THE COMMONER BRACHIOPODS OF THE LATEST ORDOVICIAN OF THE OSLO-ASKER DISTRICT, NORWAY

by L. R. M. COCKS

ABSTRACT. The brachiopod fauna of the upper part of the rocks of Ashgill age in the Oslo-Asker area, Norway, is reviewed prior to an assessment of the ecology of the macrofauna found in this Rawtheyan and Hirnantian regressive sequence, a regression caused by the contemporary glacio-eustatic lowering of sea level. Most of the elements of the cosmopolitan *Hirnantia* Fauna occur, some very commonly, such as *Dalmanella*, *Hirnantia*, *Eostropheodonta*, *Cliftonia*, and *Hindella*, but other elements are rare or absent; many additional genera are also noted. In sediments filling tidal channels at the top of the sequence, genera such as *Thebesia*, *Brevilamnulella*, and *Leptoskelidion* are recorded for the first time outside the North American craton. The commoner constituents of the fauna are described and illustrated, and the new species *Trematis norvegica*, *Onniella kalvoya*, *Leptoskelidion loci*, *Eoplectodonta oscitanda*, and *Thebesia scopulosa* are erected. The pentameride *Holorhynchus* is revised and reinterpreted as an ancestral stricklandiid.

THE latest Ordovician has attracted much interest in recent years since it has become established that an important glaciation occurred at that time, causing a world-wide eustatic fall in sea level in late Ashgill times and a subsequent rise in the early Llandovery. Sequences representing this stratigraphical interval are relatively uncommon, since the usual effect of the sea level fall and rise is the unconformity seen between most Ordovician and Silurian rocks; however, one such preserved sequence is in the Oslo-Asker region, Norway, where the late Ashgill rocks are unusually well represented and contain a diverse series of shelly faunas. Brenchley and Newall (1980) have described and analysed the sedimentology of this regressive sequence. Because such sequences are usually eroded as the regression proceeds, the area affords a rare opportunity to study and evaluate the animal associations to be found in such a situation. However, prior to such a study of the ecology (Brenchley and Cocks 1982), the systematics, particularly of the commoner forms such as the brachiopods, need reassessment, and this is the purpose of the present paper.

The Lower Palaeozoic strata of the Oslo-Asker region were known to the earliest geologists, and since the work of Kjerulf and Brøgger in the mid nineteenth century have also been mapped and classified. Amongst this Cambrian to Silurian sequence lie the latest Ordovician rocks, which were studied closely by Kiaer (1897, 1902, 1908) and more recently by Brenchley and Newall (1975). There were formerly known as 'Stage 5' rocks, with substages 5*a* below and 5*b* above, but they are now divided into three formations, Husbergøya Shale underlying Langøyene Sandstone in the east of the Oslo-Asker area, and the Langåra Limestone-Shale Formation developed laterally to the Langøyene Sandstone in the west of the Oslo-Asker area. There are also beds of similar age in geographically separated areas not far from the Oslo-Asker district, to the south-west at Skien-Langesund and to the north at Ringerike and Hadeland, but these other areas have a different stratigraphy and largely different faunas, and are outside the scope of this study. Further to the north, in the Mjøsa area, the Silurian lies unconformably upon rocks of late Caradoc or early Ashgill age, and beds of late Ashgill age are absent.

Previous work on the brachiopod fauna from the late Ashgill of the Oslo-Asker area has been surprisingly sparse—consisting only of Kiaer (1902), who described *Holorhynchus giganteus* and

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'*Barrandella*' *kjerulfi*; Holtedahl (1916), who reviewed the Strophomenida, though without describing new species from the upper Ashgill; Wright (1965), who recorded a rare species of *Streptis*; and Sheehan (1977), who revised *Hindella*.

AGE AND AFFINITIES OF THE FAUNA

In the east of the Oslo-Asker district there is a 2-m-thick brown sandstone which forms a useful marker horizon at the top of the Husbergøya Shale Formation. Within, and up to 5 m beneath, this brown sandstone there occur the trilobites *Tretaspis sortita broeggeri*, *Mucronaspis kiaeri*, *Stygina latifrons scotica*, *Calymene* (s.l.) sp., and *Toxochasmops* sp., which Dr. A. W. Owen considers to represent a fauna of latest Rawtheyan age, probably equivalent to the Cystoid Limestone of northern England (Ingham 1966) and the Starfish Bed at Girvan, Scotland. Thus, all of the Husbergøya Shale probably falls within the Rawtheyan Stage. Above it occurs the Langøyene Sandstone, and above that formation the Silurian Solvik Formation, from which Howe (1982) has described lower Llandovery *acuminatus* Zone graptolites collected 11 m above its base. The age of the intervening Langøyene Sandstone Formation must therefore be Hirnantian; a conclusion supported both by the shelly faunas described here and by the physical regression and subsequent transgression seen at its top, reflecting the eustatic fall and rise of sea level caused by the contemporary glaciation (Brenchley and Newall 1980). In the west of the district, the upper part of the Husbergøya Shales and all of the Langøyene Sandstones are replaced laterally by the Langåra Limestone-Shale Formation (Brenchley and Newall 1975), whose detailed age is in doubt, but whose lower part is probably late Rawtheyan, and whose bulk, including the *Holorhynchus* Beds, is probably Hirnantian.

The affinities of the fauna are noteworthy in that, although nearly all of the genera and many of the species of the widespread *Hirnantia* fauna are present in the area at various localities, the *Hirnantia* community itself is only one of several assemblages which occur. Of particular interest are the species which occur in sediments filling tidal channels at the top of the Langøyene Sandstone, representing genera such as *Leptoskelidion*, *Brevilammulella*, and *Thebesia* which have hitherto been reported only from the central North American craton (Amsden 1974). In the Norwegian channels these unusual species usually occur in great numbers, and sometimes even in virtually monospecific assemblages. The Oslo-Asker district has also long been known for its abundance of *Holorhynchus* at the top of the sequence, and this genus is also known from the USSR, China, and elsewhere at a similar stratigraphical position. However, the main impression left by the brachiopod fauna as a whole is of a relatively cosmopolitan series of assemblages, whose ecology is discussed by Brenchley and Cocks (1982), and which may prove to be even more widespread when late Ordovician faunas from elsewhere are re-evaluated.

SYSTEMATIC PALAEONTOLOGY

Five new species are described in some detail and some older species revised, otherwise only the synonymy and discussion of some of the previously described species are given. All the types are lodged in the Paleontologisk Museum, Oslo (PMO), and other material in the British Museum (Natural History) (BB).

Class INARTICULATA Huxley, 1869

A number of inarticulate brachiopods have been found at various horizons and localities within the late Ordovician of the Oslo-Asker region, and representatives of the lingulide genera *Lingula* (at least two species), *Craniops*, and *Eodinobolus*, and the acrotretides *Orbiculoidea* s.l., *Philhedrella*, and *Acanthocrania* have been identified. However, the only inarticulate brachiopod collected in substantial numbers is *Trematis norvegica*, described below.

Order ACROTRETIDA Kuhn, 1949
Superfamily DISCINACEA Gray, 1840
Family TREMATIDAE Schuchert, 1893
Genus TREMATIS Sharpe, 1848
Trematis norvegica sp. nov.

Plate 78, figs. 1–4

Description. Large trematid, biconvex but relatively thin in profile. Outline subcircular, but variable, sometimes appreciably longer than wide and vice versa. Brachial valve beak diverging widely (at 120° to 140°) and protruding just beyond pedicle valve margin. Ornament of fine radial costellae (8 per mm at 3 mm from the umbo of the holotype) and growth lines of about the same strength between and interrupted by the costellae, combining to give a mesh-shaped arrangement, the whole interrupted by occasional accentuated growth lines at sporadic intervals. V-shaped pedicle opening with margins diverging at approximately 80° and with a length of 5 mm in the holotype. Obscure muscle scars faintly impressed near the centre of the brachial value.

Material. Holotype PMO 104.018, and sixty-one other specimens, including BB 76063–76087 and BB 91662–91685, all from 25 m above the base of the Langøyene Sandstone Formation (Hirnantian), north shore of Hovedøya, Oslo. Grid Ref. NM 968416; the species also occurs at other localities of comparable horizon, for example at Gressholmen north, Oslo (Grid Ref. NM 962399).

Dimensions (in mm)	Length	Width
PMO 104.018, pedicle valve, holotype	24.6	*c.* 25
BB 91667, pedicle valve	24.5	41.8
BB 76072, brachial valve	30.8	*c.* 27
BB 76073, brachial valve	*c.* 24	35.1
BB 76076, conjoined valves	25.6	33.2

Discussion. Wright (1963) has reviewed the genus *Trematis*, and noted, following Hall and Clarke (1892, p. 139), that several different types of ornament occur within the genus. The type species *T. terminalis* (Emmons, 1842), from the Trenton of New York State, has an ornament consisting of pits arranged in a quincunx pattern and no radial striae, and other species have a similar arrangement, or pits arranged hexagonally, or pits in radial rows separated by radial ribs. This last group, with ribs, in which Wright included *T. siluriana* Davidson, *T. cancellata* G. B. Sowerby, *T. ottawaensis* Billings, *T. crassipunctata* Ulrich, *T. huronensis* Billings, *T. minneapolis* (Sardeson), and *T. foerstei* Cooper, in some instances approach the ornament seen in the new species. However, comparison of the new species is complicated by the fact that it is much larger than any other known trematid, and in the early growth stages the growth lines and ornament are crammed together in a densely packed reticulate ornament which is difficult to compare with *T. terminalis.* The listed species of *Trematis* with costae need reassessment to see whether they should be reassigned to a new genus, since *T. terminalis* and the common Caradoc *T. punctata* from Shropshire and *T. millepunctata* from the Hudson River Group lack external ribs, although a faint radial pattern can be seen on some of the inner shell layers in partly exfoliated specimens.

T. norvegica occurs abundantly along a few bedding planes as the only common brachiopod in a restricted assemblage together with modiolopsid bivalves and conulariids, and with bryozoa and cornulitids growing epifaunally upon them. The brachiopods are preserved in a muddy limestone, and their shells appear quite thin (apparently thinner than other species less than half their size, such as *T. terminalis* and *T. ottawaensis*), but to what extent this thinness is due to post-depositional compression is unknown. This appears to be the first record of the genus from Europe apart from Britain, and is also the youngest from anywhere.

