Relict Ordovician brachiopod faunas in the Lower Silurian of Asker, Oslo Region, Norway

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The diverse brachiopod fauna of the lowest part of the Solvik Formation (Lower Llandovery) in the Asker area of the Oslo Region is a well-organised association overwhelmingly dominated by relict genera more typical of the Ordovician. These taxa appear to have survived the extinction events of the late Ordovician in deep water facies in or adjacent to the central Oslo Region. The gradual disappearance of Ordovician elements through the sequence is considered to have resulted from unsuccessful competition with immigrant stocks of Silurian aspect that may have originated around the shelves of archipelagos created during the late Ordovician regression. Thus competition is suggested to account for the final pulse of faunal extinction above the Ordovician-Silurian boundary.

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An extended extinction event just prior to the Ordovician-Silurian boundary has been recognised as one of a number of significant extinction events during the Phanerozoic (Raup & Sepkoski 1984). Information regarding the earliest Llandovery faunas, however, is sparse compared with that for immediately younger and older faunas. The widely recognised glaciation at the end of the Ordovician caused a considerable fall in sea level in the order of 50-100 m (Brenchley & Newall 1980). This led to the drainage of the broad continental shelves and was followed by a rapid rise in sea-level at the beginning of the Llandovery (Sheehan 1973, 1975). The resulting disconformities seen at most Ordovician-Silurian junctions are accompanied by a marked change in fauna from late Ordovician assemblages, which still retain a degree of provincialism compared to the more cosmopolitan faunas of the Silurian (Berry & Boucot 1973, Sheehan 1973).

The change in fauna is significant and in some cases such as that of the North American epicontinental platform there is little connection between the highly endemic late Ordovician fauna and that of the earliest Silurian (Berry & Boucot 1973). Recognition and analysis of strata and faunas equivalent to those apparently missing at the boundary in many parts of the world would give a more accurate picture of the transition of Ordovician to Silurian faunas as a whole. Evidence of such a faunal transition potentially is most com-

plete at and beyond the platform edges or in intracratonic basins where sections may be continuous across the system boundary. These sequences are, however, the most likely to be destroyed during subsequent orogeny and continental collision. Nevertheless, such continuous sequences have been reported from Anticosti Island (Twenhofel 1928, Barnes & McCracken 1981, Bolton 1981) and Quebec (Lespérance & Sheehan 1976, Lespérance et al. 1981), both of which are situated at platform edges. The present paper documents a comparable section from an intracratonic setting in the central Oslo Region. Within the last twenty years there have been many records of the latest Ordovician Hirnantia fauna (see Rong 1979 and 1984a for reviews). This distinctive and widespread fauna probably inhabited intermediate shelf depths and comprised a variety of ecological associations (Rong 1984b). It was decimated during the late Hirnantian (Sheehan 1982). Thus whilst shelf faunas were clearly most susceptible to external stress, those inhabiting deeper water environments may have been shielded from such pressures by virtue of the evenness of their habitat. We discuss herein a deep-water, lowest Llandovery, fauna dominated by typically Ordovician forms whose gradual extinction was probably the result of unsuccessful competition with immigrant Silurian stocks during the period of the initial Llandovery transgression.

Geological setting

The marine Lower Palaeozoic succession of the Oslo Region was deposited in an intracratonic depression on a foreland area to the south-east of the developing Scandinavian Caledonide orogenic belt (Nicholson 1979, Bruton & Owen 1982, Worsley et al. 1983). The basin had a SSE-NNW trend with sediments of the Asker area originating at intermediate depths, whilst deposition was shallower to the west and deeper towards the east. The Asker sequences (Fig. 1) consist of mixed siliciclastic and carbonate rocks and are locally well exposed and abundantly fossiliferous. Although the exact palaeogeographic position of the Oslo Region during the late Ordovician-early Silurian is not certain (e.g. Webby 1984), the presence of sediments of the bahamitic type, including ooliths, in the highest Ordovician strata of the region, indicates a tropical to subtropical situation (Jaanusson 1973, Lindström 1984). Reconstructions by Ziegler et al. (1977) and Scotese et al. (1979) place Balto-Scandia on the southern side of the Ordovician equator.

