

LOWER CRETACEOUS BRACHIOPODA FROM SOUTH-EASTERN ALEXANDER ISLAND

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ABSTRACT. Seven new species of Brachiopoda are described from the Lower Cretaceous of south-eastern Alexander Island; one new genus, *Prochlidonophora*, is proposed. The occurrence of these brachiopods in mudstone sequences and the possibility that they may have lived attached to other animals or plants are discussed. Some elements within the brachiopod faunas described have been broadly compared to those of a similar age from Mexico, northern California and Siberia. Although it is not suggested that there is any close specific relationship between these faunas, the ubiquitous nature of some genera, formerly thought to have been restricted to the Northern Hemisphere is clearly demonstrated.

ALTHOUGH Mesozoic brachiopods were first collected in Alexander Island by members of the British Graham Land Expedition, 1934-37 (Fleming, 1938, p. 509), the specimens were never described. To date, the only available accounts of Mesozoic brachiopods from Antarctica are those of three inarticulate species from the Lower Aptian of Alexander Island (Thomson, 1971), and two articulates from the Middle Jurassic of eastern Ellsworth Land (Quilty, 1972). Most of the material described here came from outcrops in the vicinity of Fossil Bluff (Fig. 1) but it also includes specimens from northern Hyperion Nunataks and the Mount Lassel area. All of these are believed to be Neocomian or Lower Aptian in age (see below).

The preservation of the brachiopods is poor. Most of them occur as moulds of crushed individuals and have little of the original test remaining. In only one instance (p. 23) was it possible to obtain serial sections of internal structures. However, the rarity of described faunas of a comparable age from the Southern Hemisphere and the distinctive morphology of all the forms leave little doubt that they belong to undescribed species and, in most cases, to new genera.

Seven species are described:

- "Glottidia" rostrata* sp. nov.
- "Acanthorhynchia" (Echinirhynchia) setosa* sp. nov.
- "Lamellaerhynchia" sp. A.*
- Ptilorhynchia australis* sp. nov.
- Penzinothyris imbricata* sp. nov.
- "Terebratula" lamellosa* sp. nov.
- Prochlidonophora muirwoodae* gen. et sp. nov.

In addition, late Aptian or Albian species are represented by three fragmentary rhynchonellids from Succession, Waitabit and Keystone Cliffs, but these are too poorly preserved to warrant description. Similarly, several Tithonian to Berriasian rhynchonellid species from the Ablation Point area are also excluded from the present descriptions; probably the best of these has already been illustrated (Taylor and others, 1979, pl. VIIIc).

STRATIGRAPHICAL OCCURRENCE AND AGE

Fossil Bluff area

Brachiopods have a restricted distribution in the Lower Cretaceous rocks of south-eastern Alexander Island but they apparently occur most commonly in exposures near Fossil Bluff, an area studied stratigraphically in detail by B. J. Taylor. His conclusions (Fig. 2) form the

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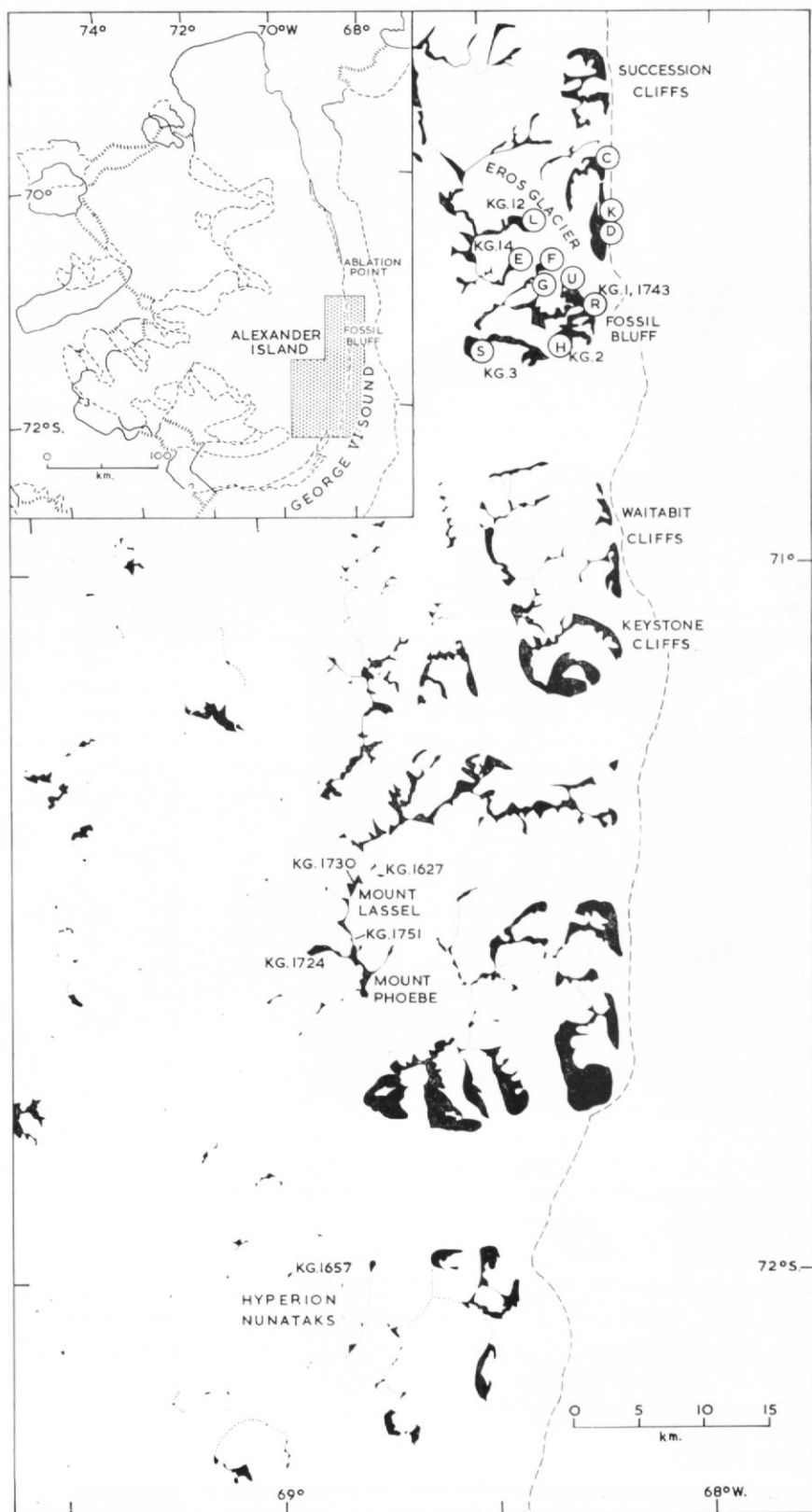


Fig. 1. Sketch map of south-eastern Alexander Island showing the localities from which the brachiopods were collected.