Class ARTICULATA Huxley, 1869
Order ORTHIDA Schuchert and Cooper, 1932
Suborder ORTHIDINA Schuchert and Cooper, 1932
Superfamily ORTHACEA Woodward, 1852

Orthaceans occur throughout most of the area, but they are often represented by only a few specimens at any one locality, and thus it is difficult to collect samples which merit formal description. Genera identified include *Dolerorthis*, *Nicolella*, *Platystrophia*, *Glyptorthis*, *Hesperorthis*, *Orthambonites* (Plate 78, fig. 5), *Skenidioides*, *Dinorthis*, and *Cremnorthis*, and several of these genera are apparently represented by more than one species. Occurring at only three localities (channels near the top of the Langøyene Sandstone at the south-west of Hovedøya and at the south-east of Langøyene; and in the middle of the Langåra Formation at Langåra), there occurs a large (e.g. BB 71255, length 29.2 mm, estimated width 40 mm) orthostrophiine which appears to be a new species of *Comatopoma* Havlíček, but with a different ribbing style, relatively larger cardinalia, and a larger size of any other species previously attributed to this hitherto exclusively Bohemian genus.

Superfamily ENTELETACEA Waagen, 1883

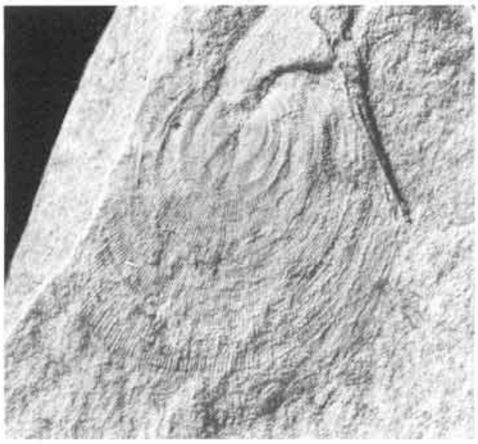
There has been some discussion as to whether there should be more than one superfamily for endopunctate orthides. However, I agree with Havlíček (1977, p. 110) that all the punctate orthides have a monophyletic origin, possibly from the Ranorthidae, and thus only one superfamily need be used, as in the Treatise on Invertebrate Paleontology (Wright *in* Williams *et al.* 1965). In addition to the genera described in more detail below, *Dicoelosia*, *Laticrura*, and *Epitomyonia* have all been found as relatively rare components of the fauna at several localities. Although the enteletaceans form the most numerous group of brachiopods in the late Ashgill of the Oslo–Asker area, they are also the most difficult to identify, partly because homoeomorphy is rife in some characters, partly because of the large number of generic and specific names available (perhaps indicating finer taxonomic splitting than in other brachiopod groups), and partly because different systematists have adopted different criteria in older and younger rocks, whilst leaving the Ashgill enteletaceans relatively poorly known, except those from Bohemia.

EXPLANATION OF PLATE 78

Figs. 1–4. *Trematis norvegica* sp. nov., all from 25 m above the base of the Langøyene Sandstone Formation, north shore of Hovedøya, Oslo, Grid Ref. NM 968416. 1, PMO 104.018, holotype, a pedicle valve, ×2. 2, BB 91667, a pedicle valve, ×2. 3, BB 76072, interior of a pedicle valve, ×4, showing ornament. 4, BB 76073, a brachial valve, ×1·5. Note that the specimens in figs. 2 and 4 have cornulitids attached to the interior of the valves.

Fig. 5. *Orthambonites* sp., BB 75311, the internal mould of a brachial valve, from Husbergøya Shales, 10 m above base of section at Ringeriksveien, Sandvika, Baerum, Grid Ref. NM 853403, ×4.

Figs. 6–10. *Hirnantia sagittifera* (M'Coy, 1851), from within 2 m of the base of the Langøyene Sandstone Formation, fig. 6 from west Rambergøya, Oslo, Grid Ref. NM 962394, figs. 7–10 from north-west Gressholmen, Oslo, Grid Ref. NM 963400. 6, PMO 104.019, internal mould of a pedicle valve, ×1·5. 7, BB 74616, internal mould of a pedicle valve, ×1. 8–10, BB 74123, internal mould of a particularly large and convex brachial valve, ×1.



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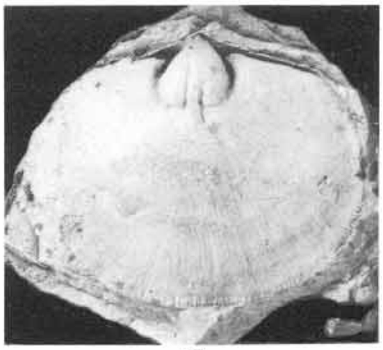

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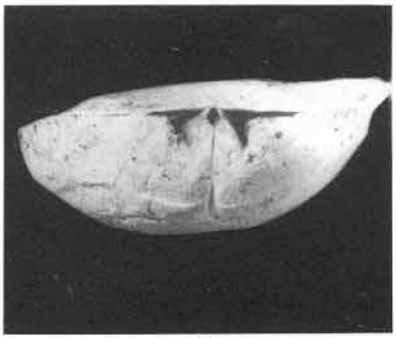

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COCKS, *Trematis*, *Orthambonites*, and *Hirnantia*

Family DALMANELLIDAE Schuchert, 1913
Genus DALMANELLA Hall and Clarke, 1892
Dalmanella testudinaria (Dalman, 1828)

Plate 79, figs. 4–12

1828 *Orthis testudinaria* Dalman, p. 115, pl. 2, figs. 4*a–e*.
1963 *Dalmanella testudinaria* (Dalman); Williams and Wright, p. 29, pl. 2, figs. 7, 8, 11–13, 16–19.
1965 *Dalmanella testudinaria* (Dalman); Temple, p. 383, pl. 3, figs. 1–7; pl. 4, figs. 1–6; pl. 5, figs. 1–7; pl. 6, figs. 1–7.
1968 *Dalmanella testudinaria* (Dalman); Bergström, p. 8, pl. 2, fig. 5.
1977 *Dalmanella testudinaria* (Dalman); Havlíček, p. 137, pl. 32, figs. 1–15, 18, 19, 23; pl. 56, fig. 13.
1980 *Dalmanella testudinaria* (Dalman); Nikitin *in* Appollonov *et al.*, p. 38, pl. 12, figs. 1–17.

Material. In the Oslo–Asker district, *D. testudinaria* is common at a number of localities, particularly at 1–5 m above the base of the Langøyene Sandstone, e.g. at Gressholmen (BB 74131–74160), Grid Ref. NM 962399, Husbergøya (BB 74231–74247), Grid Ref. NM 961376, and Hoyerholmen (BB 75572–75602, BB 75960–75968), Grid Ref. NM 874361.

Discussion. Since the species has been extensively redescribed in recent years (see selected synonymy above), a full description is not given here. *Dalmanella* was a variable and successful genus from Llanvirn to early Llandovery times, and its great variability, as well as its sheer abundance from many localities, has presented problems to many taxonomists. In late Ashgill times, *D. testudinaria* was particularly widespread, and is known both as an important constituent of the *Hirnantia* community, and as a significant, sometimes even dominant, member of other assemblages. It has been found in a wide variety of lithologies, ranging from siltstones (e.g. Västergötland, Poland, Bohemia, Aber Hirnant) to fine calcilutites (the type locality at Borenshult, Sweden, and the Oslo–Asker district) and micrites (Anticosti Island, Canada). Mitchell (1977) distinguished a subspecies for slightly wider forms, later renamed (Mitchell *in* Cocks 1978, p. 63) *D. testudinaria ripae*, from the Pomeroy area, Ireland, and Dr. D. A. T. Harper tells me that this is also the common form in the Whitehouse Group of Girvan, Scotland. Other closely related contemporary forms include *D. edgewoodensis* Savage, from central North America and reviewed by Amsden (1974), whose brachial valve is more convex and less sulcate than *D. testudinaria*; *D. portranensis*,

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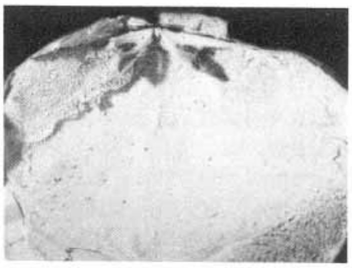
EXPLANATION OF PLATE 79

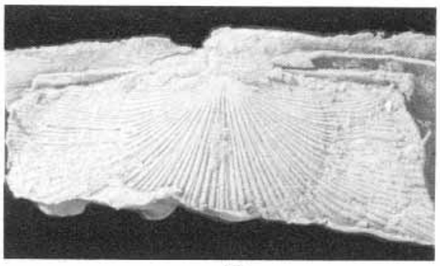
Figs. 1–3. *Hirnantia sagittifera* (M'Coy, 1851), from within 2 m of the base of the Langøyene Sandstone Formation, figs. 1 and 2 from north-west Gressholmen, Oslo, Grid Ref. NM 963400, fig. 3 from west Rambergøya, Oslo, Grid Ref. NM 962394. 1, BB 74116, latex cast of the internal mould of a brachial valve, with encrusting ceramoporoid bryozoan, ×1·5. 2, BB 93984, latex cast of the external mould of a brachial valve, ×1·5. 3, BB 74115, latex cast of the internal mould of a brachial valve, ×1·5.

Figs. 4–12. *Dalmanella testudinaria* (Dalman, 1828), all from within 2 m of the base of the Langøyene Sandstone Formation, north-west Gressholmen, Oslo, Grid Ref. NM 963400. 4, BB 74148, internal mould of a pedicle valve, ×3. 5, BB 74136, latex cast of the external mould of a brachial valve and associated pedicle valve interarea, ×3. 6, 7, BB 74145, internal mould of a pedicle valve and the latex of it, ×2·5. 8, BB 74144, internal mould of a brachial valve, ×3. 9, 10, BB 74152, latex cast and internal mould of a brachial valve, ×3. 11, 12, BB 74151, latex cast and internal mould of a brachial valve, ×3.

