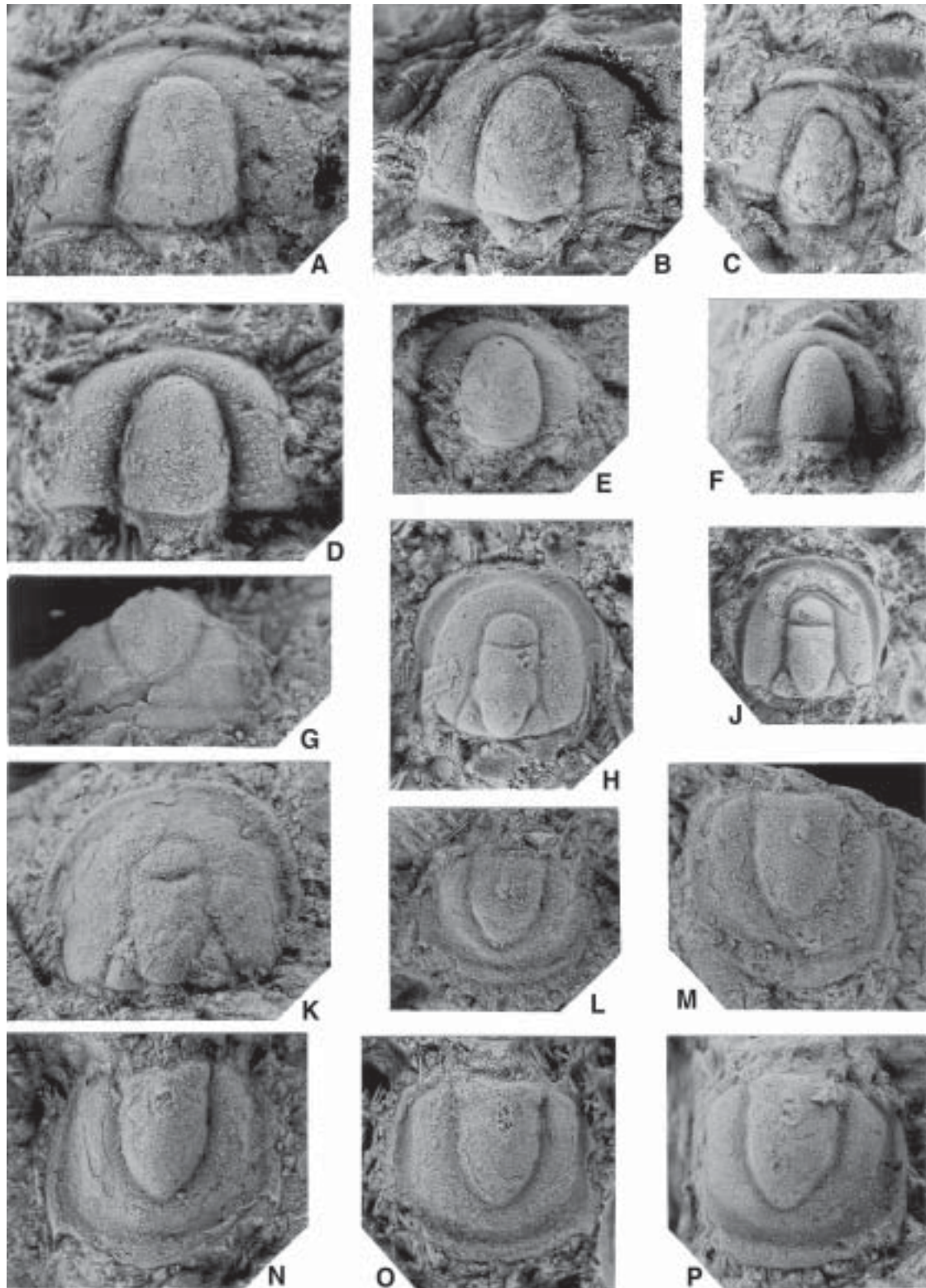


Figure 4. A-G. *Solenopleura bucculenta* Grönwall, 1902. A. PMO 164.209, cranidium, dorsal view, X7. B. PMO 164.205, cranidium, dorsal view, X8. C, G. PMO 164.200, cranidium, dorsal and frontal views, X6. D. PMO 164.211, cranidium, dorsal view, X7. E. PMO 164.203, cranidium dorsal view, X5. F. PMO 164.208, cranidium, dorsal view, X6. H, J-P. *Axagnostus fallax* (Linnarsson, 1869). H. PMO 164.212, cephalon, dorsal view, X6. J. PMO 164.210, cephalon, dorsal view, X7. K. PMO 164.199, cephalon, dorsal view, X7. L. PMO 164.201, pygidium, dorsal view, X6. M. PMO 164.204, pygidium, dorsal view, X6. N. PMO 117.050, pygidium, dorsal view, X6. Figured by Bruton et al. 1989, fig 3: 10,15. O. PMO 164.206, pygidium, dorsal view, X8. P. PMO 164.207, pygidium, dorsal view, X6.

fied as *Peronopsis* cf. *quadrata*, from which it differs in not having a pointed rachis that almost reaches the border furrow. Associated cephalons show the same broad furrow of *A. fallax*, whilst the smaller specimen has a narrower border (cf. Robison 1982, pl. 6, figs 5, 7).

Family Solenopleuridae Angelin, 1854

Subfamily Solenopleurinae Angelin, 1854

Genus *Solenopleura* Angelin, 1854

Type species. – By subsequent designation (Walcott, 1884), *Calymene holometopa* Angelin, 1851.

Discussion. – Westergård (1953) discussed the family affinities and described 8 species of *Solenopleura*. All but one of these, *S. canaliculata* (Angelin, 1851), together with a Bohemian species, were assigned by Šnajdr (1958) to a new genus *Jincella*. However, as pointed out by Öpik (1967, p. 184), *Jincella* is a synonym of *Asthenopsis* Whitehouse, 1939. Taylor & Rush-ton (1971, p. 8 footnote) have also pointed out that the type species of *Solenopleura* (*S. holometopa*), was selected by Walcott (1884), and is not, as listed by Šnajdr (1958) and Moore (1959), *Calymene canaliculata* Angelin, 1851, selected by Miller (1889). The family is in dire need of revision as it appears that not all the features used in distinguishing the various assigned genera are valid. Many species have been described from the Acado-Baltic province and have been separated on slight differences of glabellar convexity, depth of dorsal furrows and length of anterior border, all dependent on state of preservation and whether or not internal or external moulds are available for study.

Solenopleura bucculenta Grönwall, 1902

Figs 4A–G

1989 *Solenopleura* sp.; Bruton et al. fig. 3: 13.

Diagnosis and discussion. – The cranidia figured here are assigned to *S. bucculenta* on account of the following diagnostic features:

- 1) Glabella blunt to tapering, outlined by very deep dorsal and preglabellar furrows.
- 2) Deep median pit in preglabellar furrow.
- 3) Occipital ring with median node.
- 4) Anterior border furrow deep, border upturned.
- 5) Eye ridges absent.
- 6) Posterior branch of facial suture slightly divergent.
- 7) Internal moulds smooth, dorsal exoskeleton with coarse granulation. Cranidia of this species are

readily separated from other species of *Solenopleura* (and *Jincella*) on account of the deep dorsal furrows and the straighter facial sutures.

Genus *Parasolenopleura* Westergård, 1953

Type species. – By original designation, *Calymene aculeata* Angelin, 1851.

Discussion. – In defining *Parasolenopleura*, Westergård (1953, p. 21), listed differences between this genus and *Solenopleura*, pointing out that in the former the cheeks are flatter, furrows are shallower and the cranidium slopes less steeply downwards anteriorly. Many of these features of the cranidium are variable but it does seem that cranidia of *Solenopleura* s.l., as defined above, can be separated from cranidia of *Parasolenopleura* on account of the greater convexity of the fixed cheeks. *Parasolenopleura* has prominent eye ridges lacking in *Solenopleura*.

Parasolenopleura cf. *peregrina* (Wallerius, 1930)

Figs 5A–D

1989 *Parasolenopleura* sp.; Bruton et al. fig. 3: 12.

Diagnosis and discussion. – The present material is assigned to this species on account of the prominent occipital spine (see Westergård 1953, pl. 7, fig. 9). Glabella strongly convex, tapering forwards with well defined dorsal and preglabellar furrows. Occipital ring the base of a broad upwardly directed spine. Preglabellar area narrow and convex (sag.), flatter laterally; border furrow well defined. Eye ridges curved outwards and backwards, palpebral lobe at about one half glabellar length.