Summary of previous research

The Hirnantian sequences of the Oslo-Asker district have been recently described and discussed in detail by Brenchley & Newall (1975, 1977, 1980, 1984). In contrast there have been few recent studies of the lowest Silurian rocks of this district (Baarli 1985, Thomsen & Baarli 1982, Baarli & Johnson 1982). The uppermost Ordovician Hirnantian sediments appear regressive with the development towards the top of the stage of a complicated system of barrier islands, tidal channels, oolite shoals and slightly deeper areas characterised by mud deposition. To the west of the Asker area lay a zone of shallow water deposition possibly bordering land or a shallow shoal, whilst to the east offshore facies were developed (Brenchley & Newall 1980). A complex of eight benthic level bottom communities characterise the varied upper Ordovician lithofacies (Brenchley & Cocks 1982). The Ordovician sequence ends abruptly with evidence of a rapid transgression which left a reworked sandstone layer less than one metre thick over most areas. Where carbonate sediments were deposited, there was no reworking, and the transition upwards into the deeper water lower Silurian shales is fairly continuous (Brenchley & Newall 1980).

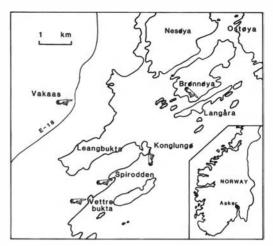


Fig. 1. Locality map for the Asker area of the Oslo-Asker district of the Oslo Region; localities from whence collections made are indicated by pointer. Inset shows position of Asker within Norway.

Immediately overlying this highest Ordovician sandstone, in some areas, is a thin nodular limestone with a sparse shelly fauna which is considered to mark a brief cessation in the transgression prior to deposition of the typical offshore shales of the Solvik Formation (Brenchley & Newall 1980). To the east of Asker, in the deeper parts of the basin, the shales are dark and include graptolites, but no shelly faunas are known. In Asker, coeval strata are represented by fossiliferous calcareous mudstones interbedded with highly calcareous seams also having a rich shelly fauna. The comprehensive and meticulous work of Kiær (1908) remains one of the most important sources of reference for Silurian research in the region together with those of the Ordovician (Kiær 1897, 1901, 1902). On the basis of his wide experience of both the Ordovician and Silurian systems in the Oslo Region, Kiær (1908, p. 478) considered there was no real change in fauna at the Ordovician-Silurian boundary since the most profound faunal changes had already occurred during the latest Ordovician.

Age of the Solvik Formation

In Asker there are no graptolites known from the base of the Solvik Formation, but a rich conodont assemblage referable to the lowest Llandovery *Icriodella discreta – Icriodella reflecta* Zone of the

British succession includes Ozarkodina oldhamensis, the species considered typical of the basal Silurian of Anticosti Island (Barnes 1982). In Asker this fauna occurs 8 m above the base of the Solvik Formation at Konglungen (Grid. Ref. NM849347) and thus indicates an earliest Silurian age for the formation (Aldridge & Mohamed 1982, Worsley et al. 1983). Graptolites are found near the base of the Solvik Formation in the adjacent Oslo area where they supply important information regarding the precise timegap between the deposition of the beds containing highest Ordovician Hirnantia faunas and the overlying Llandovery shales. Howe (1982) has reported graptolites of early acuminatus or possibly late persculptus Zone age from Ormøya about 10 km east of Asker indicating the lower Silurian to be virtually complete.

Many of the brachiopod species in the lower Solvik Formation are known from lower Silurian rocks elsewhere. For example, Schizonema subplicatum has been described from the Mulloch Hill Sandstone of the Craighead inlier, Girvan (Reed 1917) and the Haverford Mudstone Formation in Dyfed, South Wales (Bancroft 1949); 'Leptaena' reedi from the Woodland Formation of the Girvan district (Cocks 1968) and from Meifod, Wales (Temple 1970); Katastrophomena scotica from the Haverford Mudstone Formation (Cocks 1968) and Streptis altosinuata from the Woodland Formation and Meifod (Reed 1917, Temple 1970).