Figs. 13, 14, 17, 18. *Onniella kalvoya* sp. nov., all from Langøyene Sandstone Formation, 24 m above the base of Stage 5, Kalvøya north-east, Baerum, Grid Ref. NM 864401. 13, 14, PMO 104.021, holotype, internal mould of a brachial valve and latex cast of the corresponding external mould, ×3. 17, BB 91890, internal mould of a brachial valve, ×3. 18, BB 91885, internal mould of a pedicle valve, ×3.

Figs. 15, 16. *Drabovia* sp., from Husbergøya Shale Formation, 1 m below brown sandstone at the top of the formation, south-west coast of Brønnøya, Asker, Grid Ref. NM 857362. 15, BB 74649, internal mould of a brachial valve, ×3. 16, BB 74647, internal mould of a pedicle valve, ×3.





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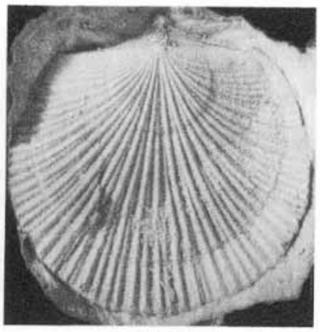

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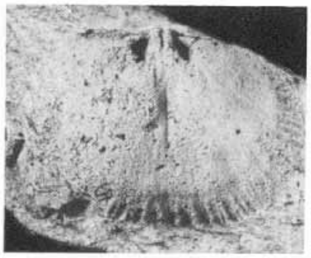

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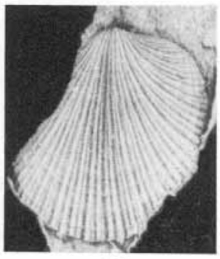

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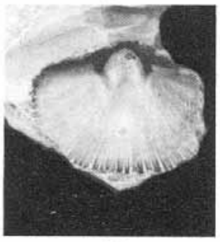

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COCKS, *Hirnantia*, *Dalmanella*, *Onniella* and *Drabovia* whose dental lamellae are more nearly parallel and whose brachiophores are longer than *testudinaria* (Wright 1964); and *D. wysogorskii*, from Swedish erratic blocks of the same age as the Leptaena Limestone of Dalarna (Wiman 1907), which needs revision. *D. cicatrica*, from Kazakhstan (Nikitin *in* Appollonov, Bandaletov and Nikitin 1980), and *D. pectinoides* Bergström, 1968, from Västergötland, both differ in ribbing style, and *D. pectinoides* also in the form of the muscle field in the pedicle valve. *D. testudinaria* itself is a very variable form, and although several authors have presented statistical analyses of various sorts, it is instructive to note the variability in the relative sizes and proportions of the cardinal process, brachiophores, shaft and median ridge (compare Pl. 79, figs. 9 and 11 with Williams and Wright 1963, pl. 2, figs. 7 and 8).

Genus ONNIELLA Bancroft, 1928
Onniella kalvoya sp. nov.

Plate 79, figs. 13, 14, 17, 18; Plate 80, figs. 1-5

Description. Exterior. Shells with subcircular outline; gently convex pedicle valve without incurved umbo; convex brachial valve with gentle sulcus. Relatively small apsacline pedicle valve interarea, narrow open delthyrium, with apex angle about 40°. Small anacline brachial valve interarea, approximately half valve width; open notothyrium partly filled with posterior of cardinalia. Primary ornament of relatively fine, even costellae (approx. 5 per mm at 3 mm anteriorly) with new ribs arising by branching; secondary ornament of concentric filae (14-16 per mm throughout valve length) more accentuated in rib troughs and rarely crossing rib crests.

Pedicle valve interior. Strong teeth supported by short stubby dental plates which merge anteriorly quickly with the valve floor; small crural fossettes present. Muscle field relatively small, extending for average of 34% valve length in five specimens, bilobed, adductor scars poorly differentiated (Pl. 79, fig. 17). Vascular markings usually obscure, but pair of thick *vascula media* diverge anteriorly from diductor scars in some specimens.

Brachial valve interior. Cardinal process relatively small, bilobed posteriorly, and continuing anteriorly in a thin shaft which merges further anteriorly with a low but distinct myophragm. Thick, stubby brachiophores which merge posterolaterally with subsidiary fulcral plates to give well-defined sockets, which are also bounded anterolaterally by thin socket plates. Tops of brachiophores diverging anteriorly at about 70°. Well-defined adductor area extending anteriorly for 50-60% of valve length; anterior scars longer and wider than posterior scars (Pl. 79, fig. 13).

Material. Holotype PMO 104.021, the internal mould and external counterpart of a brachial valve (Pl. 79, figs. 13, 14): 9 conjoined valves, 13 pedicle valves, and 7 brachial valves (including BB 74248-74253, BB 91874-91892) from the Langåra Limestone-Shale Formation, 24-26 m above the base of Stage 5, north-east end of Kalvøya, Baerum, Norway, Grid Ref. NM 864401. The species also occurs commonly at other localities in the same formation, and rarely in the Husbergøya Shales.

Dimensions (in mm)	Length	Width
PMO 104.021, brachial valve, holotype	9.9	9.5
BB 91890, brachial valve	6.3	7.1
BB 74253, brachial valve	9.5	11.6
BB 91885, pedicle valve	7.3	8.4
BB 91881, pedicle valve	12.6	*c.* 12

Discussion. Seven species of *Onniella* are known from the Caradoc of Britain (Cocks 1978; Hurst 1979), four from North America (Cooper 1956), five from Bohemia (Havlíček 1977), and seven from the Baltic area (Hints 1975). However. since '*Onniella*' *rava* and its subspecies *silvicola*, known from Ashgill and early Llandovery rocks in Bohemia and Wales (Marek and Havlíček 1967; Temple 1970), have been transferred to *Ravozetina* by Havlíček (1977, p. 145), the only nominal post-Caradoc species are the five revised by Hall (1962) from the Cincinnatian of eastern North America and *O. trigona* and *O. mediocra* from the Llandovery of Estonia (Rubel 1962); the former also identified in the late Ashgill of Estonia and Latvia by Hints (1975). This substantial and important stock needs revision as a whole; nevertheless, *O. kalvoya* appears to be different from other species in its combination of relatively finely spaced primary ribbing with the fine secondary concentric filae. The filae have also been reported in Ashgill *O. trigona* by Hints (1975, pl. 11, fig. 8*a*), but that species has coarser primary ribs, stronger brachiophores, and a larger myophragm than *O. kalvoya*.

Genus PAUCICRURA Cooper, 1956

Paucicrura sp.

Plate 80, figs. 6, 7

Discussion. Shells like BB 73781-73792, from near the top of the Langøyene Sandstone, 72-73 m above the base of Stage 5, to the south-west of Rambergøya, Oslo, Grid Ref. NM 962394, can be firmly attributed to *Paucicrura*, possessing as they do a trilobed cardinal process and flaring brachiophores like the type species *P. rogata* (Sardeson, 1892) from the Trenton of Minnesota (Cooper 1956, pl. 157F, figs. 18-24). The distinctive brachial valve sulcus is also present in the Norwegian specimens. Lack of recent revision of the genus precludes specific attribution at present; however, the Norwegian specimens appear to be the stratigraphically youngest so far attributed to *Paucicrura*, whose upper limit was previously uncertain (Cooper 1956, p. 143). The species is known from various localities and horizons within the Oslo-Asker area, for example half-way up Stage 5 at the Høvikveien-Baerumsveien road junction, Baerum, Grid Ref. NM 885431.

Family DRABOVIIDAE Havlíček, 1951

Genus DRABOVIA Havlíček, 1951

Drabovia sp.

Plate 79, figs. 15, 16

Discussion. Relatively rare shells, like BB 74647-74649 from 1 m below the brown sandstone at the top of the Husbergøya Shales at a roadside exposure in south-west Brønnøya, Asker, Grid Ref. NM 858363, can be assigned to the Draboviidae, and seem best attributed to *Drabovia* itself on the basis of their cardinalia, brachiophore shape, and ornament. This genus ranges from the Llandeilo to the Ashgill (Havlíček 1977, p. 244), and the brachial valve illustrated here (Pl. 79, fig. 15) is very comparable to *D. westrogothica*, which was described by Bergström (1968) from the late Ashgill of Västergötland, Sweden.

Genus HIRNANTIA Lamont, 1935

Hirnantia sagittifera (M'Coy, 1851)

Plate 78, figs. 6-10; Plate 79, figs. 1-3; Plate 80, fig. 8

1851 *Orthis sagittifera* M'Coy, p. 398.
1935 *Hirnantia sagittifera* (M'Coy); Lamont, p. 313, pl. 7, figs. 20-22.

Description. Exterior. Biconvex, with convexity of brachial valve considerably greater than pedicle valve. Faint trace of very weak pedicle valve fold and corresponding brachial valve sulcus seen in a few valves only. Small anacline brachial valve interarea and fairly small apsacline pedicle interarea. Open delthyrium with small pedicle collar and open notothyrium. Relatively fine radial ornament (84 ribs counted at 10 mm growth line on BB 93984, Pl. 79, fig. 2), with new costellae arising both by bifurcation and intercalation, the costellae curving round laterally to merge with the hinge line. Growth lines obscure, except anteriorly in old specimens.

Pedicle valve interior. Teeth supported by dental plates extending to the valve floor and diverging at right angles, merging antero-laterally with the variably developed muscle-bounding ridges. Thin lanceolate adductor muscle scars between well-impressed anteriorly rounded diductor muscle scars, the whole muscle field bilobed, and extending anteriorly for about one-third of the valve length. Vascular markings obscure.

Brachial valve interior. Cardinal process small, simple (Pl. 79, figs. 1, 3), becoming stronger and more bulbous in the most gerontic specimens (Pl. 78, fig. 9). Pair of stout but relatively short socket plates (the 'supporting plates' of Temple 1965, p. 400) diverging at right angles and attached to the valve floor. Variably developed, poorly defined, thin and low median septum extends for up to one-third of the valve length. Adductor muscle field weakly impressed, but each muscle scar is subcircular and extends anteriorly from between one-quarter and one-third of the valve length.