Type material of this species is apparently missing and Westergård's two cranidia are not well preserved. One specimen (Westergård 1953, pl. 7, fig. 9), shows the broad based occipital spine, whilst the other (Westergård 1953, pl. 7, fig. 10), shows the spine broken but the doubling of the occipital ring gives the impression of an entire posterior margin. This is the case in the specimen figured herein (Figs 5B,C), indicating that the spine is an extension of the dorsal surface of the exoskeleton and not a posterior extension of the occipital ring. The presence of a prominent spine separates *P. peregrina* from the type and other species figured by Westergård (1953), which have a small node or a thin, needle-like spine.

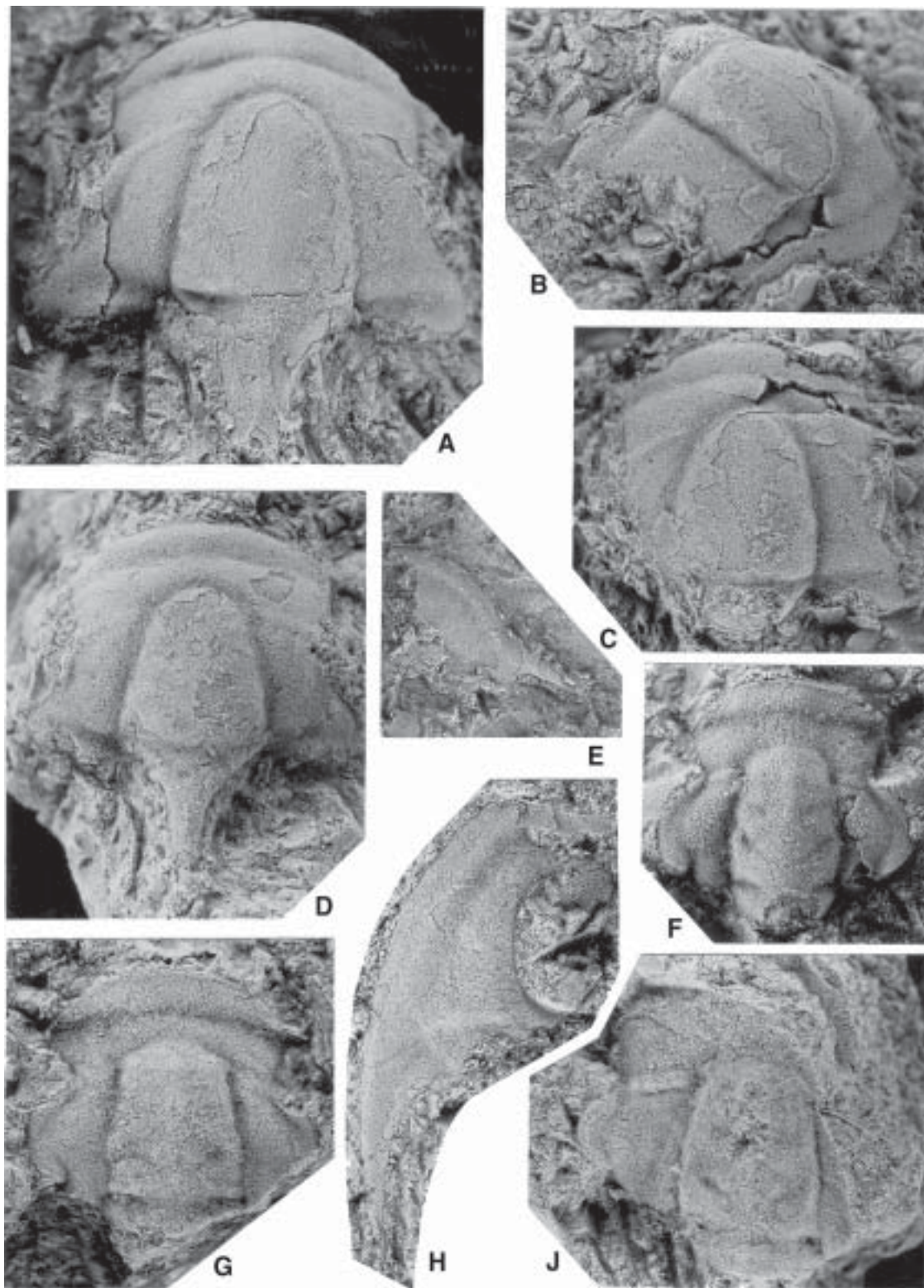


Figure 5. A-D. *Parasolenopleura* cf. *perigrina* (Wallerius, 1930). A. PMO 164.217, cranidium, dorsal view, X7. B, C. PMO 117.053, cranidium oblique frontal and dorsal views, X5. Figured by Bruton et al. 1989, fig. 3: 13. D. PMO 117.052, cranidium, dorsal view, X8. Figured by Bruton et al. 1989, fig. 3: 12. F-H. *Anomocare* cf. *laeve* (Angelin, 1852). F. PMO 164.213, cranidium, dorsal view, X7. G. PMO 164.214, cranidium, dorsal view, X5. H. PMO 164.215, free cheek, X5. E, J. ? *Nericia* sp. indet. E. PMO 164.216, incomplete cranidium, dorsal view, X4. J. PMO 164.220, free cheek, X5.

Family Anomocaridae Poulsen, 1927
Genus *Anomocare* Angelin, 1854
Type species. – By original designation, *Proetus laevis* Angelin, 1852.

Anomocare laeve (Angelin, 1852)
Figs 5F–H

- 1851 *Proetus laevis* Angelin, p. 21, pl. 18, figs. 1,1a.
1854 *Anomocare laeve* (Angelin); Angelin, p. 25.
1902 *Anomocare laeve* (Angelin); Grönwall, p. 141, pl. 4, fig. 8.
1911 *Anomocare laeve* (Angelin); Walcott, p. 87, pl. 4, fig. 8.
1930 *Anomocare laeve* (Angelin); Holm & Westergård, p. 17, pl. 4, figs 16,17.
1950 *Anomocare laeve* (Angelin); Westergård, p. 14, pl. 3, figs 1–8.
1959 *Anomocare laeve* (Angelin); Poulsen *in* Moore, O286, fig. 212: 1a.

Lectotype. – By original designation (Westergård 1950, pl. 3, fig. 3), a cranidium from the Andrarum Limestone, Scania, Sweden.

Discussion. – Westergård (1950), chose as lectotype what was thought to be one of Angelin's syntypes, a cranidium, figured by Holm & Westergård (1930). The present material is slightly larger and uncompressed. Both specimens figured here have the occipital ring damaged and the spine is missing. One cranidium (Fig. 5F) shows the characteristic median glabellar keel and the three pairs of lateral furrows; L1 is inclined inwards and backwards and is deep laterally, L2 is shorter, less inclined, L3 is shallow and transverse. The occipital furrow is deep laterally. The glabella tapers slightly forwards and is blunt to weakly rounded in front.

Westergård's illustrations are somewhat flat and do not bring out the incised furrow at the anterior and posterior ends of the palepebral lobe, nor do they show clearly the anterior furrow crossing the distal part of the eye ridge. The present material also illustrates a broad, smooth border and weakly convex brim. The free cheek (Fig. 5H) is assigned here because of the large eye, but it is much broader than the cheek figured by Westergård (1950, pl. 3, fig. 6).

Cranidia of *Anomocare* differ from those of *Macrotoxa* Lorenz, 1906 (type species *Anomocare angelini* Grönwall, 1902), in having a more rectangular glabella and narrower border. The characteristic course of the anterior facial suture and spatulate border of

Anomocarina Lermontova (type species: *Proetus excavatus* Angelin) separates this genus from *Anomocare*.

Family Marjumiidae Kobayashi, 1935
Genus *Nericia* Westergård, 1948
Type species. – By original designation, *Nericia quinquentata* Westergård, 1948.

