

A NEW OXYTOMID BIVALVE FROM THE UPPER JURASSIC–LOWER CRETACEOUS OF ANTARCTICA

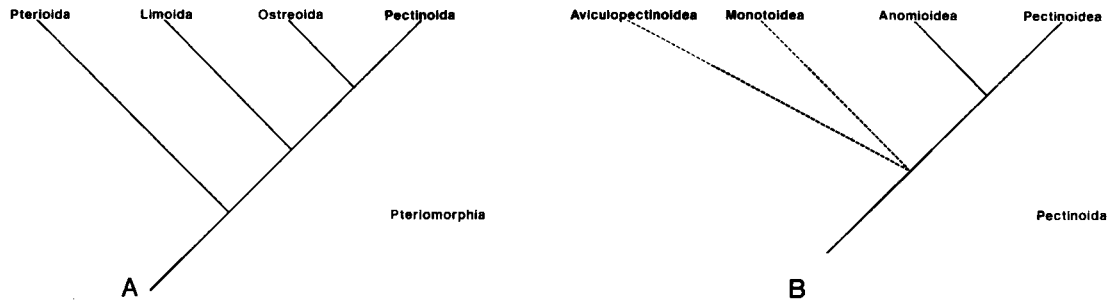
by J. A. CRAME

ABSTRACT. *Praeaucellina umbonoradiata* gen. et sp. nov. is a small pteriomorph bivalve from the Upper Jurassic–Lower Cretaceous of Antarctica which can be referred to the family Oxytomidae, within the superfamily Monotoidea. Sub-rounded to strongly obliquely elongated in outline, it is markedly inequivalve. The left valve is somewhat narrower than the right, and the latter possesses a clearly defined, but tiny, antero-dorsal ear. This feature takes the form of a rounded blade which is strongly inclined with respect to the plane of commissure. This is a typical oxytomid feature, as is the presence of a pseudotenolium. Indeed, there is now a considerable volume of morphological and stratigraphical evidence to suggest close phylogenetic ties with Late Jurassic–Early Cretaceous genera such as *Aucellina* and *Oxytoma*. Other austral oxytomids, such as *Arctotis* and *Maccoyella*, comprise a distinct morphological subgroup characterized by much thicker hinges. Whilst elucidation of the features of *Praeaucellina* helps to consolidate the taxonomic differences between the Oxytomidae and Buchiidae, it highlights further possible similarities between the former of these categories and the Monotidae. Resolution of phylogenetic relations within the Monotoidea will greatly assist studies of the evolution of Mesozoic high-latitude bivalve faunas.

WITHIN the class Bivalvia there are two major groupings of epifaunal bivalves with predominantly calcitic shells: the mussels (usually referred to the order Mytiloidea within the subclass Isofilibranchia) and the scallops and their close relatives (referred to the subclass Pteriomorphia) (Carter 1980, 1990). The latter group was particularly common from the late Palaeozoic to the late Mesozoic, when forms such as the inoceramids, bakevelliids, pinnids, pectinids, limids and oysters were major components of marine benthic invertebrate assemblages. Indeed, such was their abundance that they have been used widely in stratigraphical, ecological and biogeographical studies; this is particularly so in mid- to high-latitude regions. Nevertheless, it is true to say that, despite their widespread utility in palaeontology, we still know comparatively little about the phylogenetic relationships of many pteriomorph groups.

From the pioneering observations made by Waller (1978), it is understood that there are four calcitic orders of pteriomorphs, with the pterioids being the most primitive (Text-fig. 1A) (N.B. the classification of pteriomorphs followed here is that of Carter (1990)). This is so because they possess a nacreo-prismatic shell; in all the other groups the inner aragonitic layers are some form of crossed-lamellar structure and in the outer calcitic layers prismatic structure has been largely or completely lost (Waller 1978; Carter 1990). Foliated calcite ultrastructure is a derived character state restricted to just the orders Ostreoida and Pectinoidea (Text-fig. 1A). Within the order Pectinoidea it has been suggested that four taxa of superfamily rank can be recognized: the essentially Palaeozoic Aviculopectinoidea, the essentially Mesozoic Monotoidea, and the Anomioidea and Pectinoidea, both of which comprise a variety of fossil and living forms (Table 1). The phylogenetic positions of the Aviculopectinoidea and Monotoidea are as yet unresolved, but it is assumed generally that both taxa were ancestral to the stock yielding the Anomioidea and Pectinoidea (Text-fig. 1B).

If the distinctive oyster-like anomioids are excluded, the order Pectinoidea can be said to be characterized by small to large bivalves which are rounded to obliquely oval in outline, moderately to strongly inequivalve (LV always more inflated than RV), and typically bear stronger radial than concentric ornament. However, perhaps their most diagnostic feature is the presence of a small ear and byssal notch in the antero-dorsal region of the right valve. At some stage in their lives most



TEXT-FIG. 1. Schematic phylogenies for: A, the bivalve subclass Pteriomorphia, and B, the order Pectinoidea. Based on data contained within Waller (1978). In B the superfamily Aviculopectinoidea may well be the most primitive, as some representatives are known to possess a nacreous shell layer; such a feature is unknown within the Monotoidea (Carter 1990).

TABLE 1. Subdivision of the bivalve order Pectinoidea. Based on Hertlein *et al.* 1969 and Carter 1990, with minor amendments. Abbreviations: E, Early; L, Late; M, Mid.

Order PECTINOIDA Rafinesque, 1815	
Superfamily	Aviculopectinoidea Meek and Hayden, 1864
Family	Leiopectinidae Krasilova, 1959 (Ord.–E. Dev.)
	Pterinopectinidae Newell, 1938 (L. Sil.–E. Perm.; ?L. Perm.–E. Trias.)
	Aviculopectinidae Meek and Hayden, 1864 (L. Dev.–L. Trias.)
	Deltopectinidae Dickins, 1957 (L. Carb.–E. Perm.)
	Euchondriidae Newell, 1938 (L. Dev.–L. Perm.)
Superfamily	Monotoidea Fischer, 1887
Family	Monotidae Fischer, 1887 (L. Trias.–L. Jur.)
	Asoellidae Begg and Campbell, 1985 (L. Trias.)
	Buchiidae Cox, 1953 (?M. Perm.–E. Cret.)
	Oxytomidae Ichikawa, 1958 (E. Perm.–?E. Paleoc.)
	Pseudomonotidae Newell, 1938 (E. Carb.–E. Trias.)
Superfamily	Anomioidea Rafinesque, 1815
Family	Permanomiidae Carter, 1990 (Perm.)
	Anomiidae Rafinesque, 1815 (Jur.–Rec.)
	Placunicae Gray, 1840 (Eoc.–Rec.)
Superfamily	Pectinoidea Rafinesque, 1815
Family	Propeamussiidae Abbott, 1954 (E. Carb.–Rec.)
	Entoliidae von Teppner, 1922 (E. Carb.–L. Cret.)
	Pernopectinidae Nevevskaya <i>et al.</i> , 1971 (E. Carb.–L. Perm.)
	Streblochondriidae Newell, 1938 (E. Carb.–Perm.)
	Pectinidae Rafinesque, 1815 (Trias.–Rec.)
	Spondylidae Gray, 1826 (?E. Perm.–?L. Trias)