Material. PMO 104.019 (Pl. 78, fig. 6) and BB 75477-75485, BB 93947-93966 from Langøyene Sandstone Formation (basal Hirnantian), 1-2 m above brown sandstone, shore exposure at Rambergøya west, Oslo, Grid Ref. NM 962394. The species occurs at several localities at a similar horizon (see Brenchley and Cocks 1982), and particularly abundantly in an old quarry at Gressholmen (BB 74109-74130) at Grid Ref. NM 963400.

Dimensions (in mm)	Length	Width
PMO 104.019, internal mould of pedicle valve	28·2	*c.* 37
BB 74616, internal mould of pedicle valve	33·7	41·1
BB 74109, internal mould of pedicle valve	24·9	31·0
BB 74123, internal mould of brachial valve	33·3	45·6
BB 93964, internal mould of brachial valve	21·7	26·5

Discussion. Hirnantia sagittifera dominates the macroecology of the beds in which it occurs, both as a large species in its own right and also as the base for a common epifauna of ceramoporoid bryozoans, crinoids, cornulitids, and other forms which thrived on both live and dead *Hirnantia* shells. A fuller synonymy for the species is given in Cocks (1978, p. 79); it is well known from many studies, the topographically closest being that of Bergström (1968) from Västergötland, Sweden.

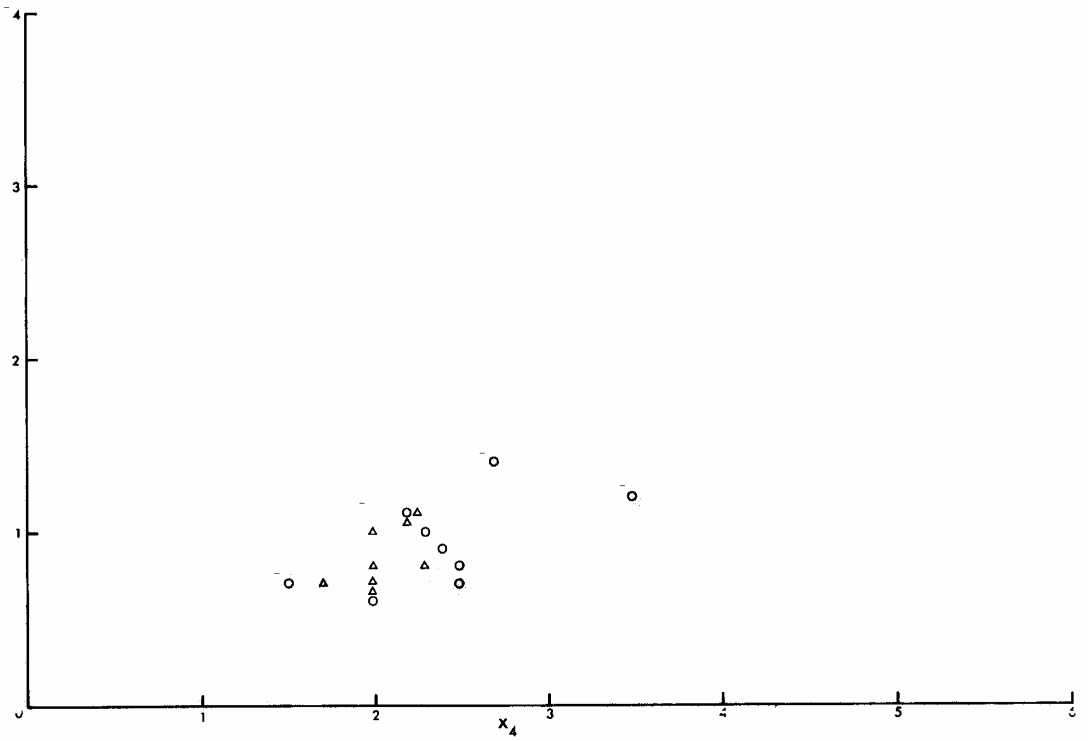
The Oslo shells are particularly large by comparison with other populations of *Hirnantia*, and thus statistical tests were made using the brachial valve parameters originally measured by Temple (1965, p. 400), i.e. x_4, the socket plate length; x_5, the socket plate width; and x_6, the crural pit depth, all measured from internal moulds (text-fig. 1). Dr. Temple has kindly provided me with his raw data from Hirnant, Wales (the type locality for *H. sagittifera*); Hol Beck, the English Lake District; and Stawy, Poland, to compare with the new data from the Oslo region (Table 1), and their allometry has been tested. When x_4 is compared with x_5, the Oslo slope is significantly different from the other three, but when x_4 is compared with x_6, then the Oslo shells are seen to group with the Welsh shells as against the Polish and Lake District specimens. The pooled slope of x_4 against x_6 is 1·75, and when the group means are adjusted using this slope then the Oslo and Welsh groups give intercepts on the vertical through $\log x_4 = 0$ of $-1·86$ and $-1·83$, which are statistically significantly different from the Polish and Lakes groups, which both give valves of $-1·51$. Some thought was given to the possibility of erecting a new subspecies for the larger and also proportionately different Oslo material, but this was rejected in favour of recognizing *H. sagittifera* as a rather variable species tolerating a relatively wide range of habitats and temperature conditions, of which the warm lime muds of the Oslo area apparently represented the optimum. Rong (1979) erected a new species *H. magna* and another new subspecies *H. sagittifera fecunda* based on Chinese material of similar age, but his illustrations suggest that both forms and their names can be included within *H. sagittifera sensu stricto* as interpreted herein.

Family LINOPORELLIDAE Schuchert and Cooper, 1931
Genus LEPTOSKELIDION Amsden, 1974
Leptoskelidion loci sp. nov.

Plate 80, figs. 9-14

Description. Exterior. Biconvex shells with subcircular but slightly transverse outline and short hinge line; no trace of fold or sulcus. Small anacline brachial valve interarea and fairly small curved apsacline pedicle valve interarea. Open delthyrium and notothyrium. Weak ribs, 6 per mm at 3 mm anteriorly from the umbo; ribs curving round laterally but not merging with hinge line. Growth lines obscure.

Pedicle valve interior. Teeth large, supported by prominent but slender dental plates initially diverging at approx. 40° and curving anteriorly (sometimes changing direction at a single sharp point) to diverge for about 20° for most of their length (even slightly incurving in two specimens) before merging quickly anteriorly with



TEXT-FIG. 1. Relative dimensions of brachial valve structures of *Hirnantia sagittifera* from various localities: plot of x_4, the socket plate length, against x_6, the crural pit depth, for populations from Oslo (solid black squares), Hirnant, Wales (open circles), and Stawy, Poland (open triangles). The Polish and Welsh data and the definitions of x_4 and x_6 are from Temple (1965).

TABLE 1. Measurements of x_4, the socket plate length; x_5, the socket plate width; and x_6, the depth of the crural pit, of samples of *Hirnantia sagittifera* from Oslo, Wales, Poland, and the English Lake District. All on natural log scale. The intercepts are on the vertical lines corresponding to log $x_4 = 0$ in each case.

	Oslo	Wales	Poland	Lakes
Sample size (brachial valves)	18	17	20	17
x_4 (means and standard deviations)	1·61 (0·15)	0·98 (0·25)	0·67 (0·41)	1·08 (0·34)
x_5 (means and standard deviations)	−0·60 (0·45)	−1·02 (0·25)	−1·75 (0·49)	−1·09 (0·55)
x_6 (means and standard deviations)	0·97 (0·28)	−0·12 (0·44)	−0·33 (0·72)	0·38 (0·47)
Pairwise correlations x_4, x_5	0·55	0·87	0·76	0·82
Pairwise correlations x_4, x_6	0·36	0·53	0·96	0·93
Pairwise correlations x_5, x_6	−0·05	0·28	0·69	0·80
Allometric slope (from major axis) x_6/x_4	3·83	2·66	1·81	1·44
Intercept (plus or minus standard error)	−1·86 (0·07)	−1·83 (0·10)	−1·51 (0·05)	−1·51 (0·06)
Allometric slope (from major axis) x_5/x_4	5·00	2·07	1·28	1·78
Intercept (plus or minus standard error)	−4·11 (0·09)	−3·15 (0·06)	−3·21 (0·14)	−3·43 (0·10)

the valve floor. Muscle field less than one-third valve length, but details of musculature obscure. Vascular markings usually obscure, apart from traces of vascula media in a few specimens immediately anteriorly of the muscle field.

Brachial valve interior. Cardinal process thin and blade-like, merging anteriorly with the median septum which swells to a maximum thickness at about 3 mm anteriorly from the umbo and extends for up to half the valve length. The expanded brachiophore bases are subparallel posteriorly and then curve round to converge anteriorly and join the median septum in a well-defined sessile cruralium. The brachiophore bases also extend laterally to fuse with the hinge line to form prominent socket plates. Suboval adductor muscle scars poorly impressed on either side of the median septum anterior to the sessile cruralium.

Material. Holotype PMO 104.022, the internal mould of a brachial valve (Pl. 80, fig. 12) from a channel fill at the top of the Langøyene Sandstone Formation, 6 m below the local base of the Silurian at south-west Hovedøya, Oslo, Grid Ref. NM 966407, and thirty-seven other specimens from the same locality (including BB 70367–70378, BB 70402–70409, BB 75998–76004), and other channels nearby (e.g. BB 35300–35304). The species also occurs rarely in the top sandstone of the couplet at the very top of the same formation, for example at south-east Langøyene, Nesodden, Grid Ref. NM 968385 (e.g. BB 74280).

Dimensions (in mm)	Length	Width
PMO 104.022, internal mould of a brachial valve, holotype	11·3	14·8
BB 70403, internal mould of a brachial valve	14·5	16·4
BB 70367, external mould of a brachial valve	10·1	*c.* 15
BB 70370, internal mould of a pedicle valve	13·9	14·8
BB 76001, internal mould of a pedicle valve	15·8	*c.* 17

Discussion. Leptoskelidion loci is closely related to the type and only other known species of the genus, *L. septulosum* Amsden from the Noix Limestone of Missouri (Amsden 1974). However, the ornament of *L. loci*, although still weak, is stronger than on *septulosum*; the 'bulb-like myophore'

EXPLANATION OF PLATE 80

Figs. 1–5. *Onniella kalvoya* sp. nov., all from Langøyene Sandstone Formation, 24 m above the base of Stage 5, Kalvøya north-east, Baerum, Grid Ref. NM 864401. 1, BB 91890, latex cast of the internal mould of a brachial valve, × 4. 2, 3, BB 74253, internal mould and latex cast of a brachial valve, ×2. 4, BB 74250, latex cast of the exterior of a pair of conjoined valves, showing interarea (interarea broken to the right), ×3. 5, BB 91884, internal mould of a brachial valve, ×3.