?*Nericia* sp. indet.
Figs 5E, J

Discussion. – The large incomplete cranidium (Fig. 5J), differs from those assigned to *Anomocare laeve* in having a very broad fixed cheek and hence a longer eye ridge and a smaller, semicircular palpebral lobe. These features and the broad glabella with lateral depressions at the proximal end of the eye ridge, allow comparison with *Nericia*, previously described from the *Lejopyge laevigata* Zone of Närke and Västergötland, Sweden. The posterior and anterior borders are incomplete but the latter shows that it was broad and flat with a furrow at least laterally. Of interest is a narrow sinuous ridge (furrow on inside of exoskeleton), on the preglabellar area extending from the anterior suture to the frontal glabellar lobe. Such a feature seems to be lacking on internal moulds of *Nericia* figured by Westergård (1948, pl. 4, figs 5–7), though it is present on a cranidium of *Parasolenopora aculeata* (see Westergård 1953, pl. 5, fig. 8; pl. 6, fig. 1a, 3a), but not on *P. cf. peregrina* figured herein (Figs 5A–D). The ridge on the preglabellar area may be a caecal tract or could outline a modified plectrum (see Öpik 1961, p. 163, figs 50, 56). One fragmentary free cheek (Fig. 5E) is like that illustrated for *Nericia septemdentata* Westergård, 1948, pl. 4, fig. 7.

Brachiopods (DATH)

Remarks. – The division of the phylum into carbonate-shelled and phosphatic-shelled taxa, first suggested by Goryanskij and Popov (1985), and elaborated by the cladistic analysis of Williams et al. (1996) is followed here. The following measurements on specimens were made (in mm) where applicable: sl (sagittal length), mw (maximum width), hw (hinge width), pmw (position of maximum width measured from posterior margin) and dpt (maximum depth), slcs (sagittal length cardinal muscle scar), mwcs (maximum width cardinal muscle scar), slas (sagittal length anterior muscle scar), mwas (maximum width anterior muscle scar), slms (sagittal length of median septum), slia (sagittal length interarea), mwia (maximum width interarea), dipf (maximum diameter of

pedicle foramen), mwpt (maximum width of pedicle tube, slpt (sagittal length of pedicle tube), pvp (position of ventral process measured from posterior margin) and lvp (length of ventral process). Where large samples were available, in the case of *Treptotreta? socialis* multivariate statistics are presented and a PCA was run for the Norwegian sample against similar Swedish material. References to the authorship of all categories of generic rank and above are to be found in the Treatise (Williams et al. 2000) and are not repeated here.

Class Lingulata Goryanskij and Popov, 1985
 Order Lingulida Waagen, 1885
 Superfamily Linguloidea Waagen, 1885
 Family Obolidae King, 1846
 Subfamily Obolinae King, 1846
 Genus *Obolus* Eichwald, 1829

Type species. – By subsequent designation (Davidson 1853, p. 135), *Obolus apollinis* Eichwald, 1829 from the Tremadoc rocks of Estonia, Ingria and Russia.

Obolus? sp.
 Figs. 6B–E

Material. – One conjoined pair and several disarticulated valves.

Description. – Minute dorsibiconvex valves of subcircular outline. Maximum width at or near midvalve length. Hinge width about two-thirds maximum width; cardinal extremities obtuse and rounded. Ventral valve about as long as wide. Anterior and lateral profile flatly convex with subdued umbo. Ventral

pseudointerarea, broad, anacline, with accentuated growth lines and broad median groove. Dorsal valve nine-tenths as long as wide. Anterior profile strongly convex medianly, flanks flatly concave and slope steeply laterally. Lateral profile with maximum convexity at umbo but flatly concave over anterior two-thirds of valve length. Umbo relatively subdued but evenly convex. Dorsal valve about twice depth of ventral valve. Ornament of variably accentuated concentric growth lines.

Dorsal interior with deeply impressed visceral area about three-quarters as wide as long and extending to about three-fifths valve length. Pair of muscle scars deeply impressed posterior to anterior margin of visceral area and divided by low median ridge which extends anteriorly to near valve margin.

Measurements

	sl	mw
Dorsal valve, PMO165.637 (Fig. 6D)	c.1.5	2.2
Dorsal valve, PMO165.638 (Fig. 6E)	c.1.7	2.1

Remarks. – These small valves are tentatively assigned to the obolines largely on account of their subcircular outline and suggestion of a raised ventral pseudointerarea (Havlíček 1982). Nevertheless the basic distinction between the *Lingulella* and *Obolus* type shells is not always obvious (Holmer 1989). Moreover the Norwegian material is insufficient to allow discrimination between *Obolus* itself and the closely related *Ungula*. The latter was previously considered a junior synonym of *Obolus* (Rowell in Williams et al. 1965), but Popov and Khazanovitch (in Popov et al. 1989) have since clarified the identities of both genera. *Ungula* differs in having a subcircular, thinner and flatter shell, shorter pseudointerareas, a less well-devel-

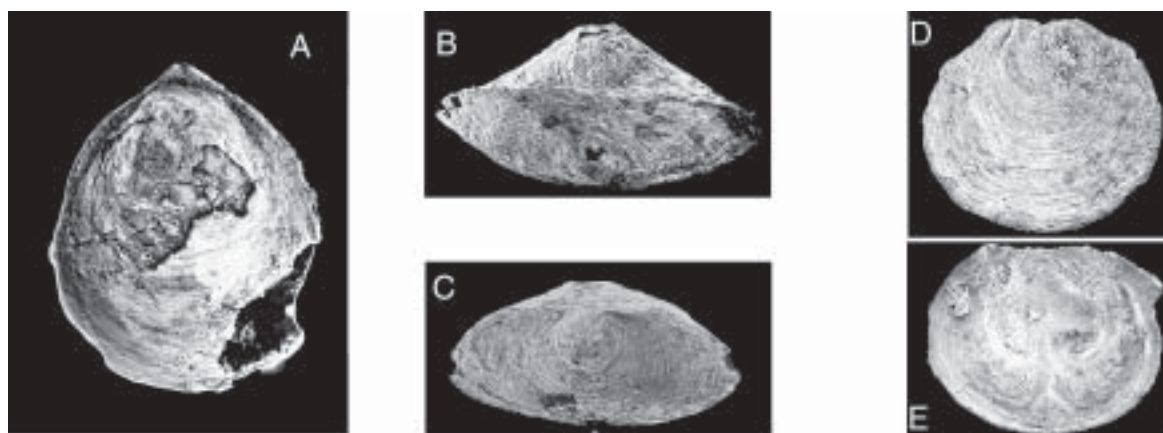


Fig. 6. *Lingulella* sp. and *Obolus?* sp. A. *Lingulella* sp., dorsal view of conjoined pair, X30, PMO165.635. B-E. *Obolus?* sp. B, C. Posterior and oblique posterodorsal views of conjoined pair, X30, PMO165.636. D. Dorsal exterior, X20, PMO165.637. E. Dorsal interior, X15, PMO165.638. All are SE photomicrographs.