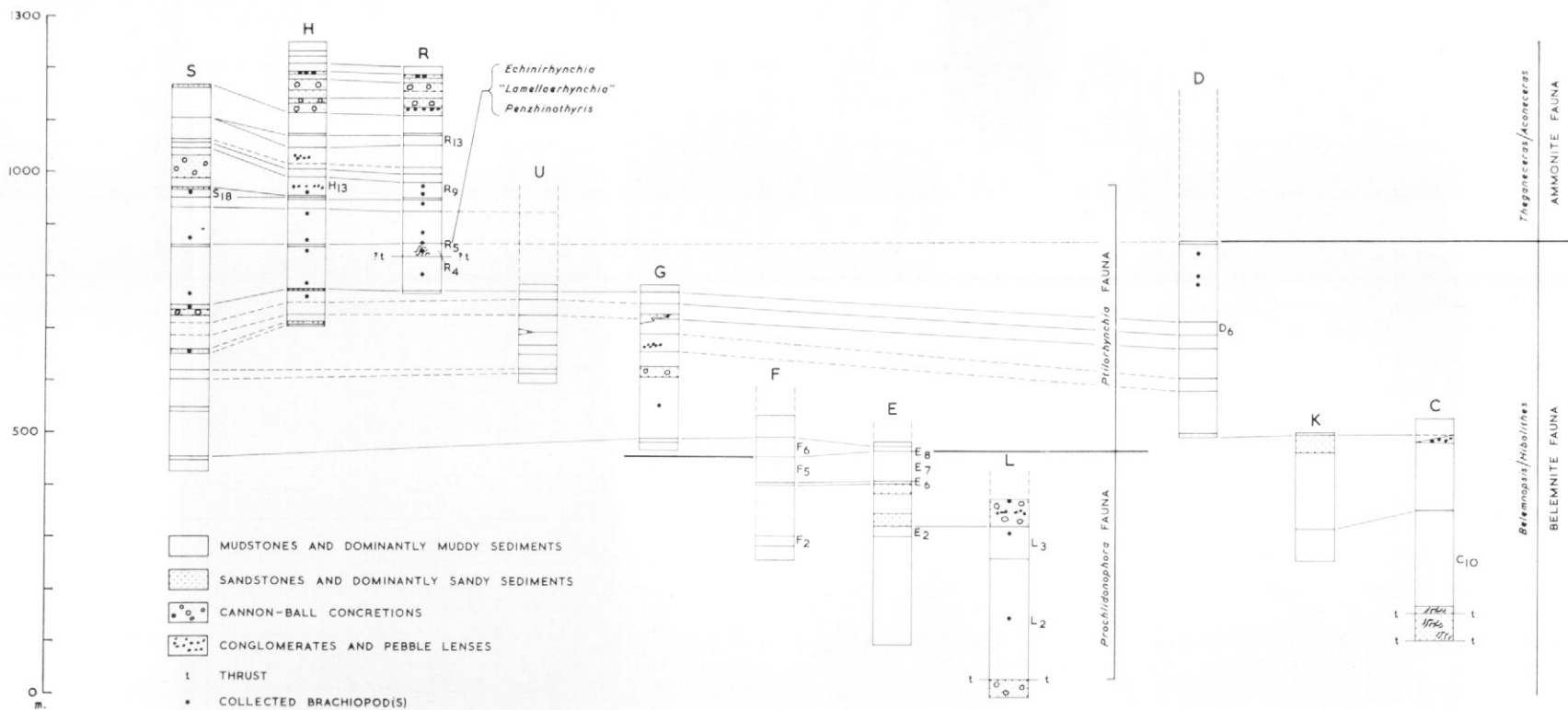


Fig. 2. Measured sections in the Fossil Bluff area to show the stratigraphical range of most of the brachiopods described. (Based on field data by B. J. Taylor; locality letters are the same as those in Fig. 1.)

basis of the stratigraphical scheme outlined here, and they are used in the interpretation of brachiopod faunas farther south.

The first species to occur is *Prochlidonophora muirwoodae*, in units C₁₀, L₂₋₃, E₂ and E₆₋₈ at localities 4 km. south of Succession Cliffs (C) and on the south-western side of Eros Glacier (Fig. 1). In the field this form was compared to "*Terebratella*" and was referred to as such in an account of the stratigraphy of south-eastern Alexander Island (Taylor and others, 1979). Although no specimens were collected from localities C and E, material from locality L confirms the identity of "*Terebratella*" and *Prochlidonophora*.

At a level marked by unit E₈ and the junction between units F₅ and F₆ there is an upward change in the brachiopod faunas when *Prochlidonophora* is almost entirely replaced by *Ptilorhynchia* (= "terebratulids" in Taylor and others (1979)). The collections suggest that *Ptilorhynchia* occurs abundantly, particularly at localities R, H and S, where it persists up to unit R₉ and its lateral equivalents. Above unit R₉ it is apparently no longer present in the sequence. The dominance of this brachiopod is only relieved at the level of unit R₅ and its equivalents where "*Acanthorhynchia*" *setosa*, "*Lamellaerhynchia*" sp. A and *Penzhinothyris imbricata* are present over a thickness of a few metres. A single specimen of *Prochlidonophora* has also been collected from unit R₅ but a field record of "? terebratelloids" (? = *Prochlidonophora*) unit D₆ is not substantiated by collected material.

The age of these brachiopod faunas is difficult to define because of the rarity of associated forms diagnostic of age, and/or the frequent lack of suitable collections. Accompanying faunas consist largely of bivalves, whereas ammonites are absent or very poorly preserved. Occurrences of belemnites at localities C, L and E were unfortunately not sampled except where the guards were infested with the borings of acrothoracic cirripedes. Belemnites from unit F₂ include *Belemnopsis gladiatoris*, *B. alexandri* and *B. aff. uhligi*, whereas *B. gladiatoris* and *Hibolithes* sp. nov. (?) were collected from Georgian Cliff in a sequence, "partly equivalent to the lower and middle parts of the stratigraphical section at locality D" (Willey, 1973, p. 56). A *Belemnopsis*-*Hibolithes* fauna has also been obtained from a new exposure approximately 50 m. below the base of the measured section at locality R, and in approximately equivalent strata at locality U. Thus the belemnite faunas of localities D, U and R are of approximately the same age (Fig. 2), whereas that of locality L is a little older. Outside Antarctica, the range of *Belemnopsis* is typically Middle Lias to Tithonian, and that of *Hibolithes* is Bajocian-Bathonian to Neocomian. However, in Antarctica there is evidence to indicate that *Belemnopsis* persisted after the Jurassic and the faunas discussed here are all believed to be Neocomian in age (Willey, 1973).

Belemnites disappear from the succession in unit R₄ and re-appear at a higher level in the sequence represented at Waitabit Cliffs. In unit R₅, the first of a variety of oppeliid ammonites belonging to the subfamily Aconeceratinae appear; these include species of *Aconeceras* and *Theganeceras* such as might be found in the Lower Aptian of the Northern Hemisphere. In unit R₁₃, nearly 100 m. above the last recorded brachiopod (*Ptilorhynchia*) in the section, the *Aconeceras* fauna is accompanied by a small heteromorph, *Acrioceras* (?) aff. *voyanum* Anderson, which appears to have strong Neocomian affinities (Thomson, 1974, p. 18). It has been argued (Thomson, 1974, p. 37) that these faunas are at least as old as Lower Aptian and it is conceivable that they could range down into the Upper Neocomian. Likewise, although at present there is only confirmatory evidence that *Belemnopsis* in Alexander Island ranges up into the Berriasian, it is possible that it may range even higher (Willey, 1973, p. 57). Since the *Aconeceras*-*Theganeceras* fauna follows directly on the *Belemnopsis*-*Hibolithes* fauna at locality R, the extension of one or both of these faunas outside their normally expected ranges is a strong possibility. The problem of defining the Neocomian stage in Alexander Island has been discussed in greater detail elsewhere (Taylor and others, 1979).

On the evidence available at present, it is not possible to date these brachiopod faunas more precisely than Neocomian to Lower Aptian.

Mount Lassel area

Any stratigraphical analysis of this area is severely hampered by the isolated distribution of exposures, the presence of faulting and the complication of east-west fold axes plunging at up to 40°. Fragmentary specimens of *Ptilorhynchia* were obtained from fine-grained indurated mudstones with a conchoidal fracture, near the summit of Mount Lassel (KG.1730). The same mudstones contain a rich ammonite fauna, mainly of crushed *Eulytoceras* and *Hypophylloceras*, but also including indeterminate *Aconeceras* and possibly some *Phyllopachyceras*. Similar forms have been collected at Fossil Bluff and in the middle part of the sequence at Waitabit Cliffs, but *Hypophylloceras*, *Phyllopachyceras* and *Eulytoceras* are widely distributed in eastern Alexander Island, and precise correlation is not possible at present. A structural analysis of the area by Bell (1975) suggests that the nunatak 3 km. east-north-east of Mount Lassel (KG.1627), with a poor fauna including *Prochlidonophora* and "*Terebratula*" *lamellosa* sp. nov., represents a slightly higher stratigraphical level than the sequence exposed on the summit of Mount Lassel. "*Terebratula*" *lamellosa* is known only from one other locality, in northern Hyperion Nunataks (see below), where it occurs in association with *Prochlidonophora* *quirwoodae*. Occurrences of *Ptilorhynchia* at stations KG. 1751 (5 km. south of Mount Lassel) and KG.1724 (7 km. south-south-west of Mount Lassel) are likely to be of approximately equivalent age to the *Ptilorhynchia* bed at Mount Lassel, but an associated ammonite fauna of *Aconeceras* and *Theganeceras* at station KG.1724 suggests a much closer correlation with the Fossil Bluff sequence than can be attempted for Mount Lassel.

Northern Hyperion Nunataks

Large numbers of *Prochlidonophora* occur over a thickness of 2 m. in a mudstone sequence at the eastern summit of the nunatak at station KG.1657 (Fig. 1). They are associated with two other brachiopods ("*Glottidia*" *rostrata* sp. nov. and "*Terebratula*" *lamellosa*), and an ammonite fauna including *Eulytoceras*, *Aconeceras* and *Theganeceras* similar to that found at Fossil Bluff (locality R; p. 18). Beneath these brachiopod-bearing beds there are at least 50 m. of poorly fossiliferous mudstones and sandstones, exposed in a near-vertical cliff. Beds above the brachiopod-bearing unit are represented in a *felsenmeer*-covered ridge to the west which spans a sequence of approximately 100 m. of westerly dipping mudstones with white tuffaceous sandstones in the top few metres. Loose slabs of mudstone, collected near the western (i.e. stratigraphically highest) end, contain the belemnite *Peratobelus*. A preliminary identification of this form by L. E. Willey suggests that it is closely similar to *Peratobelus* sp. nov. (?) (Willey, 1972, p. 34, figs. 4a-c and 5d) from the (?) Lower Aptian of Waitabit Cliffs. The stratigraphical occurrence of these *Peratobelus* specimens is thus consistent with the interpretation that the *Prochlidonophora* beds are similar in age to those with the *Aconeceras*-*Theganeceras* fauna at Fossil Bluff (i.e. unit R₅ and above).