pectinoids have been anchored to the substratum by a byssus, and always with the flatter right valve underneath (i.e. pleurothetic on the RV). The largest and most obvious 'scallops', members of the Pectinoidea, are generally subequilateral, with the anterior ear and its posterior counterpart forming subequal wing-like extensions to the hingeline. A prominent triangular ligament pit directly beneath the umbones is commonly flanked by cardinal crura (or ridges), and a primitive prismatic calcite outer shell layer may be partially or wholly replaced by homogeneous or foliated calcite. Similarly, ancestral middle and inner layers of aragonitic crossed-lamellar structure may be replaced by foliated calcite (Waller 1978; Carter 1990).

Although both the anomioideans and pectinoideans form reasonably coherent groups, the same is not necessarily true of the aviculopectinoideans and monotoideans (Table 1). At least part of the

reason for this is that the aviculopectinoid family Aviculopectinidae shows considerable stratigraphical and morphological overlap with each of the five component families of the Monotoidea. Since its redefinition in the *Treatise on invertebrate paleontology* (Cox 1969), it is apparent that at least two genera should now be removed from the Aviculopectinidae: *Claraia* is probably better assigned to the Pterinopectinidae (Zhang 1980), and *Otapiria* to the Monotidae (Begg and Campbell 1985). Nevertheless, this still leaves Triassic taxa, such as *Leptochondria*, *Ornithopecten* and *Oxypteria*?, which bear very strong resemblances to the Monotoidea (Waller 1978, p. 363).

It has been assumed generally that the Monotoidea arose from the Aviculopectinoidea by the alteration of two basic features: loss of an inner aragonitic shell layer, and interruption of a once-continuous pallial line (Ichikawa 1958; Cox 1969). However, Carter (1990) has pointed out that the putative ancestral lineage within the Aviculopectinidae contains at least one taxon, *Limipecten*, in which the outer prismatic calcite layer has been entirely replaced by homogeneous structure. As certain oxytomid genera, such as *Oxytoma* and *Meleagrinnella*, still possess a thin outer prismatic calcite shell layer, and some species, such as *Meleagrinnella curta* (Hall), may have a thin aragonitic middle shell layer in the right valve, an alternative ancestor may need to be found. *Pseudomonotis*, with its aragonitic middle and inner shell layers and at least some prismatic material in its outermost layer, is a possibility here, but it is apparent that its superfamilial placing is somewhat conjectural (Newell and Boyd 1970; Waller 1978; Carter 1990). Finally, it should be stressed that the familial subdivision of the Monotoidea has been the subject of considerable debate (see extended discussion in Ichikawa 1958; Begg and Campbell 1985; Crame 1985; Carter 1990).

It is important to emphasize that resolution of these taxonomic problems may have considerable palaeobiogeographical implications. For example, within the superfamily Monotoidea a surprising variety of taxa displays either widespread or cosmopolitan distributions, and elucidation of their phylogenetic relationships should provide important insights into the origin and evolution of high-latitude marine biotas. Of the seven Mesozoic genera currently assigned to the family Oxytomidae (*sensu* Crame 1985), two are essentially cosmopolitan (*Oxytoma* and *Meleagrinnella*), two are bipolar (*Arctotis* and *Aucellina*), and three are associated with just the southern high-latitude regions (*Malayomaorica*, *Maccoyella* and *Pseudavicula*) (Cox 1940; Kobayashi and Ichikawa 1952; Ichikawa 1958; Begg and Campbell 1985; Crame 1985, 1986). As a prelude to a full phylogenetic revision of the Monotoidea, its component genera are being reassessed in terms of morphological features (especially those of the hinge-line and shell structure) which may form potential synapomorphic character suites. Particular attention has been paid so far to the Oxytomidae, and during the course of recent fieldwork in Antarctica a new form was found which is stratigraphically intermediate between Late Jurassic (i.e. Kimmeridgian–Tithonian) taxa such as *Oxytoma* and *Arctotis* and the Early Cretaceous (?Late Barremian–Albian) *Aucellina* (Crame and Howlett 1988; Crame *et al.* 1993). It is the intention of this study to describe this new form and assess its phylogenetic and biogeographical potential.

All the specimens described in this study are deposited in the collections of the British Antarctic Survey, Cambridge, UK.

SYSTEMATIC PALAEOLOGY

Class BIVALVIA Linnaeus, 1758

Subclass PTERIOMORPHIA Beurlen, 1944

Order PECTINOIDA Rafinesque, 1815

[*emend.* Waller 1978, p. 353; Carter 1990, p. 234]

Superfamily MONOTOIDEA Fischer, 1887

[*nom. transl.* Begg and Campbell 1985; *emend.* Carter 1990]

Diagnosis. See Waller 1978, p. 362; Begg and Campbell 1985, p. 727; Carter 1990, p. 245.

Family OXYTOMIDAE Ichikawa, 1958

Emended diagnosis. Extended diagnoses and discussions have been given by Ichikawa (1958, p. 158), Begg and Campbell (1985, p. 735), Crame (1985, p. 36) and Carter (1990, p. 249). The salient features which serve to distinguish oxytomids are as follows: LV-profile can be more upright and subsymmetrical; low, rounded antero-dorsal wing commonly developed; hinge edentulous but anterior portion may bear accessory tooth-like features which articulate with inner surface of RV ear; anterior portion of hinge-line may bear shallow sulcus but this is in no way equivalent to the *Gelenkgrube* of the Buchiidae; radial ornament predominates over concentric. RV has a more rounded profile; antero-dorsal ear comparatively long and blade-like; ear not folded or turned strongly inwards; anterior portion of ligament area continues along dorsal surface of ear almost to its tip; ear tilted strongly inwards (with respect to the plane of commissure) and rests snugly beneath antero-dorsal region of LV; byssal notch can be comparatively broad; pseudoctenolium may be present; ornament typically more subdued than on LV; thin outer shell layer of prismatic calcite; thin middle shell layer of aragonitic crossed-lamellar structure may also be present.

