NEW LATE JURASSIC OXYTOMID BIVALVES FROM THE ANTARCTIC PENINSULA REGION

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ABSTRACT. Oxytomids were an important group of late Mesozoic epifaunal bivalves at high latitudes in the Southern Hemisphere. Morphologically distinct (both externally and internally) from the closely related buchiids, they were particularly conspicuous from the Kimmeridgian to Albian stages. Their presence in the late Jurassic of Antarctica is enhanced by the widespread occurrence of forms that can be confidently assigned to the distinctive Siberian genus, *Arctotis*. A new species of *Arctotis* (*A. australis* sp.nov.) is erected and shown to be clearly separable from approximately coeval specimens of the genus *Malayomaorica* (*M.* sp.nov.?). The occurrence of *Arctotis* in Antarctica adds further weight to the concept of a late Jurassic bi-polar bivalve fauna.

INTRODUCTION

As research has progressed into the late Mesozoic bivalves of the Antarctic Peninsula region, it has become apparent that many epifaunal groups have considerable stratigraphic potential. Besides the inoceramids and buchiids, which are the types most widely used in correlations, oxytomids and certain closely related forms are also proving to be of some importance. Oxytomids (i.e. members of the family Oxytomidae) are typically small to medium in size, rounded to obliquely oval in outline and moderately to strongly equivalve (LV always more inflated than RV). They bear various combinations of radial and concentric ornament but perhaps their most characteristic feature is a small ear and byssal notch in the antero-dorsal region of the right valve. Representatives of the Oxytomidae which have been recorded so far in the Antarctic Peninsula include the late Jurassic (Kimmeridgian–Tithonian) genus *Malayamaorica* (Crame, 1983*a*; see also Jones and Plafker, 1976; Jeletzky, 1983) and the early Cretaceous (Aptian–Albian) genera *Aucellina* and *Maccoyella* (Crame, 1983*b*; anonymous, 1983).

Recent field work has shown that oxytomids are particularly common at approximately the level of the Jurassic–Cretaceous boundary. They occur extensively in the late Jurassic to earliest Cretaceous Nordenskjöld Formation (and its stratigraphic equivalents) as well as overlying early Cretaceous (Berriasian–Valanginian) volcaniclastic sandstones and conglomerates (Farquharson, 1983; Crame and Farquharson, 1984). In this study a group of specimens from the Nordenskjöld Formation will be described and shown to have their closest affinities with the Siberian genus, *Arctotis* Bodylevsky, 1960. Two further specimens, from an approximately equivalent stratigraphic level in the Fossil Bluff Formation of Alexander Island, will then be described and shown to be closest to the exclusively Southern Hemisphere genus, *Malayomaorica*. *Arctotis* is clearly distinct from *Malayomaorica* and represents an important addition to our knowledge of Southern Hemisphere oxytomid bivalves.

As there has in the past been some confusion over the precise identity of oxytomids, the systematic section of this paper is prefaced by a discussion of their distinguishing features. For the purposes of Southern Hemisphere Mesozoic palaeontology it is particularly important to separate them from the buchiids, a group which apparently shows remarkably convergent morphologies. It is also necessary to briefly discuss the salient features of *Arctotis* and show that it is a valid generic category.

Definition of Oxytomid Bivalves

In the past it has been common practice in Mesozoic palaeontology to collectively refer small, inequivalve forms with a distinct byssal ear and notch on the right valve to categories such as the 'pterioids' (from the order Pterioida) or 'pectinaceans' (from the superfamily Pectinacea). However, since the publication of the *Treatise on Invertebrate Palaeontology* (Cox, 1969), a major revision of pteriomorph bivalves has been undertaken by Waller (1978) and it is apparent that the aforementioned types should now be assigned to the superfamily Buchiacea (order Ostreoida; suborder Pectinina).

In terms of gross shell morphology, buchiids and oxytomids are perhaps most readily separated by the form of their respective left valves. Whereas buchiids are invariably obliquely elongated (with respect to a horizontal hinge), oxytomids are generally much more upright and symmetrical (about an axis passing from the umbo to the extremity of the ventral margin). This difference is due to the presence of a low, rounded anterior wing on many oxytomids and its complete absence in buchiids. Viewed from the inside, it can be seen (Figs. 1a, d) that in buchiids the cardinal plate (bearing the hinge and ligament area) lies almost entirely to the posterior of the beak (i.e. the tip of the umbo), but in oxytomids a substantial part of it may be situated in front of the same feature, where it occupies the inner surface of the anterior wing. From the same viewpoint it can be seen that the buchiid beak is separated from the hingeline and protrudes over it.

The surface of the cardinal plate of the buchiid left valve bears a faintly to moderately impressed ligament pit (resilifer) which has an elongate-triangular form and tapers posteriorly (Fig. 1a). It is often bounded anteriorly by a narrow ridge which obliquely traverses the width of the plate. Directly in front of this ridge there is a short, deep excavation into the hinge margin which is often referred to as the *Gelenkgrube* (Pompeckj, 1901). Hoof-shaped in plan view and with near vertical walls, this cavity articulates with the tip of the right valve's anterior ear (Pompeckj, 1901; Pavlov, 1907; Zakharov, 1981). The resilifier in oxytomids may also be asymmetrically triangular, but it is more often oval or even rounded in outline (Pompeckj, 1901; Woods, 1905; Pavlov, 1907; Jeletzky, 1963, 1964; Marwick, 1966; Cox, 1969; Kauffman, 1976; Fig. 1d). Situated close to the centre of the cardinal plate, the resilifer is typically moderately to deeply impressed and may bear raised margins. In some forms the pit is bordered anteriorly by a tooth-like bulge of the plate's lower margin and it is possible that this projection could have articulated with the concave inner surface of spatulate right valve ears (e.g. Pompeckj 1901, pl. xv, figs. 7 and 15; Jeletzky, 1964, pl. xviii, figs 3C and 4C; Begg and Campbell, in press).