SYSTEMATIC DESCRIPTIONS

CLASS INARTICULATA HUXLEY 1869

ORDER LINGULIDA WAAGEN 1885

FAMILY LINGULIDAE MENKE 1828

Genus *Glottidia* Dall 1870*"Glottidia" rostrata* sp. nov.

Fig. 3a and b

Material

Two external moulds, presumably representing the brachial and pedicle valves, from a *felsenmeer* at station KG.1657, northern Hyperion Nunataks.

Age: Lower Aptian.

Diagnosis

Valves elongate, spatulate, characterized by rostrate posterior extremities, particularly on the pedicle valve. Both valves are more inflated than in typical lingulids. External ornament of a pair of diverging grooves flanked by narrow riblets on the (?) pedicle valve, and a median riblet flanked by shallow grooves on the (?) brachial valve are suggestive of the presence of internal septa similar to those in the genus *Glottidia* Dall.

Holotype: Specimen KG.1657.36, a (?) pedicle valve.

Description

The two moulds (KG.1657.21 and 36) appear to represent the brachial and pedicle valves respectively of two separate individuals. Both differ from typical lingulids in their greater inflation and by the possession of long acuminate or rostrate posterior extremities. The pedicle valve (Fig. 3a) has a more rostrate umbo than the brachial valve (Fig. 3b), although it should be noted that it is from a larger specimen. It is strongly inflated with a 10° wide flattened ridge or area along the mid-line. The ridge is bounded laterally by rounded grooves in turn delimited by narrow riblets, and is further ornamented with at least two faint low riblets; all of these terminate about three-quarters of the way along the valve from the umbo. The anterior margin of the valve is broken but it appears to have been bluntly terminated, and there are suggestions of small angular projections at the corners.

The brachial valve (Fig. 3b) is also inflated but it lacks the wide ridge of the pedicle valve so that the inflation is rounded in cross-section. The lateral margins of the posterior and anterior parts of the valve curve smoothly into one another and it thus tapers more evenly than the pedicle valve. A single riblet flanked by shallow grooves extends along the mid-line of the posterior three-quarters of the shell.

Remarks

Although this species is *Lingula*-like, the rostrate posterior extremity is an immediate point of difference. The internal features of its shell are unknown but the two grooves on the pedicle valve and the median riblet and grooves on the brachial valve suggest the possibility of corresponding internal structures, similar to the septa in *Glottidia* Dall. The angular projections at the antero-lateral corners of the pedicle valve are likewise reminiscent of some species of that genus. Known species of *Glottidia* range from Eocene to Recent (Rowell in Moore, 1965, p. H263). Because of this, and because of the lack of details of the internal characteristics, the present species is only broadly referred to Dall's genus; in all probability it represents a new form.

CLASS ARTICULATA HUXLEY 1869

ORDER RHYNCHONELLIDA KUHN 1949

FAMILY RHYNCHONELLIDAE GRAY 1848

SUBFAMILY ACANTHOTHYRIDINAE SCHUCHERT 1913

Genus *Acanthorhynchia* Buckman 1918

Subgenus *Echinirhynchia* Childs 1969

"*Acanthorhynchia*" (*Echinirhynchia*) *setosa* sp. nov.

Fig. 3c-e

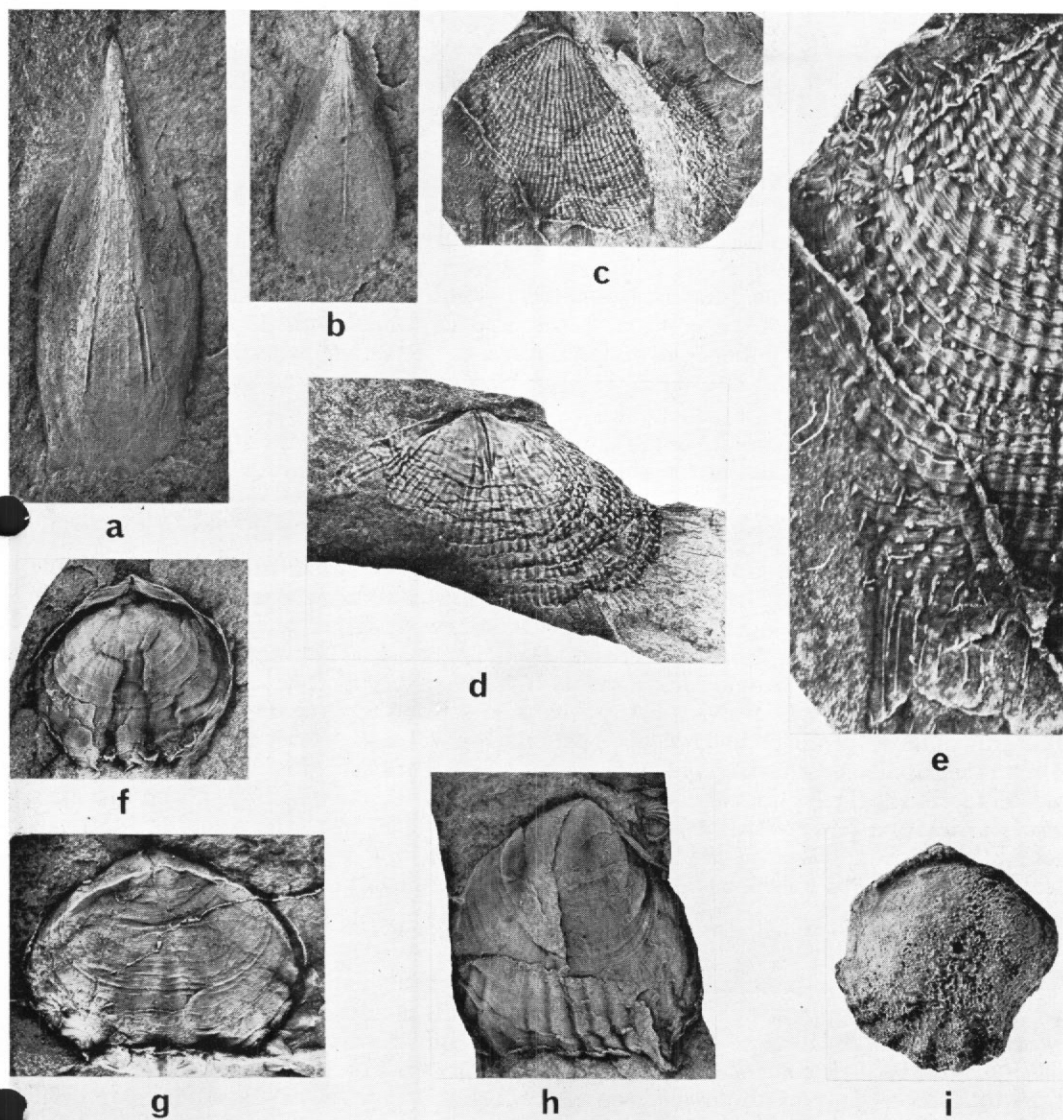


Fig. 3. a. "*Glottidia*" *rostrata* sp. nov.; latex cast from the holotype, an external mould of a (?) pedicle valve; $\times 1.5$, coated (KG.1657.36).
 b. "*G.*" *rostrata* sp. nov.; latex cast from an external mould of a (?) brachial valve; $\times 1.5$, coated (KG.1657.21).
 c. "*Acanthorhynchia*" (*Echinirhynchia*) *setosa* sp. nov.; latex cast from the holotype, a fragmentary external mould cut by a shear plane; $\times 1.5$, coated (KG.1743.27).
 d. "*A.*" (*Echinirhynchia*) *setosa* sp. nov.; natural internal mould of a pedicle valve showing traces of an internal septum and fine spines around the commissure; $\times 1.5$, coated (KG.1.370).
 e. "*A.*" (*Echinirhynchia*) *setosa* sp. nov.; enlargement detail of Fig. 3c to show the ornament; $\times 5$, coated (KG.1743.27).
 f. *Ptilorhynchia australis* sp. nov.; latex cast from the holotype, a crushed external mould of a brachial valve also showing the area on the pedicle valve; $\times 1.5$, coated (KG.2.79).
 g. *P. australis* sp. nov.; latex cast from an external mould of a wide form; $\times 1.5$, coated (KG.2.6).
 h. *P. australis* sp. nov.; latex cast from the external mould of a large multiplicate form; $\times 1.5$, coated (KG.1.30).
 i. *P. australis* sp. nov.; plaster cast from the specimen used to make the serial sections in Fig. 5; $\times 1.5$, coated (KG.3.84).

Material

Six fragmentary and crushed moulds, all from Fossil Bluff (KG.1.348, 350, 370, 646, KG.1743.27 and 28).

Age: Probably Lower Aptian.

Diagnosis

Resembles species of the Jurassic genus *Acanthorhynchia*, although the internal structures are unknown and its systematic position is uncertain. Shell much wider than long, ornamented with bifurcating capillae and fine growth lines forming a reticulate pattern. Capillae bear long hair-like spines at irregular intervals.

Holotype: Specimen KG.1743.27, a fragmentary external mould cut by a shear plane but showing the ornament well. Specific name derived from the Latin *setosus* (= bristly).