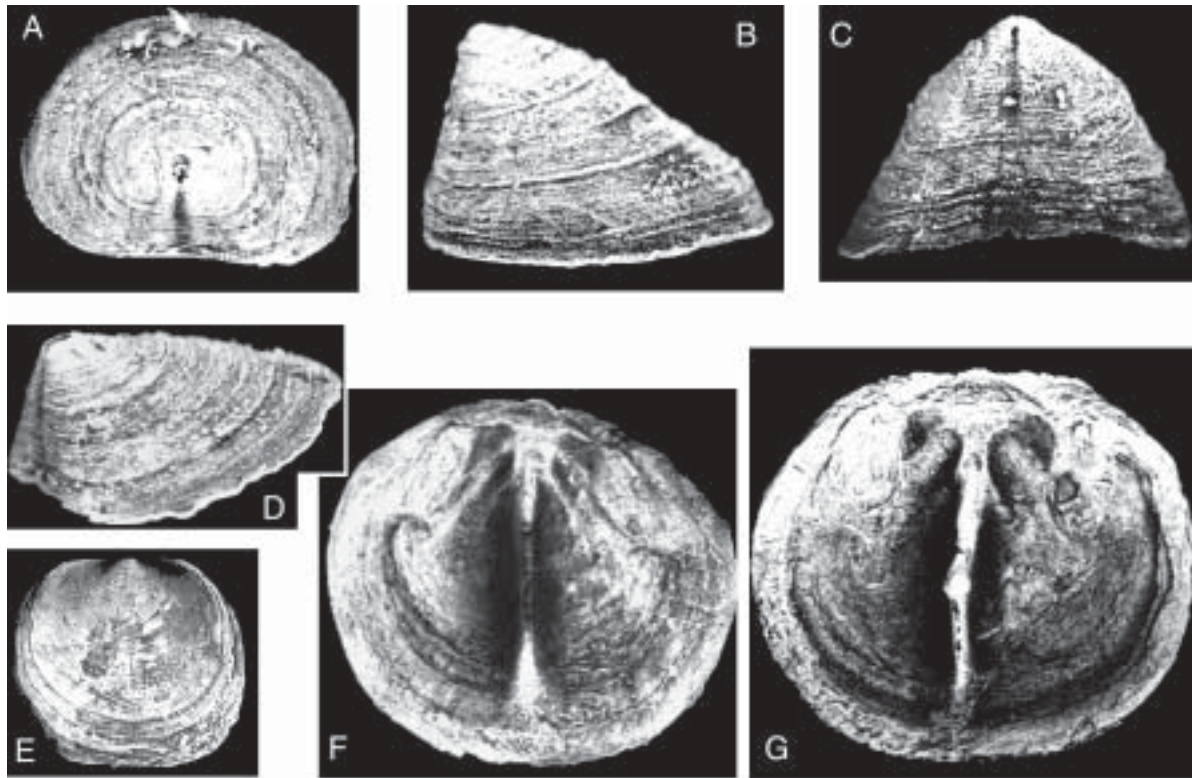


Fig. 7. *Treptotreta? socialis* (von Seebach). A,D. Posterior and oblique lateral views of ventral valve, X14, X18, PMO165.639. B,C. Lateral and posterior views of ventral valve, both X12, PMO165.640. E. Dorsal exterior, X10, PMO165.641. Figured by Bruton et al. 1989, fig.3:8. F. Dorsal interior, X20, PMO165.642. G. Dorsal interior, X16, PMO165.643. Figured by Bruton et al. 1989, fig.3:4.

oped pedicle groove and, moreover, lacks an elevated ventral visceral area with a cordate depression (Puura & Holmer, 1993). The Ritland shells are small, poorly preserved and lack interiors. Pending more adequate material they are tentatively assigned to *Obolus*.

Of particular interest is a small perforation in the anteromedian area of one of the ventral valves of this species which may be the boring of a predator into the visceral area of the animal. Chatterton & Whitehead (1987) have described similar borings into the Silurian acrotretide *Artiotreta* which they attributed to a soft-bodied predatory organism with the ability to dissolve calcium phosphate, or less likely a gastropod.

Subfamily Lingulellinae Schuchert, 1893

Genus *Lingulella* Salter, 1866

Type species. – By subsequent designation (Dall, 1870, p. 159), *Lingula davisii* M'Coy, 1851, p. 405, from the Ffestiniog Beds (Upper Cambrian - Merioneth Series), south of Penmorfa, Gwynedd, Wales.

Lingulella sp.

Fig. 6A

?1952 *Lingulella* sp. Henningsmoen, p. 19, pl. 2, fig. 4.

Material. – Two virtually complete conjoined pairs.

Description. – Minute dorsibiconvex valves of elongately oval outline. Maximum width at about mid-valve length. Hinge width about one-half maximum width with obtuse, rounded cardinal extremities. Ventral valve about four-fifths as wide as long and about one-fifth as deep as long. Anterior profile weakly convex, lateral profile slopes gently anteriorly from subdued but convex umbo. Interarea poorly preserved, but apparently modified apically, by a minute pedicle opening. Dorsal valve almost nine-tenths as wide as long and about one-third as deep a long. Anterior and lateral profiles convex. Ornament of variably accentuated concentric growth lines. Interiors not known.

Measurements

	sl	mw
Ventral valve of conjoined pair, PMO165.635 (Fig. 6A)	1.5	1.2

Remarks. – Henningsmoen (1952, p. 19, pl. 2, fig. 4) discussed and illustrated a single, small (length = 2 mm) external impression of *Lingulella* from the *Paradoxides oelandicus* Zone at Ritland Farm. The material is poorly preserved and broken; nevertheless Henningsmoen (1952) drew attention to a similar occurrence of *Lingulella?* sp. in the Oelandicus Beds of Sweden (Westergård 1936). The new Rogaland material, from higher in the sequence, though virtually complete and relatively well preserved is insufficiently abundant for detailed comparisons. It is accordingly illustrated and described under open nomenclature.

Order Acrotretida Kuhn, 1949
 Suborder Acrotretidina Kuhn, 1949
 Superfamily Acrotretoidea Schuchert, 1893
 Family Acrotretidae Schuchert, 1893
 Genus *Treptotreta* Henderson & MacKinnon, 1981

Type species. – By original designation, *Treptotreta jucunda* Henderson & MacKinnon, 1981, from the Mail-change Limestone (Middle Cambrian), northeastern Australia.

Treptotreta? socialis (von Seebach, 1865)
 Figs 7A–G, 8A–G

- 1865 *Acrotreta socialis* von Seebach, p. 341, pl. 8a, figs 1–4.
- 1876 *Acrotreta socialis* von Seebach; Linnarsson, p. 16, pl. 3, figs 32–35.
- 1902 *Acrotreta socialis* von Seebach; Matley, p. 144, figs 15, 15a–c, 16.
- 1902 *Acrotreta socialis* von Seebach; Matthew, p. 392, pl. 15, fig. 5, 5a–k.
- 1912 *Acrotreta socialis* von Seebach; Walcott, p. 711, pl. 73, figs 3, 3a–c, 4, 4a–c
- 1921 *Acrotreta socialis* von Seebach; Cobbold, p. 347, pl. 22, fig. 25
- 1971 *Acrotreta socialis* von Seebach; Poulsen, p. 269, pl. 7, fig. 1, 1a–b.
- 1989 “*Acrotreta*” cf. *socialis* (von Seebach); Bruton et al., p. 232, figs 3: 2,4,5,8.

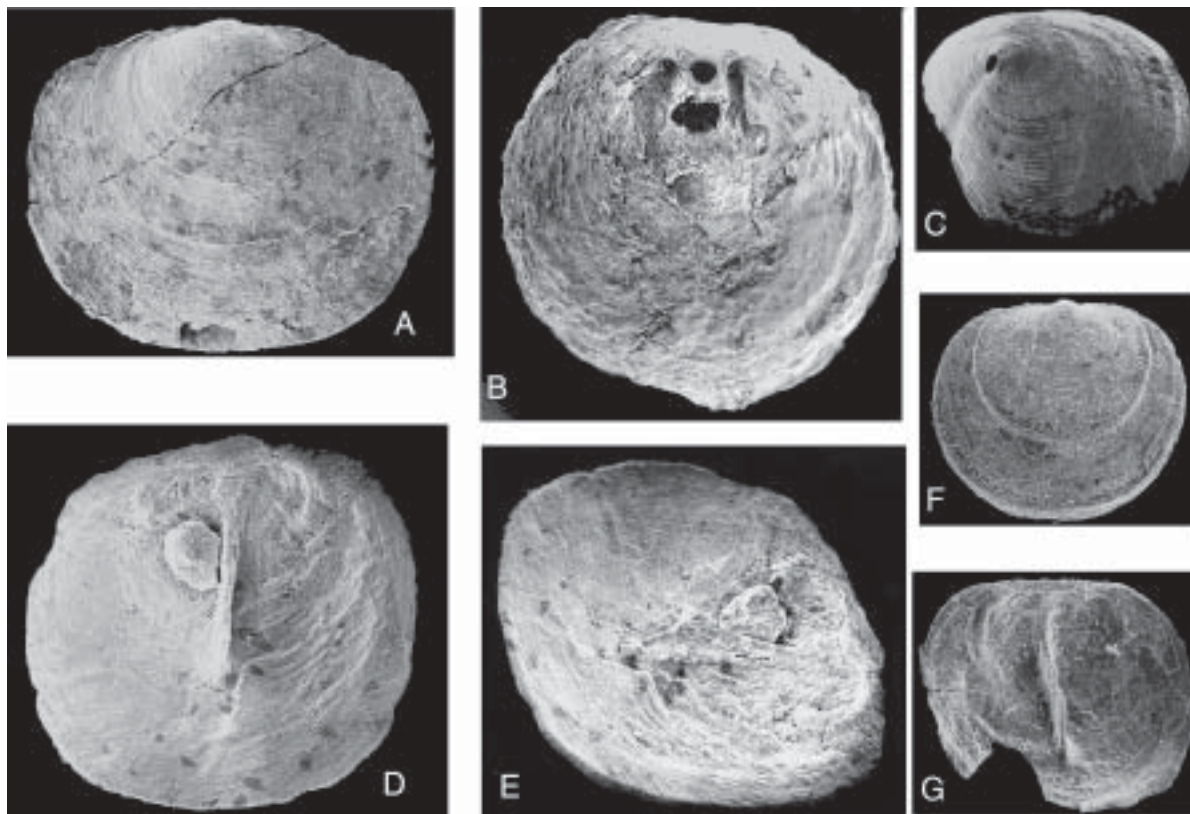


Fig. 8. *Treptotreta? socialis* (von Seebach). A. Dorsal exterior, X30, PMO165.644. B. Ventral interior, X40, PMO165.645. C. Oblique view of ventral exterior, X25, PMO165.646. D,E. Dorsal and oblique views of interior, both X30, PMO165.647. F. Dorsal exterior, X30, PMO165.648. G. Dorsal exterior, X30, PMO165.649. All are SE photomicrographs.