Component genera. *Oxytoma* Meek (*sensu lato*) (?Olenekian–Danian), *Meleagrinnella* Whitfield (Rhaetian–Tithonian), *Arctotis* Bodylevsky (Lias–Hauterivian), *Maccoyella* Etheridge, Jr (Aptian–Albian), *Pseudavicula* Hudleston (Aptian–Albian), *Avicularca* von Bubnoff? (Carnian–?Rhaetian). A Permian member of the family, *Cyrtorostra* Branson (Cox 1969), has not been considered in this study.

Remarks. Reference is again made to the previously cited sources for a full discussion of the taxonomic status of the Oxytomidae. In summary, it can be stated here that the boundaries between at least four of the component families of the Monotoidea (Monotidae, Asoellidae, Buchiidae and Oxytomidae; Table 1) are by no means rigid. The Buchiidae can usually be distinguished from the Oxytomidae by features such as a smoother form, largely opisthodontic ligament, and thickened, spoon-shaped anterior ear on the RV (Crame 1985). Articulation of the tip of this ear with a deeply recessed pit (*Gelenkgrube*) on the anterior of the LV hinge may prove to be a synapomorphy for the Buchiidae, but this feature needs further investigation. Shallower articulation pits (again, sometimes referred to as *Gelenkgrube*) have been recorded along the LV hinges of certain oxytomids (e.g. *Meleagrinnella*; Cox 1940, p. 91). Monotids can usually be distinguished by their much stronger radial ornament and tiny RV ear. Nevertheless, there are indications that the hinge region of this group, although somewhat smaller, is not significantly different in form from that of the Oxytomidae (e.g. Payevskaya 1985; Grant-Mackie and Silberling 1990). The simple hinge and large, blade-like ear may serve to establish the genera *Asoella* and *Eitalia* within the family Asoellidae (Begg and Campbell 1985), but the assignment of *Aucellina* here is questionable. Some forms of *Aucellina* exhibit a prominent pseudoctenolium (e.g. Woods 1905, pl. 10, fig. 9b), and this feature almost certainly links it closely with *Oxytoma*.

Genus PRAEAUCCELLINA gen. nov.

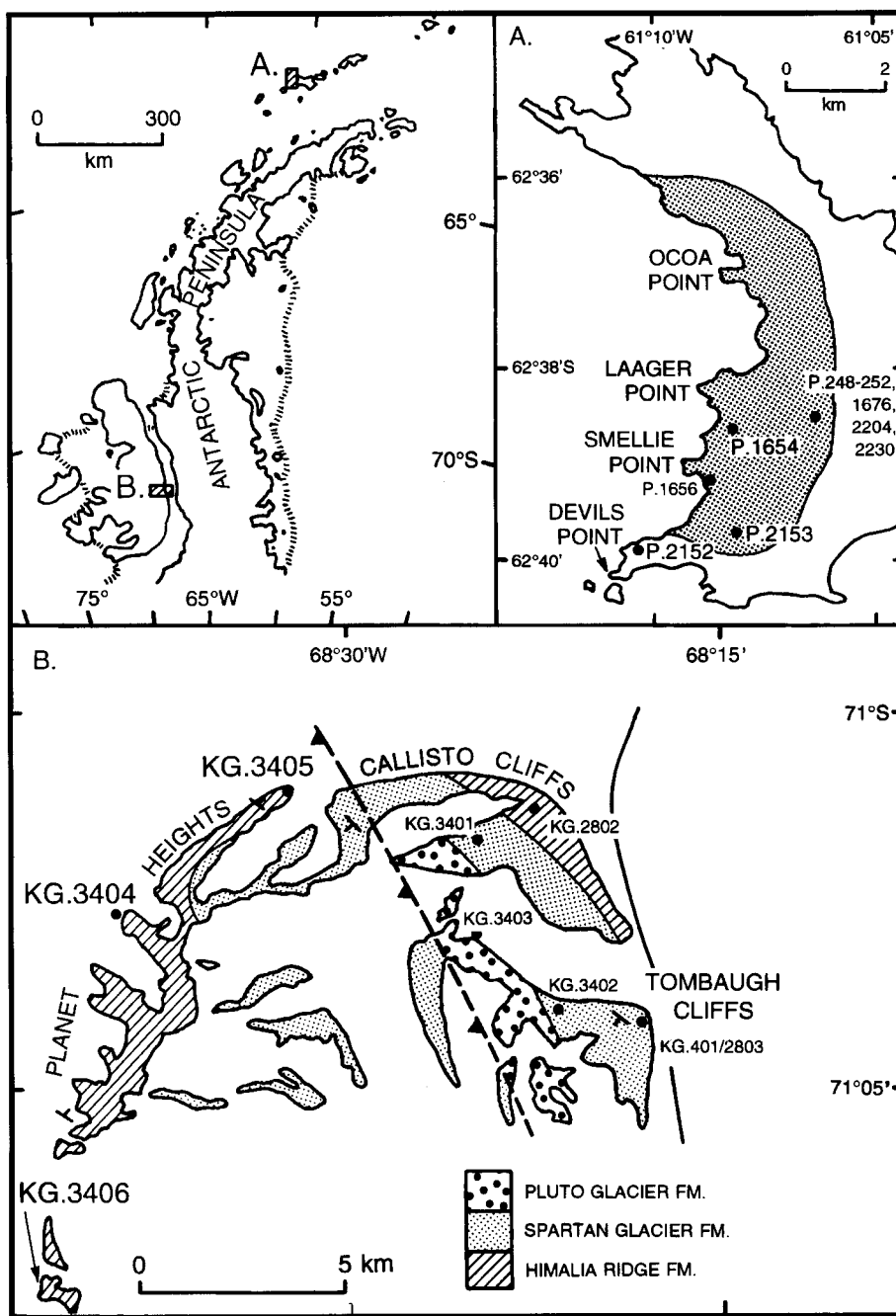
Derivation of name. Latin: *prae* (in front of: a forerunner), referring to the fact that this taxon may well be an ancestor of the well known oxytomid genus, *Aucellina*. Gender feminine.