Description

Most of the material is fragmentary (cf. Fig. 3c-d) but two specimens (KG.1.350 and 370) show that the shell was oval in outline, being much wider than long, and was at least moderately inflated. No specimens suggest the presence of an obviously larger pedicle valve, and the inference is that both valves were of approximately the same size. The commissure was probably rectimarginate as there are no indications of a sulcus or plication on any of the specimens. The ornament of this species is distinctive; sharp bifurcating capillae are crossed by numerous fine growth lines, forming a fine reticulate pattern (Fig. 3e), and at irregular intervals of about 1 mm. the capillae bear small papillae or bosses which mark the bases of fine straight spines. On all specimens these spines are seen as a fringe around the commissure, and on one example (KG.1.350) a few are still preserved on the body of the shell. The spines are extremely long in proportion to their thickness; they are commonly up to 6 mm. in length (a few were at least 8 mm. long), whereas they average about 20 μ m. in thickness.

Remarks

Despite their poor preservation, these specimens clearly represent a distinctive species which can be recognized, even from fragments, by the characteristic ornament. There are general resemblances to some of the Jurassic Acanthothyridinae, and the capillate ornament and probable rectimarginate commissure suggest closer affinities to *Acanthorhynchia* Buckman than to *Acanthothyris* d'Orbigny (cf. Ager in Moore, 1965, p. H611). However, the internal structures are unknown and it is possible that it belongs to a new genus. The shell is much wider than in described species of *Acanthorhynchia* (Childs, 1969), the ornament is much sharper and the fine reticulation does not appear to have been described previously in the Acanthothyridinae.

In a description of Upper Jurassic Rhynchonellidae from north-western Europe, Childs (1969) introduced the subgeneric name *Echinirhynchia* for certain species within the genus *Acanthorhynchia*. This name was used by Smirnova (1972) as a generic name for a species of rhynchonellid from the Berriasian of the Crimea. She (Smirnova, 1972, pl. 4, fig. 1) illustrated an elongate-oval, anteriorly sulcate specimen as *Echinirhynchia nucleatiformis*, showing what appears to be typical *Acanthorhynchia*-type spines. However, the transverse serial sections of this species show only a superficial resemblance to those of the type species figured by Childs (1969).

Nekvasilová (1975) described and figured a similar form to Smirnova's *E. nucleatiformis* as *Acanthorhynchia* (*Echinirhynchia*) *parva* from the Valanginian of Stramberk, Czechoslovakia.

The transverse serial sections which accompanied this description are very similar to those given by Smirnova (1972).

Although Childs assigned his subgenus *Echinirhynchia* to the genus *Acanthorhynchia*, the serial sections given in his original description of the type species, *A. (Echinirhynchia) senticosa* (Schlotheim), are well outside the morphological range of the original genus *Acanthorhynchia*. It is felt that the species described here as "*Acanthorhynchia*" (*Echinirhynchia*) *setosa* sp. nov. is likely to be more closely related to the forms described by Smirnova (1972) and Nekvasilová (1975) than to any species described under the subgeneric name *A. (Echinirhynchia)* by Childs.

SUBFAMILY CYCLOTHYRIDINAE MAKRIDIN 1955

Genus *Ptilorhynchia* Crickmay 1933

Ptilorhynchia australis sp. nov.

Fig. 3f-i, 4 and 5

Material

About 40 specimens, all partly crushed, from localities D, G, R, H and S in the Fossil Bluff area, and stations KG.1724 and 1730 in the Mount Lassel-Mount Phoebe area.

Age: Lower Aptian.

Diagnosis

Sub-circular, smooth-shelled polypliate *Ptilorhynchia*. Umbo short and massive; beak sub-erect with a small circular foramen. Interarea short; beak ridges poorly defined. Deltidial plates not well exposed.

Holotype: Specimen KG.2.79 from unit H₁₃ at locality H.

Description

The shell (Fig. 3f-i) is inflated, rounded in outline, and is usually wider than long, some larger specimens being markedly so (Figs. 3g and 4). No useful measurements of the thickness are obtainable due to crushing. The surface of the shell bears faint striae originating from the umbonal regions in both valves. Numerous concentric growth lines occur on the surface of the shell and these become more lamellar with increase in size. A low wide fold develops in the brachial valve when the shell is about 7-10 mm. long, and a correspondingly shallow sulcus occurs in the pedicle valve. Both valves are polypliate, with four to ten plicae developing from the mid-line and becoming more highly developed at the margins. The number of plicae on the fold in the brachial valve is usually three or four, but five or six occur in some large examples (Fig. 3h).

The short interarea is only preserved in any detail on the holotype (Fig. 3f). Two small triangular plates which probably once covered the delthyrium have been dislocated.

One specimen (KG.3.84; Fig. 3i) furnished serial sections of the internal structures (Fig. 5). The *pedicle valve* has short divergent dental lamellae which support massive, sub-quadrate, deeply inserted and inwardly projecting hinge teeth. No pedicle collar is developed. In the *brachial valve* there are crenulated, sub-quadrate or broadly rectangular hinge sockets. The inner and outer socket ridges are well developed. The hinge plates are wide, ventrally convex and have a shallow depression or V-shaped sulcus; they are supported by a high persistent median septum. The distal ends of the hinge plate are thickened and deflected towards the

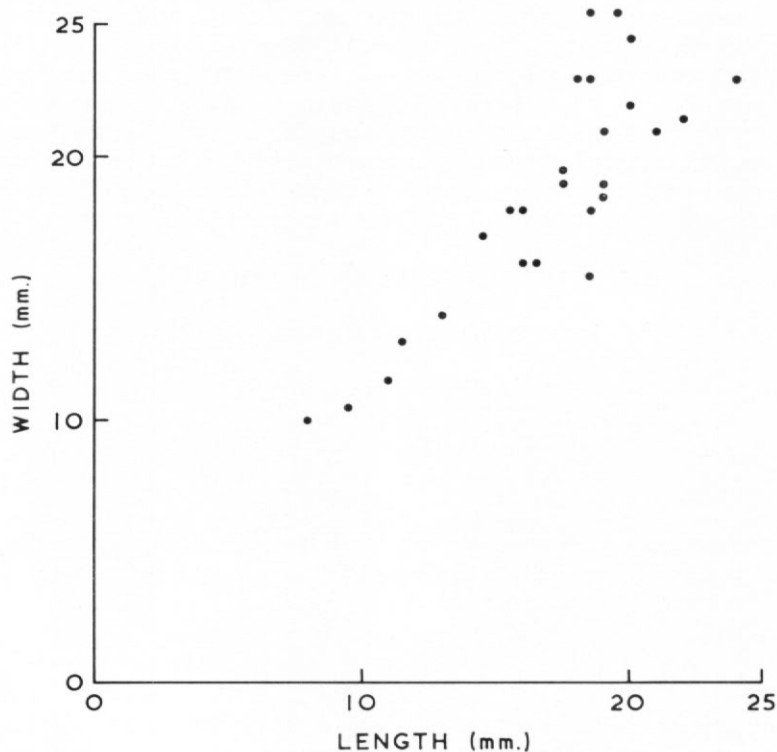


Fig. 4. *Ptilorhynchia australis* sp. nov.; graph of length against width to show the variation in shell form.

ventral valve. This feature manifests itself as two minor swellings on the dorsal surface of the hinge plates, one on either side of the septal pillar. The crural bases become more elongate and triangular in outline, turning gradually towards the dorsal cavity as they extend anteriorly.

Remarks

No comparable brachiopods of Lower Cretaceous age have yet been described from the Antarctic regions and these specimens have to be compared with material from farther afield, notably North America.

One of the earliest records of Mesozoic Rhynchonellidae from that region was that of Aguilera (1895), who described and figured a fauna from the Upper Jurassic of Mexico; most of his genera and species were assigned to well-established European taxa. From the specimens figured on pl. 1 of his work, it seems likely that the fauna was, in fact, more closely related to European tethyan faunas than any subsequent species described from that area.

Other records of Cretaceous Rhynchonellidae from North America include those of Whitteaves (1879, 1896, 1900, 1903) and Anderson (1902, 1958), both of whom described species from the Upper Cretaceous, whereas Imlay (1937) and more recently Cooper (1955) and Ager and others (1963) dealt with Lower Cretaceous forms.

The genus *Ptilorhynchia* was first described by Crickmay (1933) from the Upper Jurassic Knoxville Beds of California. *P. plumasensis*, the only representative species at that time, he nominated as type species. Subsequently, Dagus (1968) described species from both the Upper Jurassic and Lower Cretaceous of northern Siberia, and gave series of transverse serial sections of the genus for the first time. These sections were used for comparison by Owen (1972) when

he described a further species, *P. jeletzkyi*, from the Portlandian of British Columbia. A series of transverse sections through a duplicate specimen of *P. jeletzkyi* is given here (Fig. 6) for comparison.