Material. – Several hundred, complete and well-preserved ventral and dorsal valves; none recovered conjoined.

Description. – Ventral valve, high, conical, procline and of circular to transverse elliptical outline, about four-fifths as long as wide and about two-thirds as deep as long. Anterior and lateral profiles feebly convex, shell surfaces slope steeply anteriorly and laterally from apex. Procline pseudointerarea essentially flat, bisected by relatively narrow but marked median intertrough deflected dorsally by growth lines. Minute subcircular pedicle foramen situated at apex of pseudointerarea. Dorsal valve of almost circular outline, about nine-tenths as long as wide, weakly convex with subdued umbo. Interarea short, apsacline. Protegular shell with fine, shallow pits, elsewhere ornament of

variably accentuated, usually marked, growth lines.

Ventral interior. Pedicle foramen continuous internally with short oval pedicle tube surrounded by robust apical process, extending dorsally to about one-third valve depth.

Dorsal interior. High, triangular, median septum surmounted by cylindrical rod and extending anteriorly virtually to the anterior margin. Large cardinal muscle scars deeply impressed. Central scars elongate, less well defined, extending forward to about four-fifths valve length.

Remarks. – The widely quoted lingulate *Acrotreta socialis* von Seebach, 1865, as currently understood, is unstable and in urgent need of revision on the basis of type and topotype material. It is by far the most common and best-preserved brachiopod in the Rit-

Measurements and Statistics

	sl	mw
Ventral valve, PMO165.639 (Fig. 7A,D)	2.4	3.3
Ventral valve, PMO165.640 (Fig. 7B,C)	4.0	4.0
Dorsal valve, PMO165.641 (Fig. 7E)	2.9	3.1
Dorsal valve, PMO165.642 (Fig. 7F)	2.5	2.8
Dorsal valve, PMO165.643 (Fig. 7G)	3.4	3.1

Vector of means and variance-covariance matrix for 30 dorsal valves:

Means	sl	mw	pmw	slcs	mwcs	slas	mwas	slms	slia	mwia
	5.3	6.0	2.6	1.8	3.4	3.2	3.2	3.9	0.4	3.4
Var-	1.43	1.25	0.52	0.48	0.67	0.82	0.76	0.93	0.14	0.80
Covar		1.20	0.41	0.46	0.62	0.78	0.71	0.88	0.13	0.75
Matrix			0.60	0.14	0.22	0.26	0.30	0.38	0.05	0.32
				0.24	0.29	0.33	0.29	0.33	0.06	0.27
					0.41	0.46	0.41	0.47	0.08	0.39
						0.63	0.53	0.57	0.09	0.50
							0.59	0.48	0.07	0.43
								0.78	0.09	0.56
									0.02	0.09
										0.62

Vector of means and variance-covariance matrix for 15 ventral valves:

Means	sl	mw	dept	slia	mwia	dipf	mwpt	slpt	pvp	lvp
	4.7	5.6	3.4	2.3	2.5	0.2	0.5	1.1	1.8	0.63
Var-	0.24	0.22	0.21	0.10	0.06	-0.004	0.07	0.05	0.08	0.12
Covar		0.29	0.22	0.13	0.05	-0.01	0.08	0.05	0.13	0.07
Matrix			0.45	0.15	0.14	-0.01	0.05	0.09	0.10	0.10
				0.15	0.06	-0.005	0.06	0.08	0.09	0.06
					0.08	-0.002	0.02	0.05	0.05	0.06
						0.002	-0.003	-0.002	-0.0001	0.003
							0.04	0.02	0.03	0.03
								0.09	0.08	0.009
									0.21	-0.003
										0.15

land fauna. The species was first established by von Seebach (1865) based on material from the island of Bornholm. Linnarsson (1876, pp. 17–18), basing his redescription entirely on sparse Swedish material from Öland, had no access to interiors. He did, however, suggest that more than one species was probably used in von Seebach's description of *A. socialis*, possibly even including specimens from the Middle Ordovician rocks on Bornholm. Nevertheless Linnarsson (op. cit.) restricted his understanding of the species to forms from principally the *Paradoxides forchhammeri* beds and more rarely the lower *Paradoxides oelandicus* beds on Öland.

Walcott (1902) revised the species on the basis of material recollected by the Swedish Geological Survey from the Borgholm locality, Öland. He concluded that *A. socialis* (sensu von Seebach) occurred with *Paradoxides oelandicus* whilst a different species of *Acrotreta*, *A. schmalenseei* Walcott, 1902 was associated with *P. forchhammeri*. The latter is defined as a small species lacking the strong concentric ornament and marked groove on the ventral proparea, typical of *A. socialis*.

Henningsmoen (1952) recorded *A. socialis* from the *Paradoxides oelandicus* zone at Ritland, Rogaland. He noted that bedding planes covered with the valves of *Acrotreta* displayed forms conforming to both *A. socialis* and *A. schmalenseei* together with intermediate forms. In this regard he followed Westergård (1936) who suggested the latter was a junior synonym of von Seebach's species. It is possible that the variable development of the groove on the pseudo-interarea and concentric ornament may be related to ontogenetic rather than genetic factors. The larger, more mature specimens, are thus characterised by a well-developed groove and a marked concentric ornament. A reinvestigation of type and topotype material is required to clarify this analysis.

Holmer & Popov (1994) have revised, in detail, the type species of *Acrotreta*, *A. subconica* Kutorga, 1848 based new material including a neotype from the lower Arenig Päite Beds near St. Petersburg, Russia. *Acrotreta* s.s. is, in fact, most similar to *Spondylotreta* Cooper, and quite different from *Conotreta*, with a stratigraphical range now restricted to the Ordovician (Holmer & Popov, 1994). Accordingly Cambrian records of the genus, including *A. socialis*, are probably invalid and the generic assignment of *A. socialis* is thus in need of revision.

The combination of a long median septum with a surmounting rod together with narrow propareas and a marked groove on the wide ventral pseudointerarea which fades from the apex, are distinctive features of this species. These characters together with the development of a prominent apical process suggest a

provisional assignment to *Treptotreta*. This genus is best known from its Australian and New Zealand species (Henderson & MacKinnon 1981, Engelbretson 1996). However, firm generic placement of *A. socialis* should be deferred until type and topotype material of this problematic species is properly revised.

Multivariate statistics are presented for samples of both the ventral and dorsal valves of the Norwegian material. Principal Component Analysis (PCA), based on the correlation matrix, was performed on a pooled sample (N = 30) of the dorsal valves of 'A.' *socialis* from Ritland and a small sample (N = 5) of presumed conspecific material from the type locality of von Seebach's species. The PC scores of specimens were plotted against all the eigenvectors; no separation between the Norwegian and Swedish samples was apparent. Thus in terms of the variates measured (see vector of means above) the two samples are considered conspecific. There is some obvious morphological variation particularly in the shape of the ventral valves (cf. Figs 7C and D). This variation is currently considered to be intraspecific although larger samples may demonstrate a range of different morphotypes.

Family Acrothelidae Walcott & Schuchert, 1908

Subfamily Acrothelinae Walcott & Schuchert, 1908

Genus *Acrothele* Linnarsson, 1876

Type species. – By original designation, *Acrothele granulata* Linnarsson, 1876, from the *Paradoxides forchhammeri* zone on Bornholm and in Västergötland, Sweden.