Type species. *Praeaucellina umbonoradiata* gen. et sp. nov.

Other species. The genus is monotypic.

Diagnosis and remarks. As for the type species, see below.

Occurrence. Lower Cretaceous (Berriasian) of the Byers Group, western Livingston Island, and Upper Jurassic (Tithonian)–Lower Cretaceous (Berriasian) of the Fossil Bluff Group, Alexander Island; both these localities lie off the west coast of the Antarctic Peninsula. Further details given below.



TEXT-FIG. 2. Locality map for the Antarctic Peninsula region. Inset A shows the western margins of Byers Peninsula, Livingston Island, South Shetland Islands. Shaded area represents the outcrop of the President Beaches Formation; more extensive geological map given in Crame *et al.* (1993). Inset B shows localities within the Fossil Bluff Group of eastern Alexander Island. The Jurassic-Cretaceous boundary is located within the Himalia Ridge Formation (see also Crame and Howlett 1988, fig. 1).

Praeacellina umbonoradiata gen. et sp. nov.

Text-figures 4A-S, 5A-B, 6A-B

- vp 1984 *Otapiria* sp. nov. 1; Crame, pl. 2, fig. 6 (*non* pl. 2, fig. 5).
 v. 1984 *Otapiria* sp. nov. 2; Crame, pl. 2, figs 3-4.
 v. 1984 *Buchia* sp. nov. (small form); Crame and Howlett, fig. 10b-c.

Derivation of name. Latin: *umbo*; *radiata* (radiate, bearing rays); referring to the common restriction of fine, radial ornament to the umbonal regions of the shell.

Type material. Holotype: P.250.36 (Text-fig. 4A; internal mould LV). Paratypes: P.248.9; P.250.3b, 4, 6a-c, 8, 10, 11a-d, 14, 17a, b, 31-32, 34, 38-41, 44-45, 55, 64, 176; P.251.2a-c; P.252.3, 5; P.1654.33, 36, 45; P.1656.14, 24, 30-31, 39, 47, 51, 53, 70, 72, 75-78, 80, 82-84, 86-87; P.1676.1a-b, 2-4, 7-9, 14-16, 25; P.2152.20; P.2153.11, 21-23, 26-27, 31-32, 34, 37, 53-54, 56, 57b, 61, 90-129; P.2204.7, 9-10, 11a-c, 13, 15; P.2230.7, 9, 21, 23; KG.2802.346-348, 501-503, 516, 518-519, 530, 547, 553, 560, 570, 610; KG.2803.6, 31, 37, 47, 59, 65; KG.3404.302-306, 308-311, 313, 388, 415, 418a-b, 450; KG.3405.8.

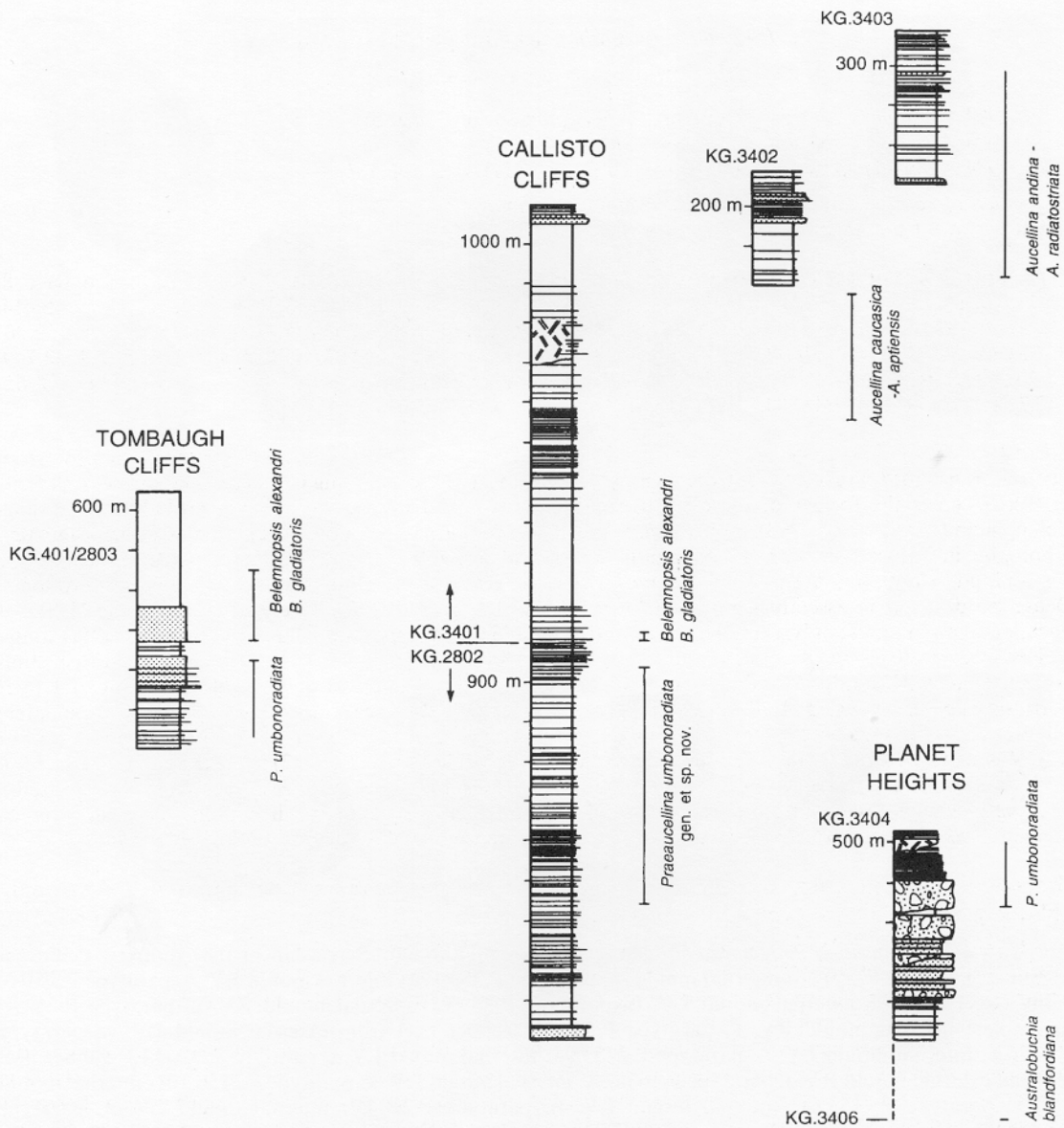
Most of the specimens prefixed by 'P.' are from the President Beaches Formation, Byers Group, western Livingston Island; however, those from locality P.2152 are from the overlying Chester Cone Formation (Text-fig. 2). Whereas the former of these stratigraphical units is Berriasian, the latter is probably Berriasian-Valanginian (Crame *et al.* 1993). *Praeacellina umbonoradiata* gen. et sp. nov. occurs in mudstone-dominated lithologies in association with a bochianitid-spiticeratid ammonite assemblage and bivalves such as the pergamidiid *Manticula*, a small *Inoceramus*, nuculids, grammatodontids and several small heterodonts. Dense bedding plane assemblages in the lower levels of section P.2153 were nucleated on the shafts of bochianitid ammonites; only a small, representative sample of these specimens has been included in this study.