In a description of Lower Cretaceous fossils from Mexico, Imlay (1937) figured a similar series of transverse serial sections of a specimen from Tamaulipas which he described as "*Rhynchonella*" *miquihuanensis*. These sections have much in common with those figured by Dagis (1968) and by Owen (1972) for species of similar ages. It is largely on these grounds, together with a broad similarity in external morphological characters, that the species here described as *P. australis* is somewhat tentatively referred to the genus *Ptilorhynchia*.

The paucity of well-preserved material from the Lower Cretaceous of Alexander Island has made it impossible to give a more accurate determination of the generic characters, and it may be necessary to revise the taxonomic situation of this species in due course, should better material become available.

Genus *Lamellaerhynchia* Burri 1953

"*Lamellaerhynchia*" sp. A

Fig. 7a and b

Material

Five, possibly six, crushed moulds from a single stratum at Fossil Bluff (KG.1.356, 358 (?), 359, 361, 365 and 366) and a single loose specimen from near locality U (KG.1743.15) thought to be from the same level.

Age: Lower Aptian.

Description and remarks

Although poorly preserved, these specimens (Fig. 7a and b) represent a distinctive rhynchonelloid brachiopod characterized by sharp, deeply incised radiating costae, and a slightly produced beak. The commissure of the shell appears to have been rectimarginate. Since the internal structures are unknown, the assumption that it is, even in the broadest sense, referable to the European genus *Lamellaerhynchia* is based entirely on its general appearance. Particular consideration is given to the form of the costae and the faint somewhat lamellar nature of the additional transverse ornament, which is just visible on the surface of the better preserved parts of the shell.

Lamellaerhynchia was originally described from the Lower Cretaceous of north-western Europe by Burri (1953), but the genus has also been recorded from the Upper Aptian-Lower Albian of Trans-Pecos, Texas, by Ager and others (1963), who described and figured four specimens as *L. indi*. The serial sections which accompanied the description of this species showed hinge plates and other internal structures typical of the subfamily Cyclothridinae, but they further showed crural bases acutely deflected towards the dorsal cavity, a character observed in the type species of *Cyclothyris*, *C. latissima* (J. de C. Sowerby), from the Upper Aptian of Farringdon, Berkshire. In view of the age of the beds at Trans-Pecos, it is more likely that *L. indi* is referable to the genus *Cyclothyris*.

Rhynchonella rustica (Moore, 1870, p. 245, pl. X, figs. 7-9) from the Lower Cretaceous of Queensland has tentatively been assigned to the genus *Lamellaerhynchia* by Hill and others (1968, p. k6, pl. KII, figs. 7 and 8). However, published illustrations show that the ribbing on that species is denser than in "*Lamellaerhynchia*" sp. A, and that its posterior end is less produced.

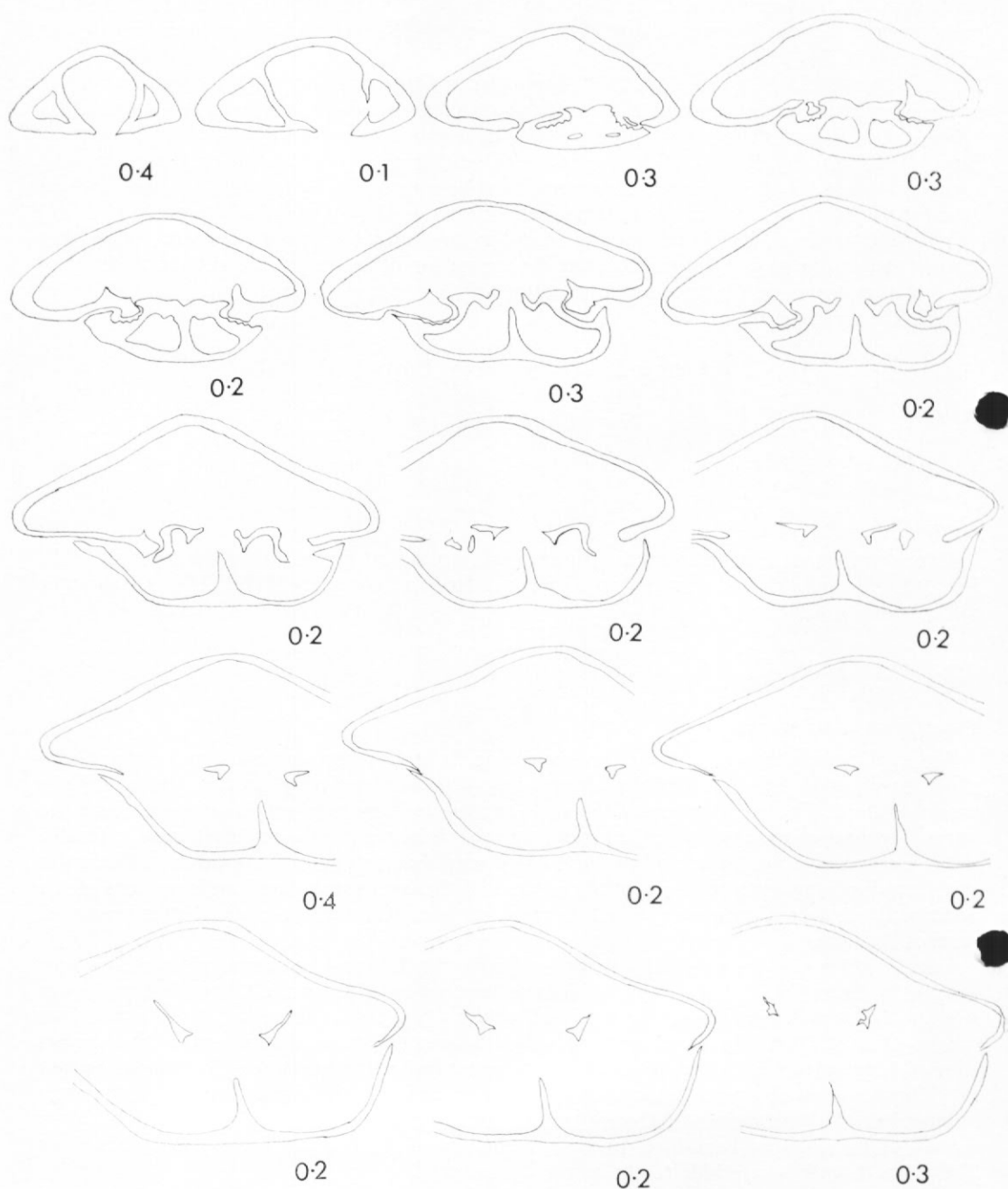


Fig. 5. *Ptilorhynchia australis* sp. nov.; 16 transverse serial sections through the umbone of specimen KG.3.84 from the Lower Aptian of Mount Ariel (locality S). The sections show a deep septalium, a high persistent median septum and similar crural development to *P. jeletzkyi* Owen from the Upper Jurassic of British Columbia, Canada (Fig. 6). The numerals denote the distance in millimetres between each section; $\times 4$.