Acrothele granulata (Linnarsson, 1876)

Figs 9A–F

- 1876 *Acrothele granulata* Linnarsson, p. 24, pl. 4, fig. 51, ?52.
- 1877 *Acrothele granulata* Linrs.; Linnarsson, p. 22, pl. 2, fig. 12.
- 1912 *Acrothele (Redlichella) granulata* (Linnarsson); Walcott, p. 663, pl. 56, figs 2a–n.
- 1923 *Acrothele (Redlichella) granulata* (Linnarsson); Hedström, p. 10, pl. 1, figs 14a–c.
- 1929 *Acrothele (Redlichella) granulata* (Lnr.); Strand, p. 341.
- 1934 *Acrothele (Redlichella) granulata* (Linnarsson); Cobbold & Pocock, p. 330.
- 1936 *Acrothele (Redlichella) granulata* (Linnarsson); Westergård, p. 24
- 1942 *Acrothele (Redlichella) granulata* Linnarsson; Poulsen, p. 216, pl. 235, figs 7–11.

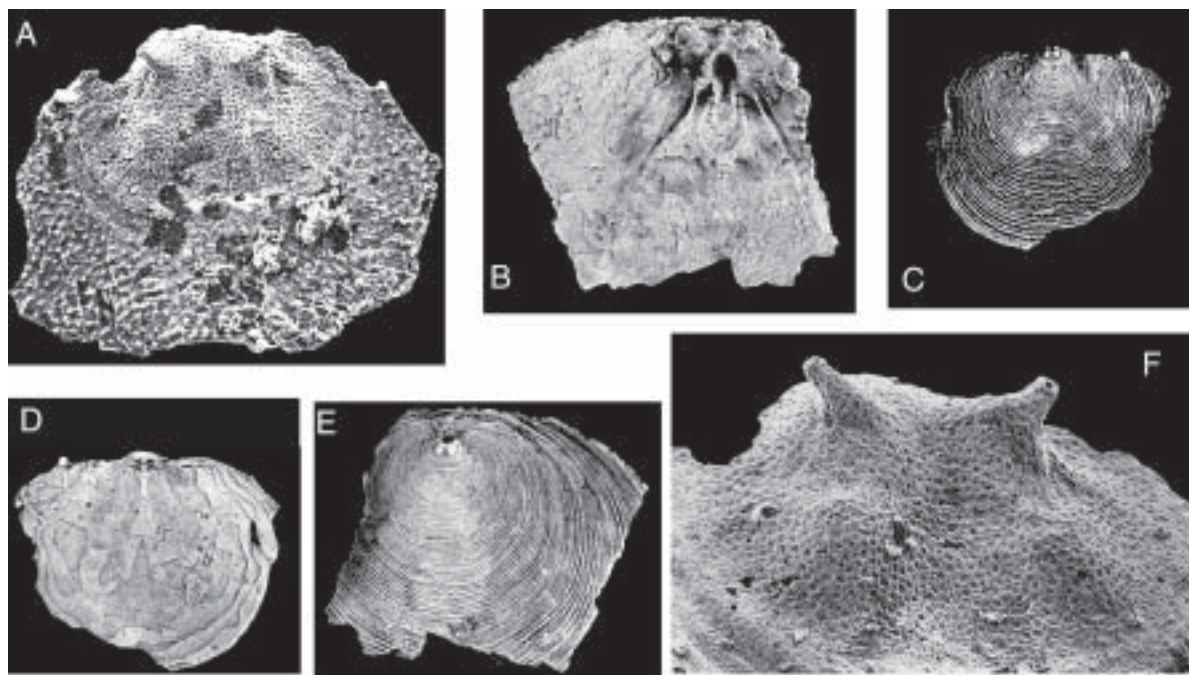


Fig. 9. *Acrothele granulata* (Linnarsson). A, F. Broken dorsal exterior with detail of posterior part, X65, X120, PMO165.650. B. Ventral interior, X9.5, PMO165.651. C,D. External and internal views of dorsal valve, X9.5, PMO165.652. E. Ventral exterior, X7, PMO165.658. A and F are SE photomicrographs.

1952 *Acrothele (Redlichella) granulata* Linnarsson; Henningsmoen, p. 20, pl. 2, fig. 3.

Material. – Two dorsal valves and two ventral valves, all broken.

Description. – Minute, ventribiconvex valves of circular outline. Ventral valve, low cone of circular outline with minute pedicle foramen situated excentrically, adjacent to posterior margin. Ventral pseudointerarea, short triangular, poorly defined by pair of grooves, convex with small subcircular pedicle foramen at apex. Dorsal valve, subcircular in outline, about nine-tenths as long as wide and virtually flat with prominent convex umbo. Micro-ornament of protogelum with network of steep-sided polygonal pits, commonly hexagonal, with weakly concave bases. Protogelum crowned by pair of dorsolaterally directed, hollow, spines arising from pair of swellings on posterior part of protogelular surface. Anterior pair of swellings on protogelum developed without spines. Ornament in front of protogelum quite different, consisting of irregular, concentric growth lamellae punctuated by tubercles presenting a markedly granulose appearance.

Dorsal interior with short median ridge, rounded and subcircular in cross-section, extending to about one-fifth valve length. Pair of deeply impressed, elongately oval cardinal scars diverge from hinge line oc-

cupying about one-half hinge width and extending anteriorly to about one-fifth valve length. Central muscles attached as pair of narrow, oval divergent scars. Elsewhere internal features barely discernible.

Ventral interior has relatively large, elongately oval, internal opening for pedicle foramen. Pair of short ridges extend forward from opening and terminate in elongately oval muscle scar. Laterally pair of longer, slightly sinuous ridges diverge anteriorly to near mid-valve length.

Measurements

	sl	mw
Dorsal valve, PMO165.652 (Figs 9C,D)	3.2	c.3.8

Remarks. – Linnarsson (1876, p. 24) considered his new species, *A. granulata*, to be allied to *Acrothele coriacea* Linnarsson, the most widespread brachiopod species in the middle *Paradoxides* beds. However Linnarsson (op. cit.) noted that *A. granulata* differed from the latter in having more pointed and excentric umbones, a distinctly granulated surface and a poorly developed proparea; moreover *A. granulata* was consistently larger.

Walcott (1908, pp. 89–90) in his substantial review of Cambrian Brachiopoda, established the subgenus *Redlichella*, type species *Acrothele granulata*, on the basis of the large and well-defined visceral area in the ventral interior together with the large cardinal

scars in the dorsal interior of that species. He (op. cit.) considered the new subgenus intermediate between the acrothelid *Acrothele* and the botsfordiid *Botsfordia*. Rowell (1965) tentatively raised *Redlichella* to generic status and added the presence of granulose ornament to its diagnosis. Granulation, however, can be a variable feature and its taxonomic significance is uncertain.

In a study of a brachiopod fauna from the Middle Cambrian of the Montagne Noire, southern France, Termier & Termier (1974) defined their new acrothelid genus, *Glyptacrothele*, on the presence of a lamellose-granular ornament, a subcircular, conical ventral valve with an excentric apex and an elliptical pedicle foramen. Linnarsson's species, *Acrothele granulata*, was considered congeneric. Although the type species, *G. courtessolei* Termier & Termier, 1974, was designated from the Calcaire de la Val d'Homs (Middle Cambrian), Montagne Noire, Linnarsson's characterization of *A. granulata* was considered fundamental to the separation of this genus from *Acrothele*, itself. There is little doubt Termier & Termier's diagnostic characteristics conform to those of *A. granulata*. Accordingly *Glyptacrothele* is considered here to be a junior synonym of *Acrothele*.

The new species from southern France is in fact very similar to *A. granulata* (Linnarsson, 1876) probably from the *Paradoxides oelandicus* Zone at Borgholm, Öland. Termier & Termier (1974) differentiated their new species from *A. granulata* with reference to the shape of the pedicle foramen, the development of the ventral vascular system and in having a less accentuated external ornament than that of the Swedish species. *Glyptacrothele bohémica* (Barrande, 1879) from the Jince Formation (*Bohemiella romingeri* Zone), Mlecice, Czechoslovakia (Mergl & Slehoferova 1989) may also be congeneric with the Scandinavian and French species. However the Czech form has a marked radial ornament (with 26–30 ribs on adult shells) and less strongly impressed muscle scars.

Both the distinctive protogelar net and spines are well preserved on the Norwegian material. Although the mode of generation of the acrotretide protogelum has been debated, the honeycomb pattern of pits clearly lightened the larval shell; adaptation to a free-swimming or pelagic life mode is thus very likely (von Bitter & Ludvigsen 1979). The function of the protogelar spines has been associated with maintenance of the stability of the larval shell after settlement - the spines could raise the gape clear of the substrate and the posterior spines may have provided a fulcrum for pedicle-powered rotation of an overturned shell (Henderson 1974). Alternatively if the species pursued an interstitial life strategy the spines may have initially prevented crushing of the fragile, protogelar

shell and permitted the development of a microenvironment around the animal.