Specimens prefixed by 'KG.' are from the uppermost levels of the Himalia Ridge Formation, Fossil Bluff Group, eastern Alexander Island (Text-fig. 2). These levels are of undifferentiated Upper Tithonian-Upper Berriasian age (Crame and Howlett 1988). At locality KG.2802 the specimens occur between approximately 338-925 m in the measured section; at KG.2803 they occur within the lower 200 m of the section, and at KG.3404 between 438-528 m. KG.3405 is an isolated spot locality (Text-figs 2-3) (Crame and Howlett 1988). In Alexander Island, *Praeacellina umbonoradiata* gen. et sp. nov. occurs in association with a berriasellid ammonite-belemnopseid belemnite assemblage. Prominent co-occurring bivalves include *Retroceramus everesti* (Oppel), *Grammatodon*, *Pinna*, *Entolium* and other taxa suggestive of a mid- to outer-shelf setting.

Diagnosis. Small-medium oxytomid; LV varies in outline from rounded-quadrate to strongly obliquely elongate; LV typically only weakly inflated and non-gryphaeoid; RV subrounded to obliquely elongate; tiny RV ear is blade-like and tilted strongly inwards towards LV; deep, curving byssal notch and pseudoctenolium; essentially alivincular ligament; generally subdued concentric ornament, but fine, sharp radial ribs which are concentrated over the umbonal region.

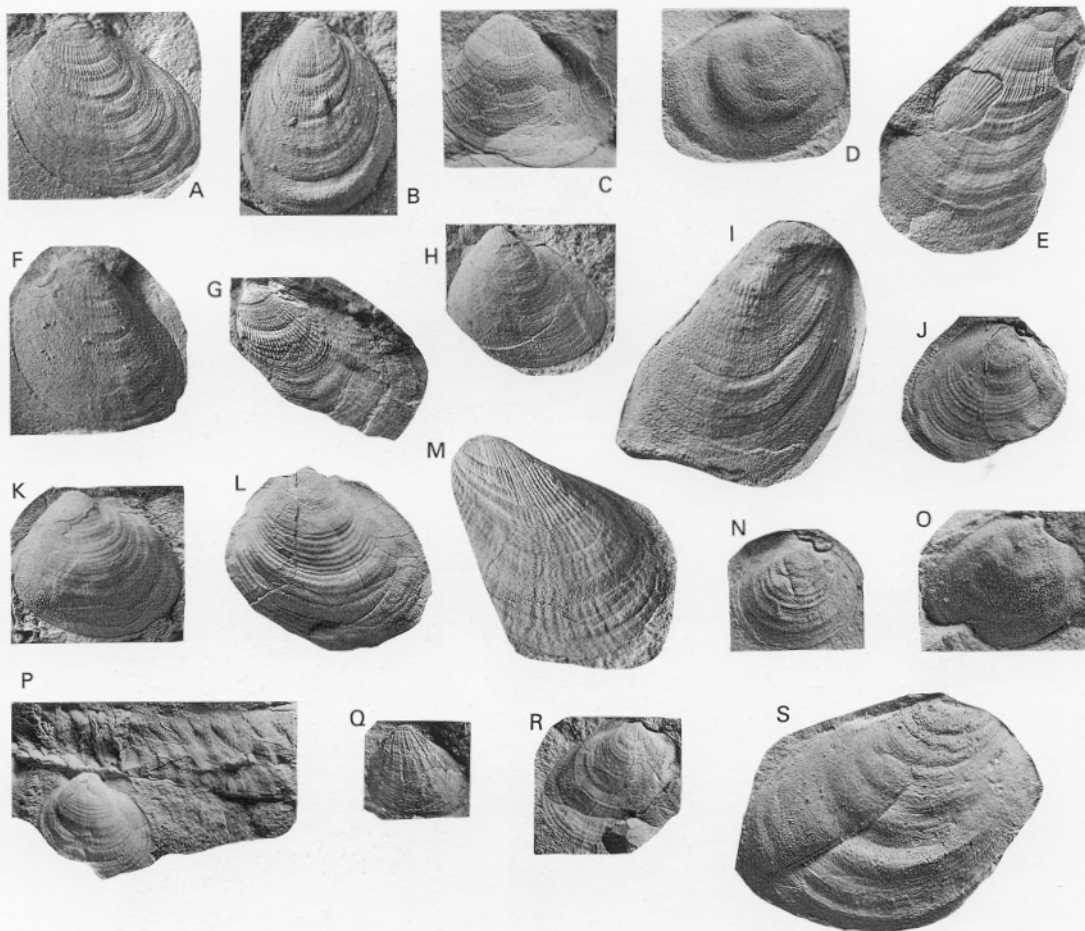
Description. Small-medium sized (for an oxytomid). Mean shell length (L , the distance from the beak to the maximum extremity of the ventral margin) of LVs is 11.9 mm (S.D. = 5.7 mm, $N = 95$), and for rights is 11.8 mm (S.D. = 5.2 mm, $N = 95$). The inequivalve nature of the shell is reflected in the somewhat narrower LV (as defined by the width, W , the maximum dimension perpendicular to L ; $\bar{x} = 9.3$ mm, S.D. = 4.2 mm, $N = 95$) compared with RV ($\bar{x}W = 10.8$ mm, S.D. = 4.2 mm, $N = 95$). These respective widths are significantly different (Student's t -test, $0.01 < P < 0.05$), as are the respective W/L ratios ($\bar{x}W/L$ LV = 0.74, S.D. = 0.2 mm, $N = 95$; $\bar{x}W/L$ RV = 0.9, S.D. = 0.2 mm, $N = 95$) ($P < 0.001$). All specimens preserved as internal or external moulds; however, some bear fragments of original shell material.