Figs. 6, 7. *Paucicrura* sp., from Langøyene Sandstone Formation, 1 m below the top of the formation, south-west Rambergøya, Oslo, Grid Ref. NM 962393. 6, BB 73785, internal mould of a pedicle valve, ×3. 7, BB 73783, internal mould of a brachial valve, × 3.

Fig. 8. *Hirnantia sagittifera* (M'Coy, 1851), BB 74615, internal mould of a brachial valve, ×2, from within 2 m of the base of the Langøyene Sandstone Formation, north-west Gressholmen, Oslo, Grid Ref. NM 963400.

Figs. 9–14. *Leptoskelidion loci* sp. nov., all from channel fill 6 m below the top of the Langøyene Sandstone Formation, south-west Hovedøya, Oslo, Grid Ref. NM 966407. 9, BB 70370, internal mould of a pedicle valve, ×2. 10, 13, BB 70403, internal mould of a brachial valve and latex cast of the cardinalia, ×2·5. 11, BB 70369, latex cast of the external mould of a brachial valve, showing faint radial ornament, ×2. 12, PMO 104.022, holotype, internal mould of a brachial valve, ×2. 14, BB 70377, internal moulds of brachial valve (above) and pedicle valve (below), ×2.

Figs. 15–17. *Cliftonia* aff. *psittacina* (Wahlenberg, 1818), figs. 15 and 17 from 1 m above brown sandstone near the base of the Langåra Limestone–Shale Formation, west Langåra, Asker, Grid Ref. NM 856356, fig. 16 from top 15 cm of Husbergøya Shale Formation, west Rambergøya, Oslo, Grid Ref. NM 962394. 15, BB 75691, posterior view of a pair of conjoined valves, ×3. 16, BB 93909, internal mould of a brachial valve, ×2. 17, BB 74619, internal mould of a pair of conjoined valves, with part of the pedicle valve broken away and showing the long cardinal process of the brachial valve, ×2.

PLATE 80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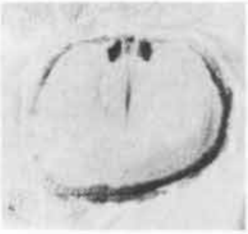
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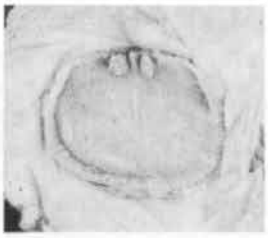
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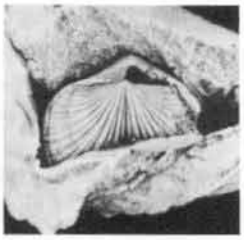
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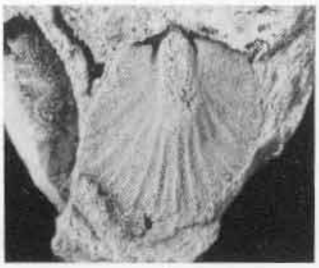
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COCKS, Enteletaceans and *Cliftonia*

of *septulosum* is much less pronounced than on *loci*; and the pedicle valve muscle-bounding ridge, which completely encircles the muscle field of *septulosum*, is scarcely developed in *loci*. The brachial valve median septum is also relatively shorter in *loci*. None of Amsden's specimens exceed 10 mm in width, whilst the Oslo material includes many shells nearly twice as large. *L. loci* is a minor constituent of the assemblage dominated by the rhynchonellide *Thebesia scopulosa*, and which appears to have lived in relatively shallow water.

Superfamily TRIPLECIACEA Schuchert, 1913
Family TRIPLECIIDAE Schuchert, 1913

Discussion. Apart from *Cliftonia*, discussed below and which occurs in swarms in some places, tripleciids occur rarely at most localities in the late Ashgill of the Oslo-Asker region. The most prevalent genus is *Triplesia* itself, tentatively identified here as *T.* aff. *insularis* (Eichwald, 1842) since some specimens appear externally similar to topotype *insularis* from Estonia: *Oxoplecia* is also known from several localities; and Wright (1965) has recorded the rare *Streptis undifera* (Schmidt, 1858) from 5*a* beds at Holmenskjaeret, Holmen, Asker.

Genus CLIFTONIA Foerste, 1909
Cliftonia aff. *psittacina* (Wahlenberg, 1818)

Plate 80, figs. 15-17

aff. 1818 *Anomites psittacinus* Wahlenberg, p. 65.
aff. 1968 *Cliftonia psittacina* (Wahlenberg); Bergström, p. 11, pl. 4, figs. 7-8; pl. 5, figs. 1, 2.

Discussion. At some localities in the middle of the Langåra Limestone-Shale Formation and in the Langøyene Sandstone Formation, *Cliftonia* occurs very commonly, for example at 1 m above the brown sandstone at Langåra west (Grid Ref. NM 856356), where it constituted 64% of the sample ($n = 171$). This is certainly the same species which occurs in the fauna from contemporary rocks in Västergötland, Sweden, which Bergström (1968) identified as *C. psittacina*, and for which he gave a full synonymy. However, the lectotype of *psittacina* comes from the Boda Limestone of Dalarna, Sweden, and without revision of the Boda form it is uncertain whether that material is specifically identical to specimens from Västergötland and the Oslo-Asker district: hence the Oslo-Asker material is left in open nomenclature.

Order STROPHOMENIDA Öpik, 1934
Superfamily PLECTAMBONITACEA Jones, 1928
Family LEPTELLINIDAE Ulrich and Cooper, 1936

Discussion. Leptellinids can be quite common in the area, particularly *Leangella* (Pl. 81, fig. 1), most of which are here identified as *L.* aff. *cylindrica* (Reed, 1917), which was originally described from the Shalloch Formation (Pusgillian) of Girvan, Scotland. *Diambonia* (Pl. 81, fig. 2) and *Sampo* (Pl. 81, fig. 3) also occur in smaller numbers. The *Sampo* is identified as *S. ruralis* (Reed, 1917), originally described from the Rawtheyan of Girvan and which appears to be a senior synonym of the type species *S. hiiuensis* from contemporary rocks in Estonia (Öpik 1933).

Family SOWERBYELLIDAE Öpik, 1930

In addition to the species of *Eoplectodonta* described below, *Eochonetes* (Pl. 81, fig. 4), *Thaerodonta*, *Sericoidea*, and *Chonetoidea* all occur sporadically in the Oslo-Asker area.

Genus EOPLECTODONTA Kozlowski, 1929

Eoplectodonta rhombica (M'Coy, 1852)

Plate 81, figs. 5, 6

1852 *Leptaena serica* var α *rhombica* M'Coy *in* Sedgwick and M'Coy, p. 239.
1871 *Leptaena sericea* var. *rhombica* M'Coy; Davidson, p. 325 *pars*, pl. 48, figs. 20–22, *non* figs. 10–19.
1928 *Sowerbyella rhombica* (M'Coy); Jones, p. 426, pl. 22, fig. 1.
cf. 1963 *Eoplectodonta* cf. *rhombica* (M'Coy); Williams, p. 448, pl. 12, figs. 9–14, 18, 19.
cf. 1977 *Eoplectodonta* (*Eoplectodonta*) cf. *rhombica* (M'Coy); Mitchell, p. 89, pl. 18, figs. 1–7.

Discussion. The lectotype of *rhombica* (selected by Jones 1928, p. 427) comes from the early Ashgill Crag Hill Beds of Horton-in-Ribblesdale, Cumbria. It is amongst the largest species in the whole family, often attaining widths of over 35 mm (e.g. BB 74577). In the Oslo-Asker area it is an intimate associate of *Holorhynchus* in the *Holorhynchus* beds near the top of the Langåra Limestone-Shale Formation, for example BB 74563–74577, BB 74594–74609 from the Ringeriksveien and Jongsåsveien, Sandvika, Baerum (Grid Ref. NM 852403 and NM 850400 respectively).

Eoplectodonta oscitanda sp. nov.

Plate 81, figs. 7–9

Description. Exterior. Concavo-convex shells of transverse outline: maximum width at hinge line. Pedicle valve interarea small, gently curved, apsacline: open delthyrium mostly filled by opposing chilidium of brachial valve. Brachial valve interarea small, catacline. Ornament of fine parvicostellae with density of 18–20 per 2 mm at 5 mm antero-medianly from umbo, and coarser costellae with 6–9 parvicostellae between each; new coarser costellae arising at intervals anteriorly to maintain a comparable distance between them throughout the valve length. Occasional traces of rugae developed in some specimens laterally. Growth lines obscure, except anteriorly in mature specimens.

Pedicle valve interior. Hinge line denticulate for one-third to one-half valve width, with 5–8 denticles seen on either side of the umbo. Teeth present, in one specimen (BB 75397) flaring anteriorly to form incipient muscle-bounding ridge, but this ridge is absent from the other shells. Flaring bilobed muscle field, deeply impressed and flabellate anteriorly (Pl. 81, fig. 7). Thick vascula media extend from anterior edge of muscle field. Median septum absent, apart from swelling between muscle scars at the very posterior of the valve.

Brachial valve interior. Hinge line fossettes corresponding with pedicle valve denticles. Trifid cardinal process with very slender central column, and the two lateral components strengthening and flaring antero-laterally to merge with the clavicular plates, whose posterior margins form the sockets. Edges of bema indistinct posteriorly, becoming stronger laterally and fading anteriorly. Inner side septa and outer side septa (Cocks 1970, p. 144) of variable strength, sometimes equal in size and at other times with the inner side septa considerably more prominent. Barely a trace of median septum developed in the centre of the valve in some specimens; apparently absent in others. Vascular system indistinct.

Material. Holotype PMO 104.023, the internal mould of a brachial valve (Pl. 81, fig. 8), and ten other brachial valves, four pedicle valves, and one pair of conjoined valves (including BB 71220–71229, BB 75395–75400), from the Langåra Limestone-Shale Formation, 18 m stratigraphically below the base of the *Holorhynchus* Beds, Ringeriksveien, Sandvika, Baerum (Grid Ref. NM 852403). The species also occurs sporadically at other localities in the same formation and in the Husbergøya Shale and Langøyene Formations.