Class Paterinata Williams, Carlson, Brunton, Holmer & Popov, 1996

Order Paterinidae Rowell, 1965

Superfamily Paterinoidea Schuchert, 1893

Family Paterinidae Schuchert, 1893

Genus *Dictyonina* Cooper, 1942

Type species. – By original designation, *Trematis pannulus* White, 1874, from the upper Lower and lower Middle Cambrian rocks of the Pioche district, Nevada, USA (Rowell 1980).

Dictyonina ornatella (Linnarsson, 1876)

Figs 10A–G

1876 *Iphidea ornatella* Linnarsson, p. 25, pl. 3, figs 42, 43.

1903 *Iphidea ornatella* Linnarsson; Wiman, p. 55, pl. 2, fig. 9.

1912 *Micromitra (Iphidella) ornatella* (Linnarsson); Walcott, p. 360, pl. 3, figs 6, 6a–d.

1936 *Micromitra (Iphidella) ornatella* (Linnarsson); Saito, p. 355, pl. 1, figs 18–21.

1936 *Micromitra (Iphidella) ornatella* (Linnarsson); Westergaard, p. 22, pl. 8, figs 8–10.

1968 *Dictyonina ornatella* (Linnarsson); Martinsson, p. 148, figs 9A, F.

1985 *Dictyonina ornatella* (Linnarsson); Berg-Madsen, p. 138, figs 4A–B.

1989 *Dictyonina* cf. *ornatella* (Linnarsson); Bruton et al., p. 232, fig. 3–1,3.

Material. – Two ventral valves and two dorsal valves, three of the shells virtually complete, the fourth is broken.

Description. – Minute ventribiconvex valves of transversely semicircular outline with maximum width at or near midvalve length. Essentially straight hinge line about two-thirds maximum width. Cardinal extremities, obtuse and rounded. Rectimarginate anterior commissure. Ventral valve about four-fifths as long as wide and over one-fifth as deep as long. Anterior profile with maximum convexity medianly with roughly flat flanks which slope laterally. Lateral profile with subdued umbo; elsewhere surface slopes anteriorly with slight convexity. Relatively short, curved, apsacline pseudointerarea with delthyrium virtually closed by robust homeodeltidium with thickened growth lines. Dorsal valve about three-quarters as long as wide and less than one-fifth as deep as long.

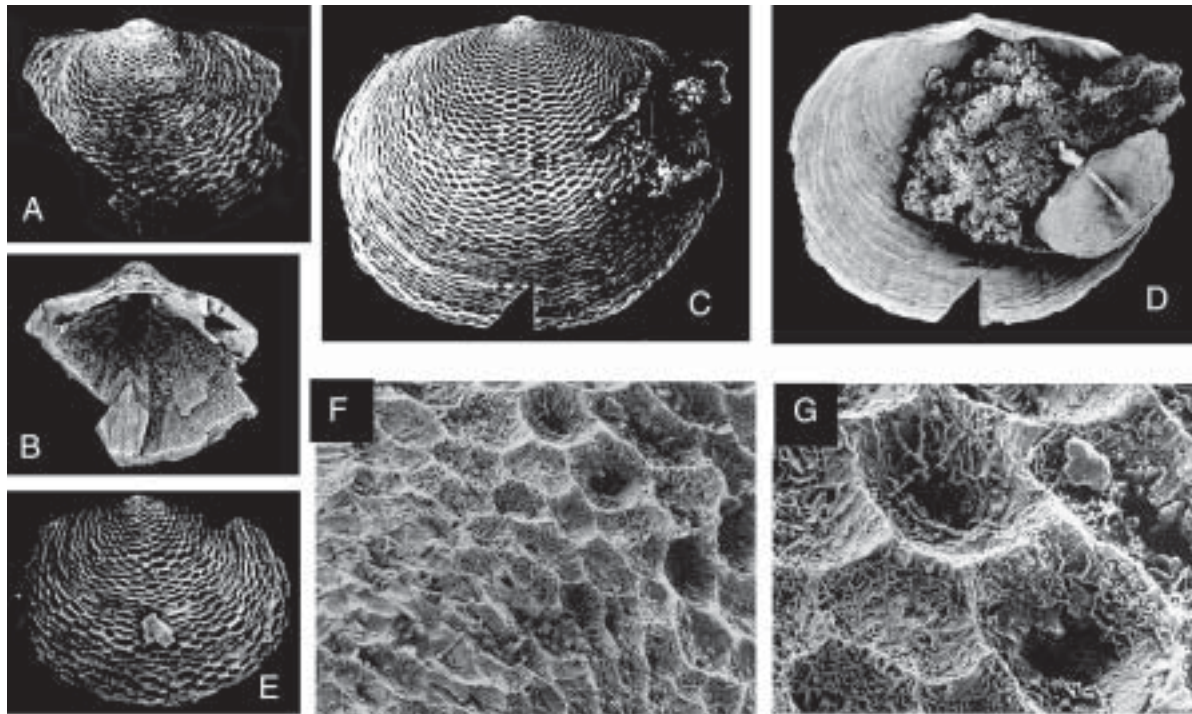


Fig. 10. *Dictyonina ornatella* (Linnarsson). A. Dorsal exterior, X8, PMO165.659. B. Ventral interior, X9, PMO165.660. C,D. External and internal views of dorsal valve, the latter with a small valve of *Treptotreta? socialis* (von Seebach) trapped in the matrix, both X7, PMO165.661. Figured by Bruton et al. 1989, fig.3:3. E. Dorsal exterior, X8, PMO165.662. Details of pitted ornament on dorsal exterior (Fig. 11C) at X25 and X60, PMO165.663. F and G are SE photomicrographs.

Anterior and lateral profiles evenly convex medianly with flat flanks sloping anterolaterally; small but prominent convex umbo. Short, curved apsacline pseudointerarea with wide, open chilidium, partly closed, apically, by small homeodeltidium with thickened growth lines. Ornament of strong concentric growth lines, variably accentuated, with about 15 per mm, anteromedianly at the 1 mm growth stage. Distinctive micro-ornament of shallow, polygonal pits with density of about 40 per sq mm at the 1 mm growth stage anteromedianly, but enlarging and losing definition, anteriorly.

Internal features poorly defined in both valves.

Measurements

	sl	mw
Dorsal valve, PMO165.661 (Figs. 10C,D)	6.0	7.4
Dorsal valve, PMO165.662 (Figs. 10E)	4.0	4.5

Remarks. – Linnarsson (1876) established this species on the basis of material from the *Paradoxides forchhammeri* Zone in Sweden and noted the occurrence of the species at Lovened, Västergötland and on Bornholm. Wright (1981) has discussed the development of pits in *Dictyonina*, noting an increase in breadth and a reduction of definition with age. The few specimens of

Dictyonina available from Ritland show a marked variation in the ornament. Although the pits in general broaden and lose definition with age there are areas on the shell surface where the concentric growth lines are accentuated and the clear development of the pits has been arrested.

The Norwegian material is placed in Linnarsson's species pending a complete revision of type and topotype material from the Middle Cambrian of Bornholm. Examination of Walcott's figured material from Borregard, Bornholm indicated both the Danish and Norwegian specimens are characterised by relatively short interareas. However the Bornholm exteriors display the sporadic development of ribs (about ten per mm at 1 mm from the posterior margin), apparently absent on the Ritland specimens.