The largest LVs are typically moderately to strongly obliquely elongate. From a prominent, pointed beak, which rises above the hingeline and ranges from orthogyrous to slightly opisthogyrous, there is a straight to gently convex antero-dorsal margin which passes into well-rounded antero-ventral and ventral margins. The postero-dorsal margin is typically straight to gently rounded and may delineate a narrow wing (e.g. Text-fig. 4H, L). Smaller (i.e. juvenile) left valves often have a more rounded-quadrate profile; indeed, in some of these there is even a tendency to develop a small antero-dorsal wing. These same small specimens are typically more strongly and evenly inflated than the larger ones (e.g. Text-fig. 4K-L). Left valve ornament comprises a combination of very fine radial ribs and low concentric folds. The radial ribs are so fine on many specimens (< 0.3 mm) as to qualify for description as striae; this is particularly so in the earliest stages of some specimens



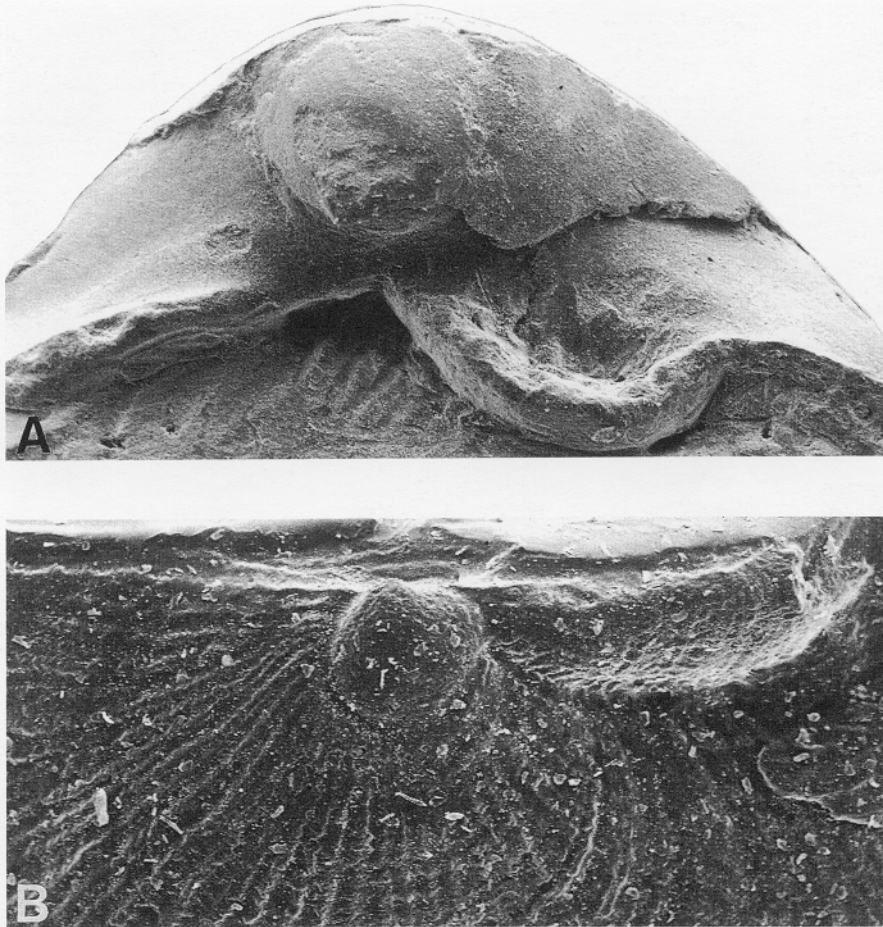
TEXT-FIG. 3. Stratigraphical correlations within the Fossil Bluff Group of eastern Alexander Island. *Praeacellina umbonoradiata* gen. et sp. nov. occurs consistently beneath the earliest representatives of *Aucellina*. The boundary between the Himalia Ridge and Spartan Glacier formations occurs at the junction between sections KG.2802 and KG.3401 at Callisto Cliffs; that between the Spartan Glacier and Pluto Glacier formations occurs at 1050 m in section KG.3401 (Callisto Cliffs) (see also Crame and Howlett 1988, fig. 9).

where very narrow secondaries occur intercalated between more prominent primaries (e.g. Text-fig. 4A-C). Superficially, the radial ribs appear to be more or less straight, but closer inspection reveals regular displacement where they cross concentric folds or depressions. They are confined essentially to the umbonal region of the valve (e.g. Text-fig. 4A-C, F-G). Concentric ornament comprises very fine growth lines which are only occasionally developed into moderately strong, regular rugae (e.g. Text-fig. 4L). In addition, broader concentric furrows, linked to distinct growth pauses, are variably developed.



TEXT-FIG. 4. *Praeacellina umbonoradiata* gen. et sp. nov.; Tithonian–Berriasian of the Antarctic Peninsula region. A, holotype P.250.36; internal mould. B, paratype P.250.17a; internal mould LV. C, paratype P.251.2; rubber peel from an external mould LV. D, paratype P.250.45; internal mould RV. E, paratype P.250.4; incomplete internal mould RV. F, paratype P.250.31; rubber peel from external mould LV. G, paratype P.1676.1; internal mould LV. H, paratype P.2153.95; internal mould LV. I, paratype P.2204.13; rubber peel from an external mould RV. J, paratype P.1656.83; internal mould RV. K, paratype P.2153.101; internal mould LV. L, paratype P.2153.61; internal mould LV. M, paratype P.2204.7; internal mould LV. N, paratype P.1656.72; internal mould RV. O, paratype KG.3404.311; internal mould RV. P, paratype P.2153.132; internal mould LV attached to the shaft of a *Bochianites* ammonite. Q, paratype P.1656.30; internal mould of a juvenile LV. R, paratype P.2153.122; internal mould RV. S, paratype, rubber peel from an incomplete external mould RV (P.250.8). All specimens from the Berriasian President Beaches Formation, Byers Group, western Livingston Island, except O which is from the Tithonian–Berriasian Himalia Ridge Formation, Fossil Bluff Group, eastern Alexander Island. All specimens $\times 1.5$, except O which is $\times 3$.