In the upper part of the Solvik Formation (above 95m from the base) the presence of members of the evolving Stricklandia lens lineage (Baarli 1986) provides information as to the age of these levels in the formation. The transition from S. lens prima to S. lens lens occurs between 122 to 130 m above the base of the formation, thus enabling a correlation with the basal A3 beds of the type Llandovery (Williams 1951). At 166 m above the base is the transition from S. lens lens to S. lens intermedia which suggests a correlation with a horizon at or near the boundary between the A and B beds of the type sequence, whilst the change from the latter subspecies to S. lens progressa occurs near the top of the unit and accordingly indicates a correlation with the highest B strata in the type Llandovery sections. Associated conodont and graptolite faunas confirm this correlation (Worlsey et al. 1983).

Lithology of the Solvik Formation

The Solvik Formation is 245 m thick and consists of 60-90% mudstones with thin to very thin limestones, calcareous siltstones and siltstones. The whole formation may be subdivided into three units, in ascending order the Myren, Spirodden and Leangen members (Baarli 1985); only the two lower members are considered and together are some 170 m thick, essentially representing a regressive sequence. The lower of the two units has a high mudstone content with frequent, very thin siltstone intercalations and few calcareous intercalations, whilst in contrast the Spirodden Member has common, highly calcareous intercalations with fewer siltstones and a rich coral and stromatoporoid fauna. The lower, Myren Member was probably deposited mainly below storm wavebase, whilst the overlying unit, the Spirodden Member, indicates shallower depths, probably near normal wavebase. Close inspection of the lowest part of the formation suggests that the late Ordovician transgression continued into the early part of the Llandovery. In all sections studied the first few metres of the Solvik Formation are characterised by diverse faunas with a high proportion of limestone intercalations, but these diminish through the next 15 m, and at Vakaas (NM828357), for example, colonies of favositid corals together with green algae (Cvclocrinites) are found in the first 6 m of the section but are absent in the subsequent 40 m, where pure limestone intercalations are also lacking. Although the limestone content and the nature and diversity of these lowest faunas vary laterally, there is a correlation between areas where the late Ordovician carbonate shoals were developed and sections where carbonate content in the Solvik Formation is high; it is therefore probable that the late Ordovician topography described by Brenchley & Newall (1980) exerted an influence on the faunal and sedimentary patterns of the early Llandovery sea prior to the achievement of a more even topography as the transgression con-

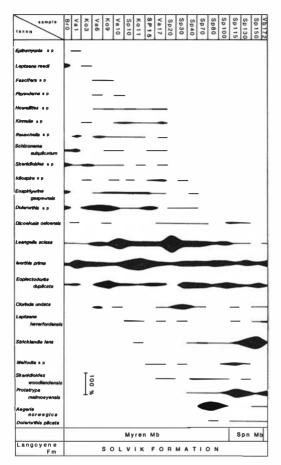


Fig. 2. Range and relative abundance data for the most common, determined brachiopods from the lower part of the Solvik Formation of the Asker area. Abbreviations in first column refer to sample sites with metres above the base of the Solvik Formation: BR- Brønnøya, VA- Vakaas, KO- Konglungen, SP-Spirodden, VB- Vettrebukta.

Faunal analysis

The lowest 20 m of the Solvik Formation have been studied in detail at four different localities east of Asker Station (Fig. 1): Brønnøya (NM-862362), Konglungen (NM849347), Vakaas (NM-828357) and Spirodden (NM842339). At the first three, the Ordovician-Silurian junction is exposed, but at Spirodden the lowest 10 m of the Solvik Formation are missing. At Brønnøya only the initial 3-4 m of the formation is exposed, whilst at Konglungen about 25 m is present. At Spirodden 164 m of the formation is exposed in an essentially undisturbed section. The sequence at Vakaas is about 130 m thick; however, it is highly tectonised.