Other taxa (DLB)

Class Hyolitha Marek, 1963

Order Hyolithida Matthew *vide* Fischer, 1962

"*Hyolithes*" cf. *obesus* Holm, 1893
Figs 11A, B

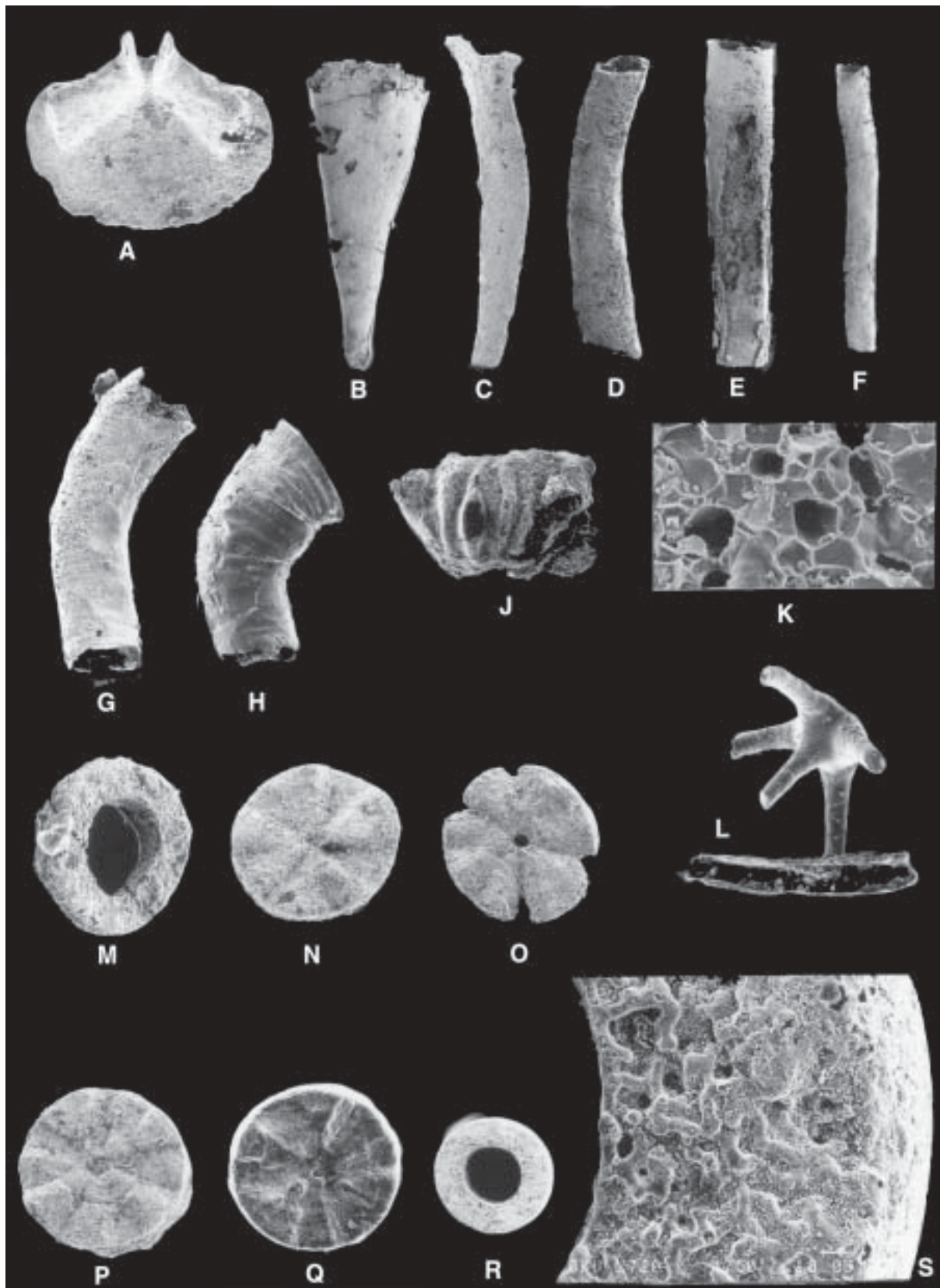


Figure 11. A-B. "*Hyolithes*" cf. *obesus* Holm, 1893. PMO 117.047. A. Operculum from inside, X100. B. conch, internal mould, X48. C-H, K. Phosphatic tubes. PMO 117.047. C, X20; K, surface detail X200; D, x. 48; E, X24; F, X24, Original Bruton et al. fig. 3:6; G, X48; H, X48. J. Bradoriid crustacean. PMO 164.202, X48. L. Hexactinellid-spicule. PMO 117.064, X60. Original Bruton et al. 1989, fig.3:11. M-R. Cystoid stem columnals. PMO 117.048. All X72. O, original Bruton et al. 1989, fig. 3:7. S, surface detail of R, X720.

Discussion. – Amongst the etched material is one phosphatic internal mould of a hyolithid conch (Fig. 11B) and one well preserved isolated operculum (Fig. 11A). The latter has been photographed from the inside and shows the paired cardinal process at the base of which is the biclavate area (for terminology see Malinky & Berg-Madsen, 1999, fig. 2). The conch has a broad apical angle comparable to that of the “*H*” *obesus* type and additional material recently figured by Malinky & Berg-Madsen (1999, pl. 1, figs 2–5; pl. 3, figs 3–4), and is short, a feature commented on by Holm (1893). The apical end shows a distinct constriction interpreted by Dzik (1994, p. 268) to represent the change from the embryonic to a later stage. Henningsmoen (1952, p. 22), listed, but did not figure, “*Hyolithes*” *obesus* Holm, 1893 from the older *Acadoparadoxides* (*Baltoparadoxides*) *oelandicus* Stage at Ritland but the poorly preserved conchs from these beds are longer. The figured operculum, if it belongs here, shows details of the interior for the first time as these are lacking on the specimen figured by Malinky & Berg-Madsen 1999, pl. 1, fig. 4.

Phosphatic tubes Figs 11C–H

Discussion. – Dzik (1994, p. 252) distinguished the early Palaeozoic hyolithellids with circular cross section (Figs 11D–H) and the flatter torellidellids (Fig. 11C). The latter shells widen at the proximal end and are curved along their length. The hyolithellids vary in shape from straight (Fig. 11E) to slightly sinuous (Fig. 11F) or curved (Figs 11G,H). Annulation is particularly well developed on one specimen (Fig. 11H).

Cystoid stem columnals Figs 11M–S

Discussion. – Berg-Madsen (1986) recovered abundant cystoid stem columnals, especially from the Andrarum Limestone on Bornholm, and similar forms are illustrated here (Figs M–R). All are phosphatised and show the lumen to be from 5–50% or more of the articulum. The latter is well preserved, apparently smooth in columnals with a large lumen (Figs 11 M,R) or with crenulae in those with a narrow lumen (Figs 11N–Q). A detail of the articulum in a specimen with a large lumen (Figs 11R,S), shows the galleried structure described and illustrated by Berg-Madsen (1986, figs 5–7). Columnals with straight sides are circular in outline but one specimen (Fig. 11O) shows bipolar and oblique lateral indentations.

Hexactinellid-spicule Fig. 11L

Discussion. – Weathered moulds of sponge spicules are common on the surface of many scree-slope shales at Ritland and Henningsmoen (1952, pl. 2, figs 8–9) illustrated two hexactinellid types including *Chancelloria*, also recorded by Berg-Madsen from the Andrarum Limestone from Bornholm (1985, fig. 5a). Though not common in the etched material, broken fragments could belong to this genus. The best preserved (Fig. 11L) seems to correspond to Bengtson’s (1986, p. 211) smooth pentacts, the most common of which, as here, has a spindle-shaped central ray. Variation is, however, enormous and the *Protospongia*? of Henningsmoen could be the same as that figured here.

Bradoriid crustacean Fig. 11J

Discussion. – The specimen with incomplete free and dorsal margins is the only one identified amongst the etched material. Bruton et al. (1989, p. 233), identified this and fragments as being a palaeocopid ostracod but Dr. Mark Williams (pers.comm. 21–04–99) has drawn our attention to the bradoriid crustacean genera *Vojbokalina* Melnikova, 1984 and *Septadella* Stubblefield, 1933 respectively from the Middle Cambrian of the area around St. Petersburg, Russia (see Melnikova et al. 1997) and Cape Breton, Nova Scotia, Canada (see Siveter & Williams 1997). *Septadella* is also recorded from the Tremadoc Series of Great Britain (Williams & Siveter 1998). Figures of the holotype of *Vojbokalina* (see Hinz-Schallreuter 1993, fig. 14: 2; Melnikova et al. 1997, pl. 3, fig. 8), show that the central node is surrounded by one strongly curved posterior lobe, whilst in the present material there are two weakly curved lobes behind the node. This may be a dimorphic or specific difference but it appears that the present material is closer to *Vojbokalina* than *Septadella* which lacks the central lobe.

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Dansk sammendrag

Den mellem kambriske skalbærende fauna fra Ritland i Vestnorge består af trilobiter, brachiopoder, hyolither, ostracod-lignende krebsdyr og svampespikler og minder meget om faunaen fra Andrarum Kalken på Bornholm. Det vises, at Andrarum Kalk facies bæltet kan følges fra Ritland, mod øst gennem den nordlige del af Oslo området og sydpå til Skåne og Bornholm.

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