Dimensions (in mm)	Length	Width
PMO 104.023, internal mould of brachial valve, holotype	7·0	15·1
BB 71228, external mould of a brachial valve	7·5	*c.* 15
BB 71220, external mould of conjoined valves	8·3	14·4
BB 75300, internal mould of a pedicle valve	8·6	13·4
BB 75301, internal mould of pedicle valve	8·7	15·2

Discussion. Relatively few species of *Eoplectodonta* have so far been described from rocks of Ashgill age. *E. oscitanda* differs from the widespread *E. rhombica* in its relatively more numerous major costellae, its more numerous and relatively finer secondary costellae, and in its smaller size. The new species may be conspecific with the *Eoplectodonta* sp. recently described by Hiller (1980, p. 183) from the Ashgill rocks of Glyn Ceiriog, Wales, although the parvicostella density appears greater in the Norwegian specimens. *E. clarksvillensis* (Foerste), from North America, requires revision, but it has common comae and the specimens seen are less incurved than *oscitanda.*

Superfamily STROPHOMENACEA King, 1846
Family STROPHOMENIDAE King, 1846

Discussion. Rare strophomenids occur throughout the area, but only *Leptaena* sp. is common enough to warrant description here. Genera identified include *Oepikina*, *Furcitella*?, *Katastrophomena*, *Kjerulfina*, *Kiaeromena*, and *Strophomena*. The specimens illustrated by Holtedahl (1916, pl. 8, figs. 7, 8) from 'Stage 5*a*, Nyborg and Bakke, Asker' as *S. asmusi* de Verneuil, 1845, appear attributable to *Strophomena sensu stricto*, although *asmusi* itself requires revision.

Leptaena sp.

Plate 81, figs. 13-15

Discussion. Leptaena occurs at many localities in the late Ordovician of the Oslo-Asker area, but unfortunately never in enough numbers at any one place to be able to characterize a new species. *Leptaena* sp. differs from the contemporary *L. rugosa* Dalman, 1828 of Västergötland, Sweden, revised by Bergström (1968), in its less regular rugae, and in the more elongate, as opposed to subcircular, pedicle valve muscle field. The only specimens similar to *L. rugosa* which are known from the area are some large specimens (e.g. BB 74589, over 50 mm wide) which were found in the base of the *Holorhynchus* Beds at the top of the Langåra Limestone-Shale Formation, and these are identified here as *L.* aff. *rugosa.*

EXPLANATION OF PLATE 81

Fig. 1. *Leangella* aff. *cylindrica* (Reed, 1917), BB 74349, internal mould of a pedicle valve, ×4, from 3 m above the base of the Langøyene Sandstone Formation, west Husbergøya, Nesodden, Grid Ref. NM 961375.

Fig. 2. *Diambonia* sp., BB 75298, internal mould of a pedicle valve, ×4, from 2 m above the base of the Husbergøya Shale Formation, west Langåra, Asker, Grid Ref. NM 856356.

Fig. 3. *Sampo ruralis* (Reed, 1917), BB 74690, internal mould of a pedicle valve, ×3, from 3 m above the base of the Husbergøya Shale Formation, south-east Brønnøya, Asker, Grid Ref. NM 869365.

Fig. 4. *Eochonetes* sp., BB 91857, internal mould of a pedicle valve, showing the perforated hingeline, ×4, from 4 m above the base of the Husbergøya Shale Formation, north-east Kalvøya, Baerum, Grid Ref. NM 864401.

Figs. 5, 6. *Eoplectodonta rhombica* (M'Coy, 1852), from 3 m above the base of the *Holorhynchus* beds, Langåra Limestone-Shale Formation, Ringeriksveien, Sandvika, Baerum, Grid Ref. NM 853404. 5, BB 74567, latex cast of external mould of conjoined valves, ×2. 6, BB 73832, internal mould of a pedicle valve, ×2.

Figs. 7-9. *Eoplectodonta oscitanda* sp. nov., from the Langåra Limestone-Shale Formation, 18 m stratigraphically below the base of the *Holorhynchus* beds, Ringeriksveien, Sandvika, Baerum, Grid Ref. NM 853404. 7, BB 75301, internal mould of a pedicle valve, ×3. 8, PMO 104.023, holotype, the internal mould of a brachial valve, ×3. 9, BB 71220, latex cast of external mould of conjoined valves, ×2.

Figs. 10-12. *Christiania* sp., figs. 10 and 11 from 6 to 7 m above the base of the Langøyene Sandstone Formation, north shore of Hovedøya, Oslo, Grid Ref. NM 967416. 10, BB 76109, internal mould of a brachial valve, ×3. 11, BB 73777, internal mould of a pedicle valve, ×2. 12, BB 74703, internal mould of a pedicle valve, ×3, from 3 m above the base of the Husbergøya Shale Formation, north-east Kalvøya, Baerum, Grid Ref. NM 864401.

Figs. 13-15. *Leptaena* sp., from 3 m above the base of the *Holorhynchus* Beds, Langåra Limestone-Shale Formation, Ringeriksveien, Sandvika, Baerum, Grid Ref. NM 853404. 13, BB 94184, internal mould of a pedicle valve, ×2. 14, 15, BB 74556, external and internal moulds of a brachial valve, ×2.

PLATE 81


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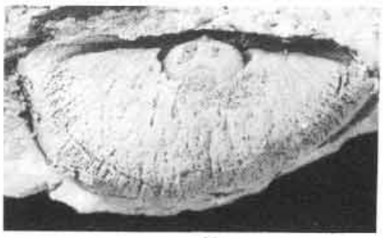
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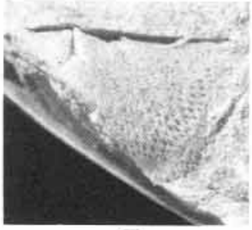
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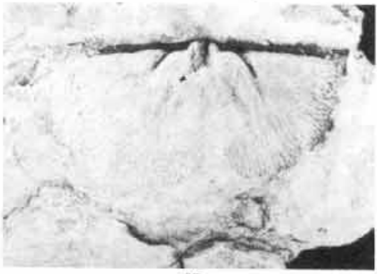
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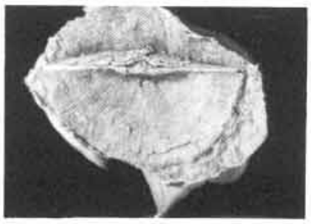
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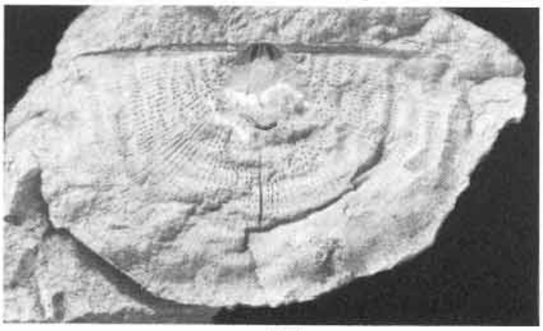
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COCKS, Strophomenides

Family CHRISTIANIIDAE Williams, 1953
Christiania sp.

Plate 81, figs. 10-12

Discussion. Identification of Ashgill *Christiania* is hampered by lack of revision of the much quoted but poorly known *C. tenuicincta* (M'Coy, 1844), originally described from the Kildare Limestone, Ireland. The chief distinguishing specific characteristic appears to be the presence and form of the subhorizontal septa in the brachial valve; other cited characters, such as the valve outline or the possession of a sulcus, appear to be less important. The genus is not common at most Oslo-Asker late Ordovician localities, but can be locally abundant, e.g. at 14·5 m above the base of the Langøyene Formation at Hovedøya north, Oslo (Grid Ref. NM 967416), where over fifty *Christiania* shells (including BB 76109-76116) were found concentrated into a single shell pocket. All these have variable subquadrate (Pl. 81, fig. 11) to semicircular (Pl. 81, fig. 12) outlines, and variably developed incipient sulci, and all the brachial valves had horizontal septa between the primary septa (Pl. 81, fig. 10), unlike the contemporary *C. portlocki* Mitchell, 1977.

Family STROPHEODONTIDAE Caster, 1939
Genus EOSTROPHEODONTA Bancroft, 1949
Eostropheodonta hirnantensis (M'Coy, 1851)

Plate 82, figs. 1-6

1851 *Orthis Hirnantensis* M'Coy, p. 395.
1871 *Strophomena siluriana* Davidson, p. 303, pl. 47, figs. 1-4.
1949 *Eostropheodonta whittingtoni* Bancroft, p. 9, pl. 2, fig. 6.

Discussion. A fuller synonymy may be found in Cocks (1978, p. 125), where Davidson's *siluriana* was provisionally regarded as a distinct subspecies, but close examination of topotype *hirnantensis*, *siluriana*, *whittingtoni*, and other samples from late Ashgill populations, including material from the Oslo-Asker district, has led to the conviction that only the one, rather variable, species of *Eostropheodonta* is present. In particular, the ribbing style, which characteristically consists of wavering costellae, is common to all of the samples. The species has also been illustrated from Västergötland, Sweden (Bergström 1968), Poland (Temple 1965), Czechoslovakia (Marek and Havlíček 1967), Wales (Cocks and Price 1975), and elsewhere, and is a common constituent of the *Hirnantia* Fauna. In the Oslo-Asker district it is relatively uncommon, and occurs chiefly as a

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EXPLANATION OF PLATE 82

Figs. 1-6. *Eostropheodonta hirnantensis* (M'Coy, 1851), figs. 1-4 and 6 from coast section at west Rambergøya, Oslo, Grid Ref. NM 962394. 1-3, BB 94003, internal mould of a brachial valve and latex casts of its external and internal moulds, ×3, from 2 m above the base of the Langøyene Sandstone Formation. Figs. 4, 6, from 15 cms below the top of the Husbergøya Shale Formation. 4, BB 93972, latex cast of the external mould of a brachial valve. ×2. 6, BB 75492, enlargement to show internal mould of cardinalia, ×5. 5, BB 74289, internal mould of a pedicle valve, ×2, from 1 m above the base of the Langøyene Sandstone Formation, south-east coast of Langøyene, Nesodden, Grid Ref. NM 968385.