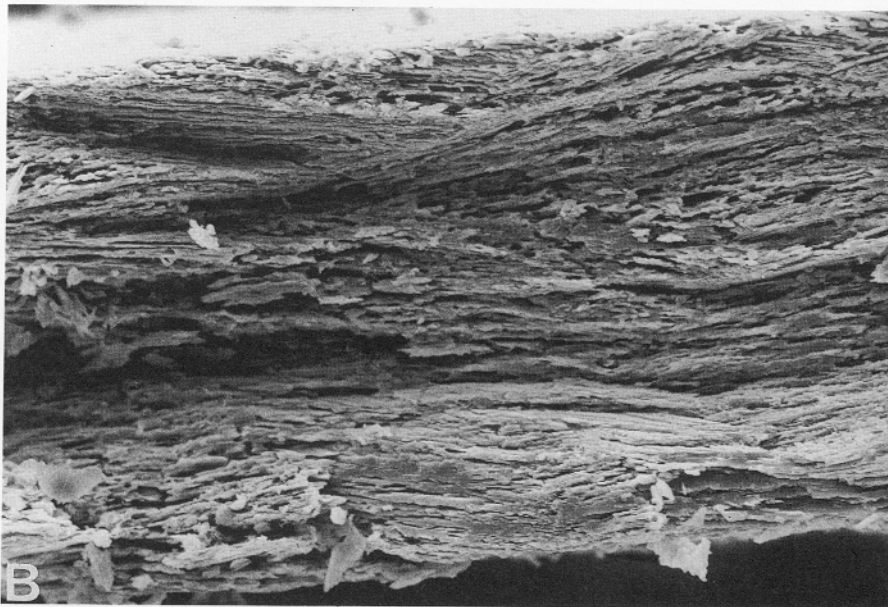
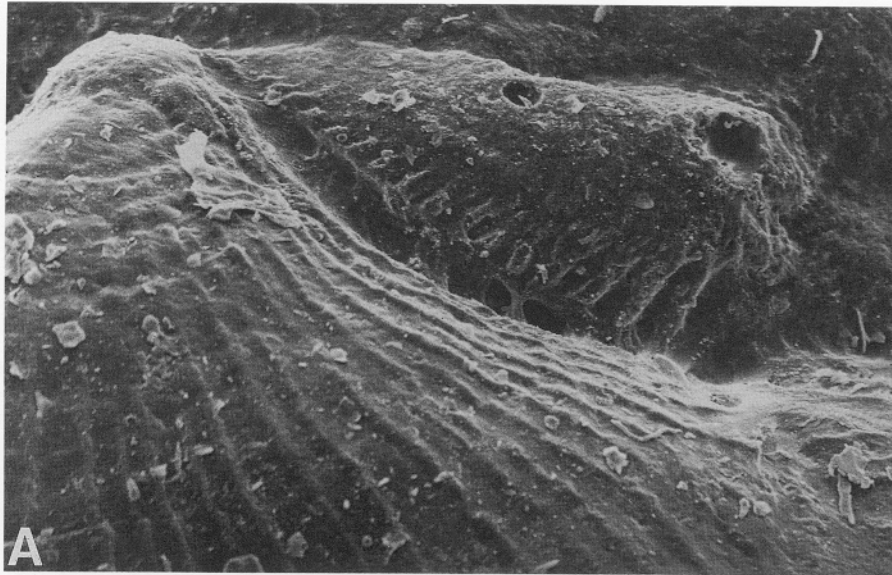
Right valve outlines vary from strongly obliquely elongate (e.g. Text-fig. 4E, I) to those which are considerably more rounded (e.g. Text-fig. 4J, N–O). In the latter forms the anterior margin is noticeably shorter and more convex, and there is a narrowly demarcated postero-dorsal wing. Right valves are typically slightly less inflated than left valves and many bear only traces of faint concentric ornament. However, the distinctive radial ornament is present on a number of both small and large specimens; it is again restricted largely to the umbonal region (Text-fig. 4E, I). The most distinctive feature of the right valve is a tiny antero-dorsal ear.



TEXT-FIG. 5. The hinge region of *Praeaucellina umbonoradiata* gen. et sp. nov. A, P.2153.133; left valve hinge region viewed from the inside and slightly from above. The posterior portion of the hinge (to the left) is relatively straight, but the anterior takes the form of shallow, sinusoidal curve. Initially, the anterior portion resembles a protruding lobe, with a concave depression on its upper surface; it then passes into a curving, recessed area. SEM, $\times 30$. B, P.2153.134; right valve hinge region, viewed from the outside and slightly from above. In a fully articulated specimen, the anterior ear (to the right) fits against and beneath the prominent bulge in the anterior region of the LV hinge. The apex of a broad, triangular resiliifer is located just beneath the top of the cap-like prodossoconch. SEM, $\times 65$.

Commonly no more than about 1.5 mm long, this feature takes the form of a gently curving blade which is tilted strongly inwards so that its upper surface comes to lie against, and largely underneath, the anterior region of the left valve hinge (Text-figs 4N, 5). The latter typically has a sinusoidal form, bulging out initially at its point of contact with the right valve ear and then curving inwards. The upper surface of the sinusoidal bulge may take the form of a shallow depression (Text-fig. 5A). As far as can be detected, the hinge and ligament surface of the left valve are essentially smooth; no form of tooth or socket has been detected.

In the right valve it is apparent that the ligament area extends along the dorsal surface of the ear, almost to its extremity. In its centre there are traces of a distinct, obtuse-angled triangular pit (or resiliifer), the apex of which lies directly beneath the beak (as marked by a smooth, cap-like prodossoconch of some 250 μm diameter) (Text-fig. 5B). The sides of the pit diverge away from the beak at an angle in excess of 130° and its



TEXT-FIG. 6. *Praeacellina umbonoradiata* gen. et sp. nov. A, P.2153.135; enlargement of the RV anterior ear to show pseudoctenolium. The latex peel from an external mould shows a broad, blade-like ear expanding from the beak region. The row of teeth-like ridges and sockets forming the pseudoctenolium is located along the ventral margin of the ear; they abut a deep, channel-like byssal notch which curves in sinusoidal fashion from the beak to the free tip of the ear. SEM, $\times 100$. B, P.2153.136; fragment of original shell material from the central region of a LV. Section normal to the shell surface (uppermost) to show crossed-foliated shell structure. SEM, $\times 1000$.

base may be slightly curved. The right valve ligament would thus appear to conform to the classic alivincular form; further details of the left valve ligament are not yet known. The right anterior ear is clearly separated from the main disc of the shell by a narrow and deep byssal notch. This can be traced from the anterior tip (where it is at its widest) to the prodissoconch, and on its upper border (i.e. the ventral surface of the ear) there is a distinct comb-like row of teeth (Text-fig. 6A). These constitute a pseudoctenolium (*sensu* Waller 1984).