The faunal information was gained mainly from 5-10 kg bulk samples collected from units no thicker than 20 cm in the mudstones. Casual collections made in the field supplement the data. The bulk samples are almost all from the first 20 m of the formation, but to demonstrate the transition from a typical Ordovician brachiopod fauna to one more characteristic of the Silurian, a few samples were taken from higher strata in the Spirodden section. The bulk samples were broken up and treated in dilute hydrochloric acid and thereafter all identifiable specimens were registered. In this study only the brachiopod biofacies is considered in detail. A fuller account of the brachiopod fauna together with monographic descriptions will be published elsewhere by the first author.

The brachiopods comprise about 50% of the total fauna, although proportions may vary locally from 30 to 95%. Small rugose corals are locally dominant, commonly comprising 20-30% of the fauna, whilst encrusting bryozoans and trilobites are also locally important. Only in the upper part of the Spirodden Member, for example, are tabulate corals, stromatoporoids, and cyclocrinid algae particularly common. However, whilst the diversity of the brachiopods is relatively low, that of the total fauna is high. The main brachiopod taxa and their mutual quantitative relationships as a percentage of the total brachiopod fauna retrieved from the bulk samples are shown on Fig. 2. The samples are arranged in stratigraphical order but not to scale. An additional 26 species are present mainly in the lowest 20 m but are represented by only a single specimen or several fragments. These are not included on the range chart because of their long ranges or poor taxonomic determination due to inadequacy of material. Inspection of the range chart (Fig. 2) indicates that two genera are dominant throughout the complete sequence. These genera Eoplectodonta and Isorthis occur in six different associations within the Solvik Formation and are represented by the species E. duplicata and I. prima in the Myren and Spirodden members. The associated species, however, are quite different in each assemblage. A clear faunal change occurs within the Myren Member 17-40 m from the base, whilst only the highest assemblages are typically Silurian. Besides E. duplicata and I. prima, Leangella scissa dominates in the remainder of the Myren Member, while Stricklandia lens and Protatrypa malmoeyensis are co-dominant in the Spirodden Member. Dolerorthis plicata, Clorinda undata,

Skenidioides woodlandiensis and Dicoelosia osloensis occur as minor but persistent elements in both members. Aegeria norvegica is dominant in a number of samples but nevertheless is not a persistent element of the fauna as a whole. The brachiopod fauna in the Myren Member is similar to that from the Mulloch Hill Sandstone (Lower Llandovery) of the Craighead inlier of the Girvan district, Scotland. The Scottish fauna is dominated by Leangella scissa together with Eoplectodonta sp., Dolerorthis sp., Clorinda sp., and Skenidioides sp. (Cocks & Toghill 1973); Isorthis prima is also common, there in its type stratum. It is interesting to note that where S. lens and atrypoids like P. malmoeyensis are dominant, L. scissa, D. osloensis and C. undata are reduced in abundance; the negative relationship between these two groups is commonly observed in Llandovery faunas and has often been used to characterise the Stricklandia and Clorinda communities of Ziegler (1965) and Ziegler et al. (1968). The lowest 40 m of the Solvik Formation are dominated by L. scissa, E. duplicata and I. prima; however, the associated brachiopods are diverse and include, as persistent elements, a species of Dolerorthis similar to D. sp.nov. Temple (1970), Skenidioides sp. (more finely ribbed than the stratigraphically younger S. woodlandiensis), Reuschella sp., Kinnella sp., Howellites sp., and Eospirigerina gaspeensis (Fig. 2). The assemblages of the lowest Solvik Formation have nothing in common in terms of the associations as a whole or constituent individuals, with the underlying shallow to mid-shelf communities of the Hirnantian sequences in Asker (Brenchley & Cocks 1982). The Solvik Formation, however, was clearly deposited in deeper water; comparable facies in the uppermost Ordovician succession are rare and not well known. Moreover the faunal associations in the Solvik Formation are not comparable, as a whole, to any described assembalges from the highest Ordovician or the lowest Silurian.