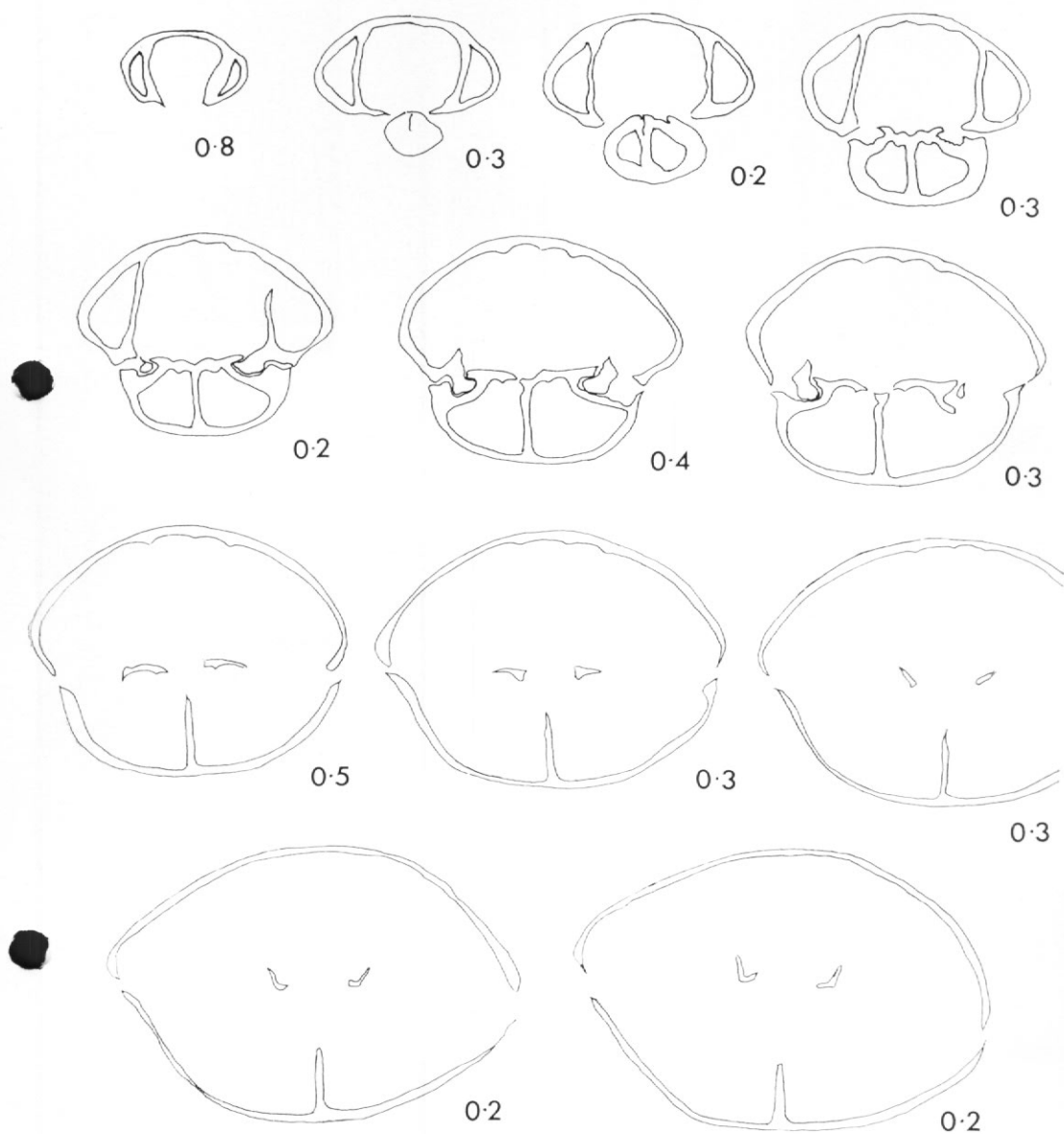


Fig. 6. *Ptilorhynchia jeletzkyi* Owen; 12 transverse serial sections through the umbone of a duplicate specimen from the Upper Jurassic of British Columbia, Canada. In addition to the deep septalium and high persistent septum in the brachial valve, the gutter-like distal ends of the crura are clearly visible. A similar but not identical arrangement of the crura is present in *P. australis* sp. nov. (Fig. 5); $\times 4$.

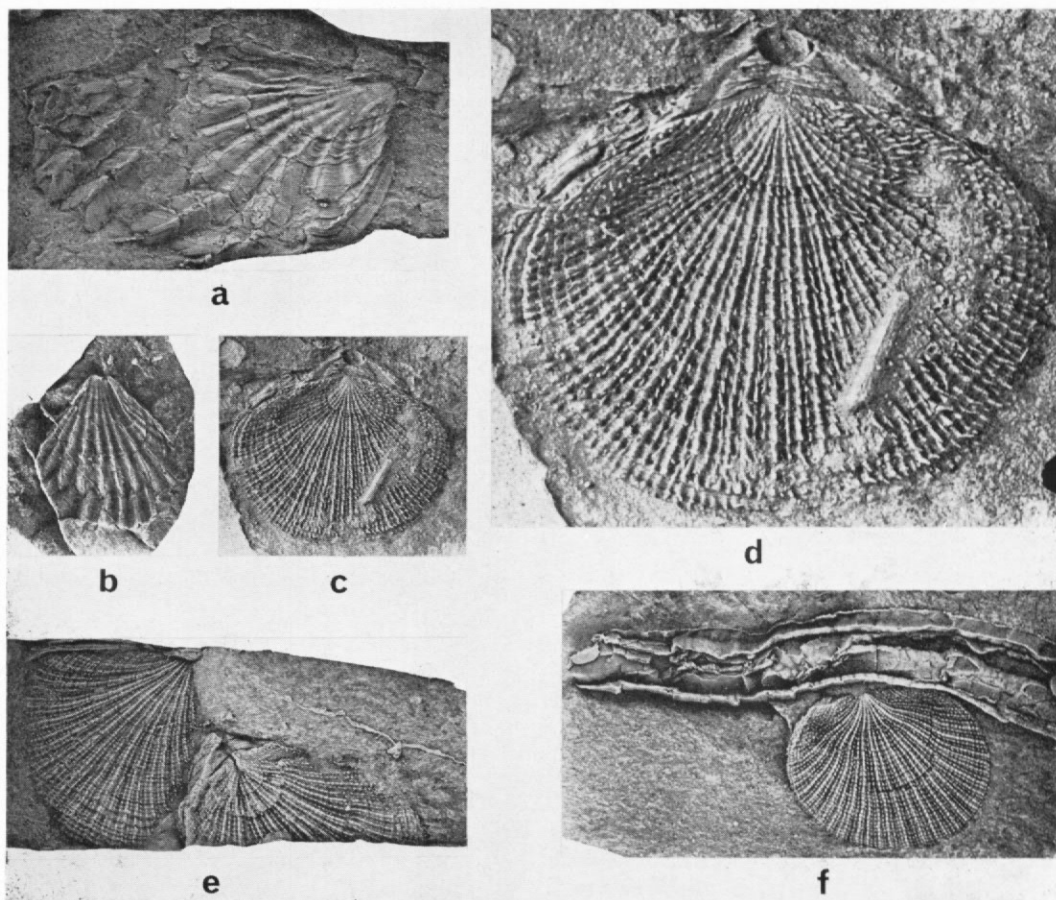


Fig. 7. a. "*Lamellaerhynchia*" sp. A; latex cast from the external mould of a large badly crushed individual; $\times 1.5$, coated (KG.1.366).
 b. "*Lamellaerhynchia*" sp. A; latex cast from a small external mould; $\times 1.5$, coated (KG.1743.15).
 c. *Prochlidonophora muirwoodae* gen. et sp. nov.; silicone rubber cast from the holotype, an external mould; $\times 2$ (KG.12.19).
 d. *P. muirwoodae* gen. et sp. nov.; silicone rubber cast of the holotype, enlarged to show the spinose ornament; $\times 5$ (KG.12.19).
 e. *P. muirwoodae* gen. et sp. nov.; latex cast from an external mould of two fragmentary specimens, one showing details of the interarea; $\times 2$, coated (KG.14.2).
 f. *P. muirwoodae* gen. et sp. nov.; latex cast from an example apparently attached to a serpulid worm tube; $\times 2$, coated (KG.1751.5).

ORDER TEREBRATULIDA

SUBORDER TEREBRATULIDINA WAAGEN 1883

SUPERFAMILY TEREBRATULACEA GRAY 1840

FAMILY CANCELLOTHYRIDIDAE THOMSON 1926

SUBFAMILY CHLIDONOPHORINAE MUIR-WOOD 1959

Genus *Prochlidonophora* gen. nov.

Type species: *P. muirwoodae* sp. nov.

Diagnosis

Sub-circular, costellate, plano-convex to incipiently biconvex. Umbo slightly produced, beak almost erect, foramen large and circular. Hinge line slightly extended, interarea long, beak ridges distinct. Delthyrium well exposed, deltidial plates conjunct.

Prochlidonophora muirwoodae sp. nov.

Fig. 7c-f

Material

More than 14 specimens from localities L, E, R, the Mount Lassel area (KG.1627 and 1751) and northern Hyperion Nunataks (KG.1657).

Age: Most specimens from the Fossil Bluff area pre-date the *Ptilorhynchia* fauna and are probably Upper Neocomian in age. A single specimen from locality R, and those from the Mount Lassel area and northern Hyperion Nunataks are associated with aconeceratid ammonite faunas of probable Lower Aptian age.

Description

The shell is almost circular in outline; some individuals (like the holotype, 12.2 mm. long and 13.0 mm. wide) are slightly wider than long but in others it is the reverse. The surfaces of both valves (Fig. 7c-f) are covered by numerous costellae originating from the umbonal regions. These increase by bifurcation or intercalation from a fairly early stage in the development of the shell and multiply at irregular intervals throughout growth. On the holotype (Fig. 7c-d) the final number of costellae is about 100. Additional concentric ornament of raised rings or periodic growth lamellae produces a strong reticulation (Fig. 7d) with the development of small spinules. Similar reticulate ornament occurs on some Recent *Chlidonophora*, although not to the extent of developing spinules.

The massive but slightly produced umbo (Fig. 7d and e) forms a broad-based triangle with a slightly extended hinge line and it is pierced by a large, circular mesothyridid foramen. The beak ridges are sharply defined and the deltidial plates are conjunct perhaps even fused.

Holotype: Specimen KG.12.19, an external mould showing the brachial valve and cardinal area, from the top of the measured section at locality L.

Remarks

The assignment of a brachiopod species to any genus depends very largely upon knowledge of its internal structures. In this case, the cardinalia and loop structure of *P. muirwoodae* are unknown due to the lack of suitable material for dissection or transverse serial sectioning. However, the external morphology of the specimens available certainly suggests that the present species is readily assignable to the family Cancellothyrididae, and it seems likely that it is fairly closely affined to the Recent genus *Chlidonophora* Dall. Notable differences from that genus are the enclosed mesothyridid foramen and the development of spinules on the surface of the shell.