Figs. 7-13. *Coolinia dalmani* Bergström, 1968, all from 1 m below the top of the Husbergøya Shale Formation, south-west Brønnøya, Asker, Grid Ref. NM 859363. 7, BB 74636, internal mould of a pedicle valve, ×2. 8, BB 74626, latex cast of the external mould of a brachial valve, ×2. 9, BB 74632, internal mould of a pedicle valve, ×2. 10, BB 73776, latex cast of the external mould of a pedicle valve, ×2. 11, BB 74641, internal mould of a pedicle valve, ×2. 12, BB 74630, internal mould of a brachial valve, ×1·5. 13, BB 74629, internal mould of a brachial valve, ×2.

Figs. 14-16. *Brevilamnulella kjerulfi* (Kiaer, 1902), PMO 40466, syntype, conjoined valves, ×3, the original of Kiaer 1902 p. 64, figs. 5, 6, from Jorgenslökken, Asker.

PLATE 82

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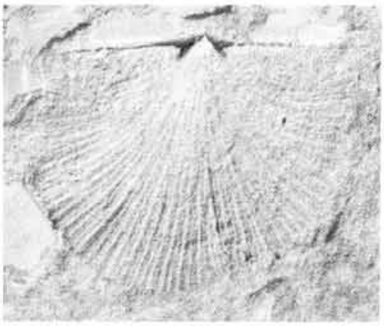

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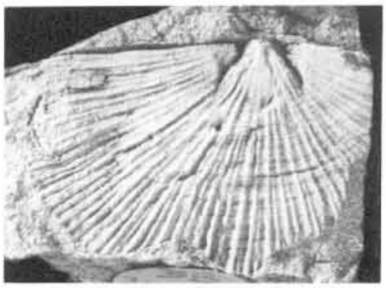

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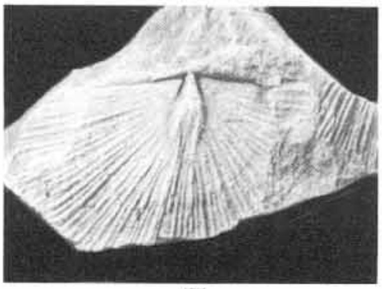

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COCKS, *Eostropheodonta*, *Coolinia* and *Brevilamnulella* minor constituent of the assemblages, but at some localities, e.g. near the base of the Langøyene Sandstone Formation at south-west Rambergøya, Oslo, Grid Ref. NM 962394, it can be abundant.

Superfamily DAVIDSONIACEA King, 1850
Family CHILIDIOPSIDAE Boucot, 1959
Genus COOLINIA Bancroft, 1949
Coolinia dalmani Bergström, 1968

Plate 82, figs. 7-13

1828 *Orthis*? *pecten* (Linnaeus) Dalman, pp. 110-111 *pars*, pl. 1, fig. 6*a-d*.
1968 *Coolinia dalmani* Bergström, p. 17, pl. 6, fig. 10; pl. 7, figs. 1-4.

Discussion. The chief difference between *Fardenia* and *Coolinia* lies in the chilidium, which is present in the latter and absent in the former. *C. dalmani* has a chilidium, but it is a very thin and fragile structure when compared with that of the Silurian *C. pecten*. The Oslo-Asker specimens may be confidently identified with Bergström's species not only in their brachial valve structures, valve form, and ribbing, but chiefly in the distinctive shape of their pedicle valve muscle-bounding ridges (Pl. 82, fig. 7), which distinguishes *C. dalmani* from all other species of the genus. In the Oslo-Asker District the species occurs sporadically, but is occasionally common, e.g. BB 74625-74642 from the top of the Husbergøya Shale Formation at south-west Brønnøya, Asker, Grid Ref. NM 858364.

Order PENTAMERIDA Schuchert and Cooper, 1931

Various pentamerides, in particular porambonitaceans such as *Parastrophina* and others (Wright 1974), occur very sporadically in the Oslo-Asker district, but the only abundant species are *Holorhynchus giganteus* and *Brevilamnulella kjerulfi*.

Superfamily PENTAMERACEA M'Coy, 1844
Family STRICKLANDINIIDAE Hall and Clarke, 1894
Genus HOLORHYNCHUS Kiaer, 1902
Holorhynchus giganteus Kiaer, 1902

Plate 83, figs. 12-17

1902 *Holorhynchus giganteus* Kiaer, p. 68, figs. 1-7.
1938 *Holorhynchus giganteus* Kiaer; St. Joseph, p. 292, pl. 4, figs. 1-5.

EXPLANATION OF PLATE 83

Figs. 1-11. *Brevilamnulella kjerulfi* (Kiaer, 1902), figs. 1-4 and 8, from near the top of the Langåra Limestone-Shale Formation, roadside exposure south of Semsvatnet, Asker, Grid Ref. NM 799364, figs. 5-7, and 9-11 from south shore of Semsvatnet, Grid Ref. NM 800364, from about 20 m stratigraphically higher than the previous specimens. 1, 2, BB 93757, posterior and vertical views of the internal mould of a brachial valve, ×2. 3, BB 91591, internal mould of a pedicle valve, ×2. 4, 8, BB 91603, vertical and posterior views of conjoined valves, ×3. 5-7, BB 91574, three views of a partly exfoliated pair of conjoined valves, ×2. 9, BB 91576, internal mould of a brachial valve, ×2. 10, 11, BB 91585, vertical and posterior views of the internal mould of a brachial valve, ×2.

Figs. 12-17. *Holorhynchus giganteus* Kiaer, 1902. 12, PMO 73241, posterior view of a prepared pedicle valve, ×1, the original of Kiaer 1902, p. 73, fig. 5, from *Holorhynchus* beds, Sandviksåsen, Baerum. Figs. 13-15 from 3 m above the base of the *Holorhynchus* beds, Langåra Limestone-Shale Formation, Ringeriksveien, Sandvika, Baerum, Grid Ref. NM 853404. 13, BB 73774, internal mould of a pair of conjoined valves of a small, presumably young, individual, ×2. 14, BB 73775, internal mould of the posterior part of a brachial valve demonstrating its similarity to a stricklandiid, ×2. 15, BB 74526, posterior view of the internal mould of an adult pedicle valve, ×1. 16, 17, PMO 12431, lectotype, conjoined valves, the original of Kiaer 1902, pp. 70, 71, figs. 1-3, ×1, from *Holorhynchus* beds, Aspelund, Asker.


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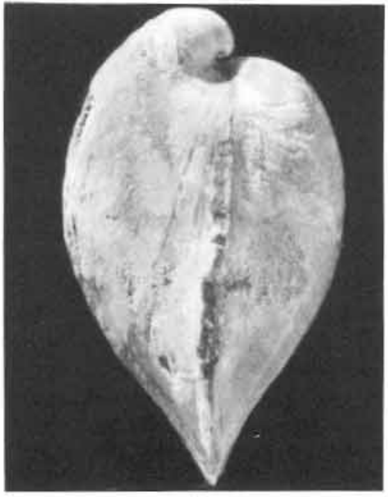
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COCKS, ***Brevilamnulella*** **and** ***Holorhynchus***

Remarks. The opportunity is taken here, not only of refiguring the lectotype, PMO 12431 (selected St. Joseph 1938, p. 293), which is a typical large specimen of conjoined valves with full calcite, but also of figuring the interior of the brachial valve for the first time (apart from serial sections), in both half-grown (Pl. 83, fig. 13) and fully mature (Pl. 83, fig. 14) specimens. It can be seen that the brachial valve interior of the mature specimen is virtually identical to brachial valves of the early Llandovery *Stricklandia lens lens* (J. de C. Sowerby, 1839), and indeed the pedicle valve structures are also similar, apart from the median septum, which is strong but short in *Stricklandia*, and virtually absent in mature *Holorhynchus* (Pl. 83, fig. 15), although weakly present in juveniles (Pl. 83, fig. 13) The similarities are close enough to transfer *Holorhynchus* unequivocally from the Pentameridae or the Virgianidae, where it had been classified by most authors, into the Stricklandiniidae, where its phylogenetic position needs reassessment among other late Ordovician genera such as *Prostricklandia* and others (Sapelnikov and Rukavishnikova 1975). In the Oslo-Asker district, millions of *Holorhynchus* shells dominate a widespread assemblage in the *Holorhynchus* Beds at the top of the Langåra Limestone-Shale Formation to the west of the area.

?Family VIRGIANIDAE Boucot and Amsden, 1963
Genus BREVILAMNULELLA Amsden, 1974
Brevilamnulella kjerulfi (Kiaer, 1902)

Plate 82, figs. 14-16; Plate 83, figs. 1-11

1902 *Barrandella kjerulfi* Kiaer, p. 63, figs. 1-7.
1938 *Clorinda kjerulfi* (Kiaer); St. Joseph, p. 307, pl. 7, figs. 1-6; pl. 8, figs. 1-13.

Discussion. At first sight, comparison is difficult between the reconstructions from the serial sections of *kjerulfi* given by St. Joseph (1938, pl. 7), and the interior views of silicified specimens given by Amsden (1974, pls. 1, 2) of the type, and hitherto only known, species of *Brevilamnulella*, *B. thebesensis* (Savage, 1913) from the late Ordovician Edgewood Formation of Missouri and Illinois and the Keel Formation of Oklahoma. However, there is no doubt that, when specimens of *kjerulfi* are prepared to reveal the interior (Pl. 83, figs. 1-4, 8-11), then the two species are seen to be very closely similar, although *B. kjerulfi* has a greater tendency to show lateral ribs. *B. kjerulfi* occurs in large numbers in restricted horizons at the very top of the Langåra Limestone-Shale Formation in the Asker area, particularly at Hvalsbakken, Grid Ref. NM 835350, and Semsvatnet, Grid Ref. NM 800364. The number of lateral ribs on either side of the median fold and sulcus varies within each sample from zero to four, with one or two being the most common. Kiaer (1902, pp. 65, 100) distinguished between a 'wide' and a'narrow' form, but there are specimens of intermediate width within each assemblage.