Of the genera in the lowest Solvik Formation, Dolerorthis, Eoplectodonta, Idiospira, Leangella, Leptaena, Streptis and Triplesia have become well established by the Caradoc or early Ashgill and continue relatively high into the Silurian. Coolinia, Dicoelosia, Epitomyonia, Eospirigerina and Schizonema appear first during the Ashgill (Boucot 1975, Sheehan 1975). In contrast, Isorthis, Clorinda, Meifodia and Stricklandia are known only from rocks of Silurian age, although the first and last have close relatives in rocks of late Ash-

gill age; whilst Fascifera, Reuschella and Epitomyonia are more typically identified with upper Ordovician faunas but nevertheless have been recorded from lower Silurian strata (Boucot 1975, Williams & Wright 1982). Kinnella is known only from highest Ashgill strata (Rong 1979, 1984a,b) but both Howellites and Pionodema range upwards from the Caradoc to the Ashgill (Cocks 1978, Cooper 1956), but have hiterto not been recorded from the Silurian. The species Leangella scissa and Eospirigerina gaspeensis are known to occur in both Ashgill and Llandovery rocks (Boucot & Johnson 1967, Cocks 1978, Hiller 1980).

In summary the first 20 metres of the Solvik Formation contain a definite assemblage of mixed Ordovician and Silurian elements. Many of the genera represented are known to become extinct close to the Ordovician boundary. This association persists until the peak of the transgression, when faunal elements more typical of the Silurian gradually arrive. Higher in the succession taxa typical of the Ordovician are no longer present, but here the assembalge is of low diversity dominated by either new Silurian species or long ranging forms. Both the lower and higher faunas in the Solvik Formation show recurrent species and a consistent organisation.

Discussion

The faunal extinctions at the end of the Ordovician Period have been recognised as one of five major extinction episodes (e.g. Newell 1967, Raup & Sepkoski 1982, 1984, McLaren 1983). Close scrutiny of the event reveals that the extinctions occurred over a considerable period of time, achieved by increments from the late Caradoc through the Ashgill (Brenchley & Newall 1984). Moreover the extinctions documented in the various fossil groups were not synchronous (Jaanusson 1979). Whilst the most marked disappearance of trilobites, cystoids and graptolites occurred at the Rawtheyan - Hirnantian boundary, brachiopods and corals apparently suffered the most heavy losses during the early part of the Hirnantian, but with a further reduction at the Ordovician-Silurian junction (Brenchley 1984). These faunal extinctions have been related to a broadly concurrent late Ordovician glaciation which, at its climax, created cooler surface waters and a drainage of the continental shelves. The direct cause or causes of the extinctions correlated

with the glacial event has promoted much debate (see e.g. Johnson 1984, Stanley 1984c). The latest Ordovician extinctions have been related to a major cooling event (Stanley 1984a,b), a restriction of the area of the continental shelves by drainage (Sheehan 1973, 1979, Jaanusson 1979, Brenchley 1984) or to major tectonic events (Campsie et al. 1984). The present study, however, demonstrates that extinction of the brachiopods did not cease at the boundary but continued for some time into the earliest Silurian. As a consequence a further cause for these later extinctions must be sought, though this is difficult since the majority of sections across the Ordovician -Silurian boundary exhibit either a hiatus, a marked change in facies from shelf deposits to graptolitic shales, or merely unfossiliferous strata. Jaanusson (1979) has noted the lack of data on earliest Llandovery faunas, while Leggett et al. (1981) noted that the lowest Llandoverv fauna in Great Britain exhibits an extremely low faunal diversity compared with that of the upper Ashgill and moreover concluded that this trend was also worldwide. They attributed this to slow recolonisation of the shelf environment following the latest Ordovician regression. This explanation does not seem valid in the central Oslo Region where diverse associations are already present during the course of the early Llandovery transgression and are only later replaced after the peak of the transgression by a typical early Llandovery assemblage, of low diversity and comprising eurytopic species.