Consideration has been given to the genus *Cruralina*, which was erected by Smirnova (1966) for three species of Cancellothyrididae from the Lower Barremian-Lower Aptian of the Crimea. Cooper (1973) remarked on Smirnova's original description of the genus, pointing out the lack of serial sections or illustrations of the internal structures of the type species, *C. cruralinica*. Conversely, two other species figured at the same time, *C. belbekensis* and *C. rotunda*, were well illustrated with transverse sections and reconstructions of the internal

structures. The shell ornament in Smirnova's (1966, fig. 4e-l) illustrations of these two species greatly resembles that of specimens figured as *Gyrosoria gracilis* by Cooper (1973, pl. 45, figs. 14-18) from the Upper Chalk of Trimmingham, Norfolk, England, and to a large extent it is also similar to the ornament of *P. muirwoodae* (Fig. 7d). However, the Antarctic species differs in having a more pronounced and spinose reticulation due to the more highly developed concentric ornament.

It may become necessary to review the taxonomic position of *Prochlidonophora muirwoodae* when more material becomes available and a closer comparison can be made with other genera and species within the Cancellothyrididae.

SUPERFAMILY LOBODOTHYRACEA MAKRIDIN 1964

FAMILY LOBODOTHYRIDAE MAKRIDIN 1964

Genus *Penzhinothyris* Smirnova 1969

Penzhinothyris imbricata sp. nov.

Fig. 8a and d

Material

Remains of nine crushed individuals on five rock slabs from unit R₅ of the section measured at locality R, Fossil Bluff (KG.1.348-50, 353 and 362). One (KG.1.350) occurs on the same slab as an example of "*Acanthorhynchia*" (*Echinorhynchia*) *setosa* sp. nov.

Age: Lower Aptian.

Diagnosis

Cinctiform, feebly inflated terebratuloid, resembling *Penzhinothyris* Smirnova in external appearance, but internal structures unknown. Ornament of faint radiating striae and lamellar growth rings. Almost equivalve, cardinal area very small.

Holotype: Specimen KG.1.349, an internal mould of an obliquely crushed pedicle valve.

Description

All available specimens of this thin-shelled species are crushed to thin disc-like forms. The shell is cinctiform, oval in outline and, despite the poor preservation of the available specimens, it was probably not much inflated. It is slightly wider than long, the largest specimen (KG.1.348) measuring 35.1 mm. long and 40.9 mm. wide. Both valves are of more or less the same size. The shell surface is finely punctate with faint longitudinal striae radiating from the umbonal regions. Numerous concentric growth lines are sometimes marked by lamellar or step-like development.

Remarks

The genus *Penzhinothyris* was first described by Smirnova (Smirnova and Pergament, 1969) from the Upper Albian of north-western Kamchatka, Penzhino area, north-eastern U.S.S.R. Later (Smirnova and Terekhova, 1972), she used the name for a terebratulid, *P. subtilis*, from the Barremian-Aptian of the Pekul'ney Range, Krivaya River, Khabarovsk Territory, north-eastern U.S.S.R. The holotype of *P. subtilis* (Smirnova and Terekhova, 1972, pl. 12, fig. 5a-d) is a sub-circular cinctiform specimen, somewhat crushed, but in many ways resembling the specimens described here as *Penzhinothyris imbricata* (Fig. 8a and d).

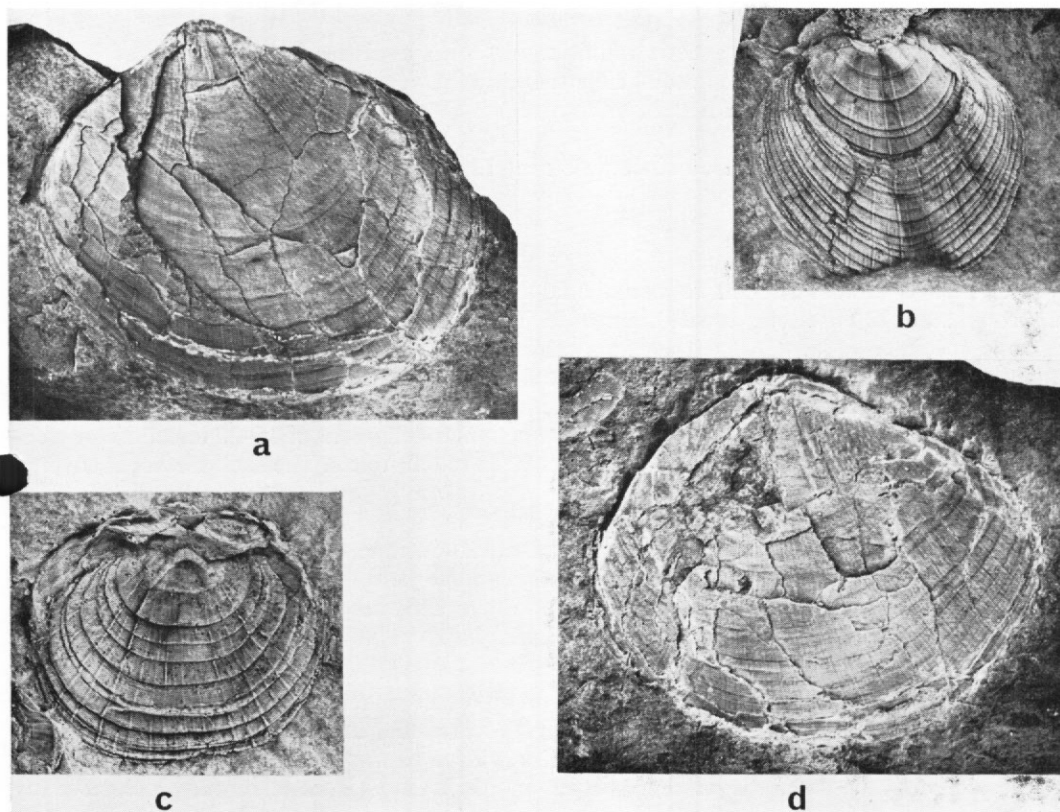


Fig. 8. a. *Penzhinothyris imbricata* sp. nov.; holotype, the natural internal mould of a crushed pedicle valve, $\times 1.5$, coated (KG.1.349).
 b. "*Terebratula*" *lamellosa* sp. nov.; latex cast from the holotype, an incomplete external mould of a pedicle valve; $\times 1.5$, coated (KG.1627.3).
 c. "*T.*" *lamellosa* sp. nov.; latex cast from an external mould of a brachial valve, also showing the crushed remains of the interarea and foramen; $\times 1.5$, coated (KG.1657.4).
 d. *Penzhinothyris imbricata* sp. nov.; the natural internal mould of a crushed example showing fine superimposed radial striae; $\times 1.5$, coated (KG.1.348).

It is interesting to note that the geographical distribution of *Penzhinothyris* (Smirnova and Pergament, 1969; Smirnova and Terekhova, 1972) is similar to that of *Ptilorhynchia*, as outlined by Dagis (1968), and, if the records given for the genera described here are correct, it follows a similar pattern from boreal Arctic to Antarctic regions.

Genus *Terebratula* Müller 1776 *s.l.*

"*Terebratula*" *lamellosa* sp. nov.

Fig. 8b and c

Material

Three adult specimens (KG.1627.3, 1657.4 and 5) from northern Hyperion Nunataks and near Mount Lassell; a fourth specimen (KG.1657.7) may represent a juvenile of the species.

Age: Lower Aptian.

Diagnosis

Terebratulid of uncertain generic affinities but with a distinctive ornament of lamellar growth rings and widely spaced radial riblets. Pedicle valve shallowly sulcate and with a large circular foramen. Internal characters unknown.

Holotype: Specimen KG.1627.3, an incomplete internal mould of a pedicle valve from northern Hyperion Nunataks.

Description

The shell is almost circular to pentagonal in outline, the holotype (Fig. 8b) measuring approximately 22 mm. long and 24 mm. wide. The foramen and interarea are only preserved on one specimen (Fig. 8c) and then in a crushed condition; the hinge line is straight and slightly extended, the interarea appears to be flat, and the foramen is large and circular. In the pedicle valve there is a shallow sulcus, whereas in the brachial valve there is a corresponding but feebly developed fold. Both valves have a similar ornament of 15–20 lamellose or step-like concentric growth lines and 27–30 widely spaced radial riblets. The shell surface is covered with numerous microscopic granules.

No details of the internal structures are preserved.

Although it was found in association with the other specimens, the (?) juvenile (KG.1657.7) is included only tentatively because it also has capillae between the radial riblets and these are not preserved on the larger specimens, even in the early stages.

Remarks

The specimens available for study are poorly preserved and slightly crushed. Although it is not possible to indicate more than general terebratulid affinities at a generic level, the material clearly represents a distinctive species with a characteristic ornament. There is a vague similarity between the present species and a dallinoid species recently described by Smirnova (1974) as *Clathrithyris clathriensis* from the Hauterivian of the Penzhin basin, north-eastern U.S.S.R., but the lack of internal morphological features in "*Terebratula*" *lamellosa* sp. nov. makes a detailed comparison impossible.