Original shell material is preserved on a number of small specimens, especially from locality P.2153 (Text-fig. 2A). Unfortunately, this is nearly all in a poor state of preservation and it has not yet been possible to examine variation in shell structure on a systematic basis. The dominant material, on both left and right valves, is a form of crossed-foliated calcite in which rather poorly defined first order lamellae intersect at a comparatively low angle (Text-fig. 6B). No trace of a prismatic calcite layer or any form of aragonite has yet been found in either valve.

Remarks. The general form of this bivalve links it firmly with the superfamily Monotoidea, and the spatulate, strongly inclined right valve ear suggests particular affinity with the Oxytomidae. Such a connection is strengthened by the presence of a pseudoctenolium, which is also present in both *Oxytoma* Meek (?Olenekian–Danian) and *Aucellina* Pompeckj (Barremian–Cenomanian) (Cox 1940; Duff 1978; Waller 1978, 1984). *Praeaucellina* is particularly similar to the latter form, but may be distinguished consistently by the following criteria: its smaller size (*Aucellina* typically having a shell length in the 20–30 mm range); the less strongly inflated and less gryphaeoid form of the left valve; restriction of radial ornament to essentially the umbonal region of both valves (for comparative *Aucellina* specimens see Cox 1953, pl. 1, figs 1–10 and Macellari 1979, pls 1–2). Nevertheless, it should be stressed that, in form alone, right valves of the two genera are very similar. There are some valves too (e.g. P.2204.7; Text-fig. 4M), in which radial ornament does indeed stretch across the entire width of the valve; such forms are very difficult to separate from small *Aucellina*.

The presence of dense radial ornament on a number of specimens also raises the question of allegiance with another monotoidean family, the Monotidae Fischer (?Carnian–Tithonian; Table 1). Although generally held to be readily distinguishable by their thinner-shelled and less inflated form, stronger radial ornament and tiny right valve ear, it is apparent that representatives of this taxon do show considerable morphological overlap with the Oxytomidae; this is particularly so for the finely ribbed members of the genus *Otapiria* Marwick. Indeed it is not easy, at first sight, to separate certain Jurassic species of *Otapiria*, such as *O. marshalli* (Trechmann 1923, pl. 15, figs 6–9) and *O. tailleuri* Imlay (1967, pl. 1, figs 1–23) from some Cretaceous *Aucellina* (see e.g. Cox 1953, pl. 1, figs 1–9). *Otapiria* can be distinguished from *Praeaucellina* by its shape, more variable valve outlines (especially LV), and stronger radial ornament; nevertheless, the differences here are by no means profound.

Recent observations on the hinge region of both *Monotis* (*sensu lato*) and *Otapiria* have revealed the presence of a subcentral, triangular resilifer, and a tiny, blade-like ear in the right valve which is strongly inclined towards the left (Ando 1987, 1988; Grant-Mackie and Silberling 1990). Furthermore, it is apparent that both genera are characterized by a pseudoctenolium (e.g. Marwick 1935, pl. 34, fig. 4; Ando 1988, fig. 4). There would appear to be very close phylogenetic ties between the Monotidae and Oxytomidae (see below).

SOME STRATIGRAPHICAL AND PHYLOGENETIC CONSIDERATIONS

Associated macro- and microfossils confidently establish the age of *Praeaucellina umbonoradiata* gen. et sp. nov. in the President Beaches Formation, Byers Peninsula as Berriasian (Crame *et al.* 1993). Furthermore, all known occurrences of this species lie beneath the Valanginian ammonite-belemnite assemblage obtained from the Sealer Hill Member (Crame *et al.* 1993). The less well preserved specimens of *P. umbonoradiata* gen. et sp. nov. from Alexander Island are all located within the Upper Tithonian–Lower Berriasian upper levels of the Himalia Ridge Formation (Crame and Howlett 1988; Text-figs 2–3); again, all localities are below a distinctive Valanginian ammonite-belemnite assemblage in the base of the Spartan Glacier Formation (Text-figs 2 and 3).

The first occurrences of the genus *Aucellina* are within the higher levels of the Spartan Glacier Formation (Text-fig. 3). Initially, these are finely ribbed forms that are referred provisionally to an *A. caucasica* (Abich)–*A. aptiensis* d'Orbigny species group (?Barremian in age); these in turn lie stratigraphically below the more familiar southern forms, *A. andina* and *A. radiatostrata* (Aptian–Albian; Cox 1953; Crame and Howlett 1988). The long stratigraphical sections of eastern Alexander Island confirm that *Praeaucellina* is the older taxon and in phylogenetic terms it is the very probable ancestor of *Aucellina*.

The possible ancestral relations of *Praeaucellina* are less clear. Within the Jurassic Oxytomidae, *Oxytoma* is the most realistic putative ancestor as it has a closely comparable hinge region and right valve anterior ear. *Arctotis*, in comparison, has a somewhat broader and thicker hinge, and a different style of ornament; it would seem to be more closely related to the Aptian–Albian genus, *Maccoyella* (Crame 1985). An alternative link between *Praeaucellina* and the Monotidae could be established through the occurrence of taxa such as *Otapiria masoni* Marwick (1953, pl. 11, figs 10–11) in the Ohauan (Tithonian) of New Zealand. However this sole Late Jurassic representative of the Monotidae is still poorly known and its precise taxonomic status needs to be confirmed. In the Himalia Ridge Formation of eastern Alexander Island (Text-fig. 2), *Praeaucellina umbonoradiata* gen. et sp. nov. may occur only a few hundred metres above the last records of *Australobuchia blanfordiana* (Stoliczka) (Text-fig. 3). Unfortunately, the hinge region of this form too, is still imperfectly known and it is not yet possible to distinguish clearly between the southern buchiids and oxytomids.

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