Jaanusson (1979) has suggested that further extinctions during the early Llandovery may have been caused by the development of large euxinic basins where bottom conditions were inimical to the colonisation of benthic organisms. In contrast Leggett et al. (1981) argue that with transgression, large shelf areas suitable for colonisation are created, whilst those faunas of the deep euxinic basins continue largely unaffected.

The sections of the Solvik Formation examined have yielded important information regarding the hitherto poorly documented earliest Llandovery shelly faunas and events which in the lowest part of the formation may be summarised as follows: (1) the establishment of a relict Ordovician fauna persisting during the early Silurian transgression; (2) new eurytopic elements arrive as the transgression continues until finally, (3) a typical lowdensity lower Llandovery fauna is firmly established. We suggest that the initial fauna consists of the more eurytopic species of the regressive

Ordovician fauna which survived the terminal Ordovician extinctions in the deeper parts of the intracratonic basin of the Oslo Region. These species were subsequently able to create and participate within new community structures during the early Silurian transgression. As the transgression proceeded, immigration occurred of more offshore elements originating around unstable continental margins or achipelagos where both isolation and speciation may have taken place during the late Ordovician regression (see e.g. Eldredge 1974, Fortey 1984, Neuman 1984 Bruton & Harper 1985). In due course the relict Ordovician elements were displaced gradually by competition with the immigrant species whilst a different less diverse recurrent assemblage evolved consisting of a mixture of the more eurytopic native species and successful immigrants. We therefore conclude that a period of competition is possibly a further aspect of the late Ordovician-early Silurian extinction event which requires consideration.

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Appendix

PLATE 1.

Orthacea and Enteletacea from the Solvik Formation, Asker Schizonema subplicatum (Reed)

- a,b. External mould and latex cast of brachial valve, PMO 107590, ×2.
- c. Internal mould of pedicle valve, PMO 107591, ×2.
- d,e. Internal mould and latex cast of brachial valve, PMO 107592, ×2.

Dolerorthis sp.

- f. Internal mould of brachial valve, PMO 107593, ×2.
- g,k. Internal mould and latex cast of pedicle valve, PMO 107594, ×2.
- h,l. External mould and latex cast of pedicle valve, PMO 107595, ×2.

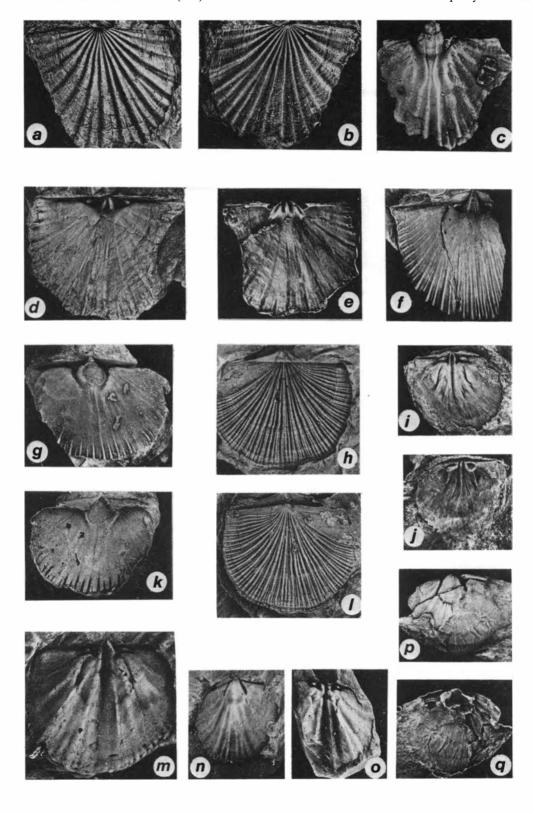
Kinnella sp.