PALAEOECOLOGY

It is believed that much of the thick Upper Jurassic–Lower Cretaceous succession of south-eastern Alexander Island (Fossil Bluff Formation) was deposited rapidly, and the apparently anomalous occurrence of articulate brachiopods in the mudstones of this sequence has already been briefly discussed (Taylor and others, 1970). Over a number of years, the problem of how brachiopods may have attached or anchored themselves on soft-sediment bottoms has received some attention (e.g. Rudwick, 1961; Ager, 1965). Several mechanisms have been described and these may be grouped into two main categories:

- i. The use of substitutes for hard bottoms.
- ii. Specialized adaptations.

The first group includes the pedicle attachment of some modern brachiopods to other organisms (sponges, corals, tunicates, other brachiopods, bivalves, horny worm tubes, etc.) or algae, with the inference that some fossil groups would also have behaved likewise. Rudwick (1961) further suggested that, since algae, sponges and horny worm tubes would not normally be fossilized, it is possible that some reported "nests" of brachiopods might represent small colonies once attached to such substrates. *Ptilorhynchia* frequently occurs grouped or "nested" in Alexander Island, sometimes in association with other fossils. The similarity in size of

brachiopod individuals in some of these grouped occurrences could suggest colonization of a "substrate" by a single spat fall, but it is also suggestive of sorting, and at least some of them may represent current-transported assemblages. *Rotularia* and small gastropods have also been reported in grouped occurrences from the succession in the Fossil Bluff area. The mode of occurrence of some discinid brachiopods in the Aptian of the Fossil Bluff area strongly suggests that they were attached to terrestrial plant debris washed into the sea (Thomson, 1971), but other individuals were attached to more conventional substrates; a *Lingula* shell and a gastropod.

In the Upper Jurassic rocks of the Ablation Point area, rhynchonellids have been found in positions suggesting attachment to a giant *Lytoceras* conch (Taylor and others, 1979, pl. VIIIc), and one specimen of *Prochlidonophora muirwoodae* (Fig. 7f) may have lived on a calcareous worm tube.

Among the specialized adaptations are the modifications to the pedicle shown by different brachiopod groups. On the basis of relative variations in length and width, the size of hold-fast papillae and the presence of "rootlets", Bromley and Surlyk (1973) distinguished seven types of pedicle in modern brachiopods. Some dredged specimens of *Chlidonophora* have an exceedingly long pedicle with numerous rootlets which pierce the shells of Foraminifera, presumably once buried in the bottom sediments and thus providing anchorages. No obvious shell characteristics related to this pedicle modification have been recognized, and therefore the likelihood of proving such an adaptation in fossil material is highly improbable. The present *Prochlidonophora* gen. nov. closely resembles *Chlidonophora* in external form and it may have been capable of securing itself in the same way, but at least one specimen (see above) suggests that its pedicle was of the "normal" short type, and that it fixed itself to solid objects on the sea bed.

The pedicle of the adult in some living brachiopods is reduced to a tethering function (Rudwick, 1970, p. 87) and in many fossil species it is clear that the pedicle had atrophied altogether. In the latter case, there is usually some adaptation of the shell which can be ascribed a stabilizing function. Sometimes this takes the form of external modifications to the shell (e.g. wings, spines, etc.) but it may alternatively consist of extra shelly material deposited on the inner surface of the shell and acting as a weight. There is little information on the longevity of brachiopods which may be lying loose because they have accidentally been torn off their anchorage.

Although poorly preserved, it is clear that the pedicle foramen of *Penzhinothyris imbricata* was extremely small in relation to the size of the shell. This is also the case in other described species of *Penzhinothyris* (Smirnova and Pergament, 1969; Smirnova and Terekhova, 1972) and in morphologically similar species of *Cincta* Quenstedt. If such species were still pedicle-attached, it seems unlikely that their pedicles could have performed more than a tethering function, and that the animals probably lived under quiet-water conditions.

The fine hair-like spines of "*Acanthorhynchia*" (*Echinirhynchia*) *setosa* resemble those studied by Rudwick (1965) in Jurassic *Acanthothyris*. Although there are no analogues of these structures in modern brachiopods, Rudwick (1965) concluded that their function was sensory; the spines of *Acanthothyris* were hollow and presumably contained an extension of the sensitive mantle. "Dead" spines on the earlier stages of the shell probably performed a stabilizing function as the pedicle of this species is believed to have atrophied. However, the spines of "*A.*" (*Echinirhynchia*) *setosa* are many times finer than those of *Acanthothyris* (cf. Fig. 9), they are now partly decalcified so that their structure is unknown, and it must therefore be questioned whether the spines of the two forms are necessarily analogous. Because of their delicacy, it is unlikely that a stabilizing function was their primary purpose, and a sensory function seems the more likely. Their preservation around the commissure and sometimes on the body of the shell is suggestive of quiet-water conditions and rapid burial.

It is interesting to note that a superbly preserved specimen of *Acanthothyris spinosa* (Fig. 9),

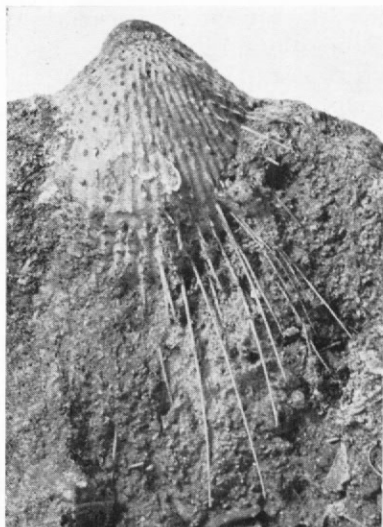


Fig. 9. *Acanthothyris spinosa* (Linné); exceptionally well-preserved example from the Inferior Oolite of Somerset, showing spines attached; $\times 1.5$ (British Museum (Nat. Hist.) No. B.10617).

to which the long spines are clearly still attached, came from the Inferior Oolite, a deposit traditionally regarded as having formed in a high-energy environment.

The internal features of the present "*Acanthorhynchia*" are unknown and its generic position is therefore doubtful. The two spinose Jurassic rhynchonellid genera, *Acanthothyris* and *Acanthorhynchia*, are externally similar but they have different internal structures, and different modes of life have been suggested for the two forms (Ager, 1965; Childs, 1969). *Acanthothyris* is frequently found grouped, suggesting attachment to some soft-bodied organism (Ager, 1965), whereas earlier defunct sensory spines may have assisted in stabilizing the brachiopod on the substrate, since it appears that the pedicle atrophied at some time (Rudwick, 1965). The somewhat sporadic distribution of *Acanthorhynchia* was considered by Ager (1965) and Childs (1969) to reflect a pelagic mode of life, and it was suggested that it may have lived attached to algae or sponges and drifted long distances. In Alexander Island, "*Acanthorhynchia*" *setosa* has an extremely restricted distribution and is only known from a few metres of mudstone, typified by unit R₅ at Fossil Bluff (Fig. 2). Unless this is an extreme expression of sporadic distribution, it agrees with neither of the distribution patterns noted for *Acanthothyris* and *Acanthorhynchia* in Europe, and its significance remains problematical.

SIGNIFICANCE OF THE FAUNAS

Lower Cretaceous brachiopods are poorly known in the Gondwana continents and thus, despite their fragmentary preservation, the present faunas offer an important contribution to our knowledge of the group. Available descriptions indicate that in this whole region the Lower Cretaceous marine invertebrate faunas are dominated by Mollusca, particularly bivalves and ammonites.

Camacho (1966, p. 271) commented that South American Mesozoic brachiopods were practically unknown and this remark still holds good today. Few species have been described and most of those were referred to the sack genera "*Rhynchonella*" and "*Terebratula*". In southern Africa and India, published accounts of Lower Cretaceous brachiopods are restricted to isolated occurrences, and in New Zealand all but the later stages of this part of the sequence are missing or represented by terrestrial deposits. Of the few species known from Australia,

only Moore's (1870) *Rhynchonella rustica* shows even a superficial resemblance to any of the species described here (p. 25).

To find comparable material, it has been necessary to look elsewhere. *Ptilorhynchia australis* is the only one of the present species from which it has been possible to obtain details of the internal structures. It is thus the one species whose generic affinities can be determined with some degree of confidence but, even then, distortion due to crushing casts a certain amount of doubt on the identification. The genus *Ptilorhynchia* was previously known only from California, Mexico and Siberia. Similarly, the Acanthothyridinae were only known from Europe and Asia and, until recently, had only been described from the Middle and Upper Jurassic. To find described material comparable to the unusual terebratulids here referred to *Penzinothyris imbricata* and "*Terebratula*" *lamellosa*, it was again necessary to look to Siberia.

The significance of this lack of comparable material closer to Antarctica is difficult to assess at present but it may well be explained by collecting failures and/or a lack of published descriptions. It is clear that several "Northern Hemisphere" genera are more widely distributed than was previously appreciated, and that more attention should therefore be given to Southern Hemisphere Mesozoic brachiopod faunas, rare though they may be. More data are needed from all the Gondwana continents to try and establish the presence of faunas intermediate between those of Antarctica and the Northern Hemisphere.

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