EXPLANATION OF PLATE 84

Figs. 1-11. *Thebesia scopulosa* sp. nov., all from 6 m below the top of the Langøyene Sandstone Formation, coast exposure on the south-west of Hovedøya, Oslo, Grid Ref. NM 968407. 1, 2, BB 70386, internal mould of a brachial valve and latex cast of it, ×4. 3, 4, BB 70400, internal mould of a pedicle valve and latex cast of it, ×4. 5-7, PMO 104.027, holotype, conjoined valves; in fig. 7 the brachial valve is uppermost, ×3. 8, 9, BB 70398, conjoined valves, ×4. 10, 11, BB 70399, conjoined valves, ×4.

Fig. 12. *Plectothyrella crassicostis* (Dalman, 1828), BB 71265, internal mould of a brachial valve, ×1·5, from 15 m above the base of the Langøyene Sandstone Formation, shore exposure at north-west Hovedøya, Oslo, Grid Ref. NM 965415.

Fig. 13. *Protatrypa* sp., BB 75306, conjoined valves viewed ventrally, ×3, from Husbergøya Shale Formation, 8 m from base of section at Ringeriksveien, Sandvika, Baerum, Grid Ref. NM 854403.

Figs. 14-19. *Hindella cassidea* (Dalman, 1828), from within 2 m of the top of the Husbergøya Shale Formation, shore exposure at the western end of Langåra, Asker, Grid Ref. NM 856356. 14-16, BB 76156, three views of the internal mould of a pedicle valve, ×1·5. 17-19, BB 74880, three views of an articulated specimen, ×2.


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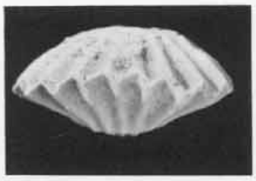
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COCKS, *Thebesia* and atrypoids

Order RHYNCHONELLIDA Kuhn, 1949

Rhynchonellides occur sporadically at several localities and horizons in the late Ashgill of the Oslo-Asker district, but, apart from the abundant *Thebesia* described below, they are never common enough to form more than a few per cent of the local assemblages. Forms identified include *Rostricellula*, *Stegerhynchus*?, and *Plectothyrella crassicostis* (Dalman, 1828), figured here in Plate 84, fig. 12; the latter is important elsewhere as a distinctive constituent of the *Hirnantia* community (e.g. Temple 1965; Bergström 1968).

Family TRIGONIRHYNCHIIDAE McLaren, 1965
Genus THEBESIA Amsden, 1974
Thebesia scopulosa sp. nov.

Plate 84, figs 1-11

Description. Exterior. Outline subtriangular, with prominent erect pedicle valve beak with relatively straight sides, which often curve anteriorly to become laterally concave in outline. Small but functional pedicle opening. Variable convexity, from nearly flat to fairly globose. About twelve ribs, difficult to count laterally since they merge with the flat shell sides; ribbing stronger anteriorly from about half valve length, the ribs curving gently antero-laterally. Anterior commissure usually fairly straight, but simple fold and sulcus sometimes weakly developed.

Pedicle valve interior. Teeth supported by well-developed but slender dental plates, subparallel on valve floor, but diverging slightly dorsally. Small transverse pedicle collar weakly developed at approximately the same distance anteriorly as the teeth. Muscle field not impressed.

Brachial valve interior. Cardinal process absent. Median septum present to half or two-thirds of the valve length. Prominent socket plates extend anteriorly to form crural bases, underneath which a small crurualium is present posteriorly. Indistinct suboval impressions of adductor muscle scars present on either side of the median septum.

Material. Holotype PMO 104.027 (Pl. 84, figs. 5-7), also BB 70379-70400, BB 76007-76056 from a channel fill near the top of the Langøyene Sandstone Formation, 6 m below the base of the Silurian at south-west Hovedøya, Oslo, Grid, Ref. NM 968408. The species also occurs abundantly in another channel fill 10 m further north and 5 m below the base of the Silurian (BB 70414-70147, BB 74823-74836). Occasional specimens doubtfully attributed to the species occur lower in the Langøyene Sandstone, for example BB 74327 from near its base at east Konglungen, Asker, Grid Ref. NM 850347.

Dimensions (in mm)	Length	Width	Thickness
PMO 104.027, conjoined valves, holotype	10·7	10·3	5·3
BB 70398, conjoined valves	7·4	6·4	4·4
BB 70399, conjoined valves	9·6	8·3	4·3
BB 76055, conjoined valves	8·2	9·3	4·0
BB 75974, conjoined valves	10·5	10·4	5·1

Discussion. Amsden's (1974) admirable redescription of the type species, *Thebesia thebesensis* (Foerste, 1909), leaves no doubt that the Norwegian material can be attributed to *Thebesia*. However, *T. scopulosa* reaches only two-thirds the size of *thebesensis*; it also differs in the occasional development of a slight sulcus, in the lesser divergence of the dental plates (compare Pl. 84, figs. 3 and 4 with Amsden (1974), pl. 14, fig. 1*e*), and in the relative proportions of the cruralium in the brachial valve. The mean perpendicular of the *T. thebesensis* points (in text-fig. 2) from the major axis based on the *T. scopulosa* plotted points was compared to zero using a normal deviate. The valve of the normal deviate was $-1{\cdot}63/0{\cdot}58$ (mean/standard error) $= 6{\cdot}3$. This is highly significant ($P < 0{\cdot}0001$), and indicates that there is a real difference in the growth patterns of the two species. One feature common to both species, and leading to its nineteenth-century identification for Norwegian specimens as '*R. cuneata*' on museum labels (e.g. on shells registered B 3899, presented by T. Kjerulf), is the elongate beak which tends to be concave laterally, a feature externally reminiscent of the true Silurian *Rhynchotreta*.

Order SPIRIFERIDA Waagen, 1883
Superfamily ATRYPACEA Gill, 1871

Atrypaceans occur rarely at several localities, but usually at scattered intervals through the rock, and there are not enought for systematic revision. Genera identified include *Zygospira*?, *Cyclospira*, *Eospirigerina*, and *Protatrypa* (Pl. 84, fig. 13).

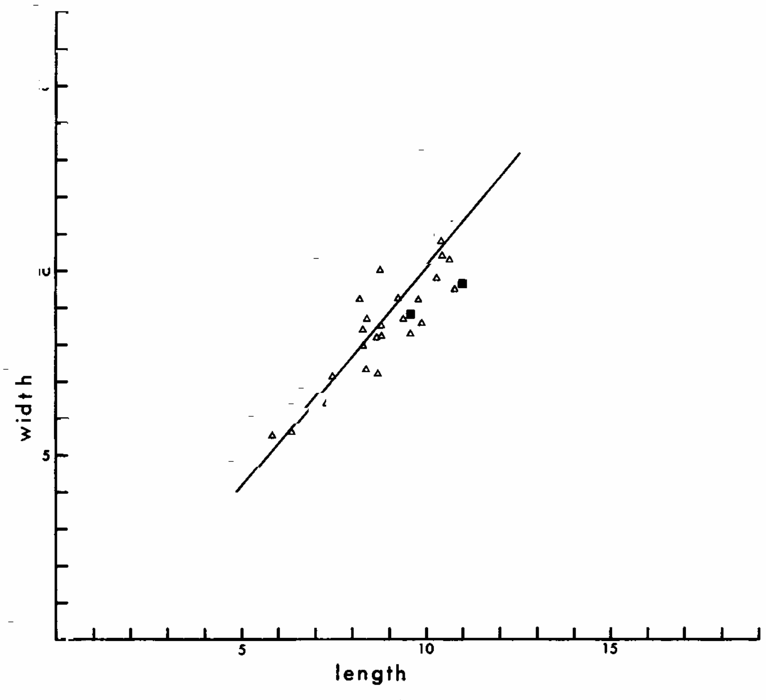
Superfamily ATHYRACEA M'Coy, 1844
Family MERISTELLIDAE Waagen, 1883
Genus HINDELLA Davidson, 1882
Hindella cassidea (Dalman, 1828)

Plate 84, figs. 14-19

1828 *Atrypa cassidea* Dalman, p. 134, pl. 5, fig. 5*a*-*d*.
1977 *Hindella cassidea* (Dalman); Sheehan, p. 29, pl. 1, figs. 1-25.
1977 *Hindella kiaeri* Sheehan, p. 37 *pars*, pl. 2, figs. 12-14, 16, 17, ?figs. 15, 18-22.

Material. In the Oslo-Asker district the species is common at a number of localities, for example in the Langåra Limestone-Shale Formation, particularly in and near the brown sandstone, e.g. at Langåra west (BB 74878-74886, BB 75250-75260), Grid Ref. NM 856356, and at Konglungen East (including BB 74330-74337), Grid Ref. NM 850347, and also in the Langøyene Sandstone Formation, for example in channel fills near the top of the formation at Hovedøya south (e.g. BB 76014-76031), Grid Ref. NM 968408.

Discussion. Sheehan (1977) has reviewed late Ordovician and early Silurian meristellids from Scandinavia, and redescribed Dalman's species *cassidea* from Borenshult, Östergötland, Sweden.



TEXT-FIG. 2. Relative dimensions of *Thebesia scopulosa* in mm from Hovedøya, Oslo (open triangles), and *Thebesia thebesensis* from Illinois and Missouri, USA (black squares); the American data from Amsden (1974, p. 90). The reduced major axis for the Norwegian sample is also shown.

Sheehan also described a new species, *H. kiaeri*, partly on material showing only the exterior (including the holotype) from the late Ashgill of Nesøya, Oslo-Asker region, and partly on material including internal moulds from the early Llandovery of Baerum. Sheehan (1977, p. 38) lists five differences between *H. cassidea* and *H. kiaeri*: four of these are internal differences (based on the early Llandovery material), and the fifth is the 'more inflated shell' of *H. kiaeri*. *Hindella* is common in the late Ashgill of the Oslo-Asker district, and is clearly attributable to *H. cassidea*, including a wide range of shell shapes intergrading between *H. cassidea* and *H. kiaeri*. Internally the Oslo-Asker forms appear identical to *H. cassidea* (e.g. Pl. 84, figs. 14-16), and they are all identified as that species here, including topotype specimens of *H. kiaeri* (BB 75364-75366). Whether or not the early Llandovery forms ascribed to *H. kiaeri* are different from *H. crassa* (J. de C. Sowerby, 1839) requires further investigation; and if so they would require a new name.

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