- i,j. Internal mould and latex cast of brachial valve, PMO 109735, ×2.
- p,q. Internal mould and latex cast of pedicle valve, PMO 107597, ×2.

[specimens assigned to Ptychopleurella sp. e.g. pl.1, figs 2,3 in Thomsen and Baarli 1982 are determined herein as Kinnella sp.]

Reuschella sp.

- m. Internal mould brachial valve, PMO 109732, ×3.5.
- n. Internal mould of pedicle valve, PMO 111738, ×2.
- o. Internal mould of brachial valve, PMO 111713, ×3.



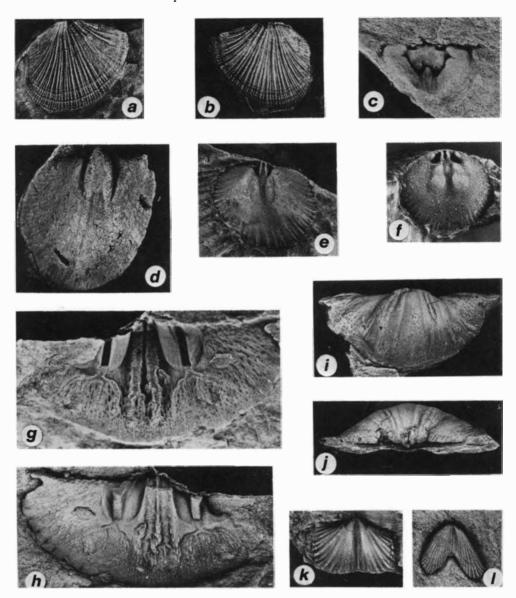


PLATE 2.

Enteletacea and Plectambonitacea from the Solvik Formation, Asker

Kinnella sp.

a,b. External mould and latex cast of brachial valve, PMO 107598, ×2.

Leangella scissa (Davidson)

c. Internal mould of brachial valve, PMO 107601, ×3.

Isorthis prima Walmsley & Boucot

- d. Internal mould of pedicle valve, PMO 111711, ×4.
- f. Internal mould of brachial valve, PMO 111709, ×4.

Fascifera sp.

e. Internal mould of brachial valve, PMO 109739, ×4.

Eoplectodonta duplicata (J. de C. Sowerby)

- g,h. Internal mould and latex cast of brachial valve, PMO 107606, ×2.
- i,j. Ventral and posterior views of internal mould of pedicle valve, PMO 107607, ×2.

Epitomyonia sp.

k. Internal mould of pedicle valve, PMO 108287, ×4. [figured as *Dicoelosia* cf. *inghami* Wright in Thomsen and Baarli 1982, pl.1, fig. 16]

Dicoelosia osloensis Wright

 Latex cast of external mould of pedicle valve, PMO 107605, ×4.

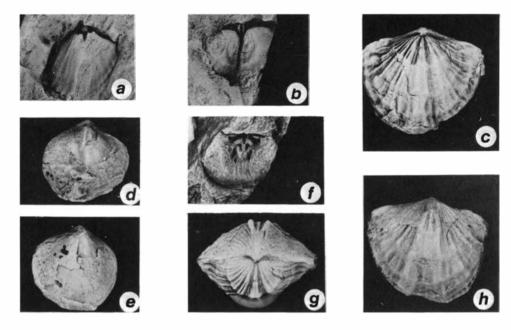


PLATE 3.

Skenidioides sp.

- Internal mould of pedicle valve, PMO 107609, ×4.
- Internal mould of brachial valve, PMO 107610, ×4.

Idiospira sp.

d,e. Ventral and dorsal views of conjoined pair, PMO 107611, ×4.

'Leptaena' reedi Cocks

Internal mould of brachial valve, PMO 105211, ×2.

Eospirigerina gaspeensis (Cooper)

cg,h. Dorsal, posterior and ventral views of conjoined pair, PMO 107613, ×4.

Repository of specimens: Paleontologisk museum, Oslo (PMO).