The most obvious difference between buchiid and oxytomid right valves lies in the nature of their anterior ears. In buchiids the ear is a comparatively small, rounded feature with a spoon-shaped to conical profile (Figs. 1b, c). The smooth, plano-convex exterior and concave, excavated interior indicate that it has been gently to strongly folded about the curving growth axis. It invariably projects upwards above the line of the hinge margin and inwards towards the left valve; in its most extreme form this latter trait is exhibited by a bend of as much as 90° (e.g. Pompeckj, 1901; Jeletzky, 1963; Jones and Plafker, 1976; Zakharov, 1981; Figs. 1b, c). In comparison with this buchiid ear, the oxytomid one is longer and flatter and, although sometimes gently

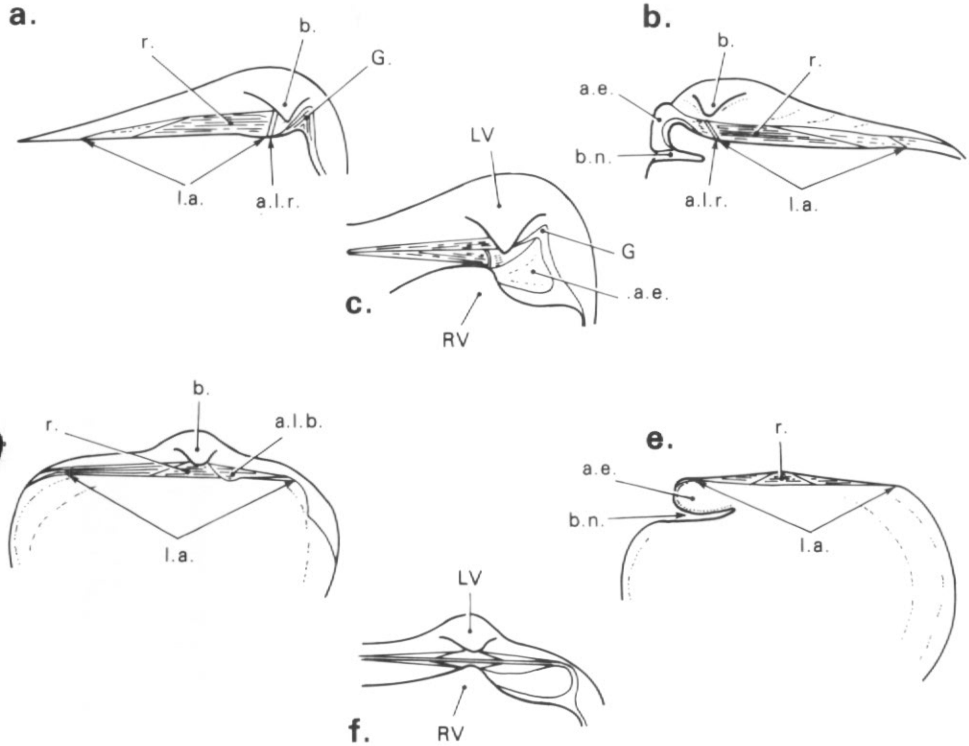

Fig. 1. Comparison of the hinge and ligament areas of buchiid (a–c) and oxytomid (d–f) bivalves. a. internal view buchiid left valve (LV), b. internal view buchiid right valve (RV), c. external view of partially articulated buchiid, d. internal view oxytomid LV, e. internal view oxytomid RV, f. external view of partially articulated specimen. Key: a.e. anterior ear, a.l.b. anterior ligament bulge, a.l.r. anterior ligament ridge, b. beak, b.n. byssal notch, G. *Gelenkgrube*, l.a. ligament area, r. reslifier. Based on illustrations given in. Pompeckj, 1901; Woods, 1905; Jeletzky, 1963, 1964; Cox, 1969; Zakharov, 1981.

flexed, is never strongly folded (Figs. 1e, f). Its dorsal margin is in alignment with the hinge (or very nearly so) and there is typically very little deflection inwards towards the left valve. A good description of it would be as a rounded blade (Pompeckj, 1901; Woods, 1905; Pavlov, 1907; Jeletzky, 1963, 1964; Marwick, 1966; Cox, 1969; Figs, 1e, f).

In a number of oxytomids the whole ear is tilted so that it dips inwards (with respect to the vertical plane of commissure); the degree of this tilt varies from only slight, as in some forms of *Oxytoma*, *Meleagrinella* and *Aucellina* (e.g. Woods, 1905, pl. x, fig. 9b; Duff 1978, text-fig. 18b; Begg and Campbell, in press), to the pronounced condition seen in some species of *Arctotis* and *Maccoyella* where it dips very steeply inwards (e.g. Etheridge, Jr., 1902, pl. 1, fig. 4; Zakharov, 1966, pl. IV, fig. 3b). The anterior ear of oxytomids rests snugly against the anterior portion of the left valve's cardinal plate which may occasionally be developed into a shallow sulcus (Fig. 1f); however, this feature is in no way analogous to the buchiid *Gelenkgrube*. In front of this sinus a slight swelling of the valve margin may be present and in *Malayomaorica* this is often developed into a pronounced callus (e.g. Jeletzky, 1963; Crame, 1983*a*).

The extent to which the inner surface of the anterior ear articulates with tooth- or ridge-like protruberances in the left valve hinge area within the Oxytomidae has yet to be fully determined. *Malayomaorica* possess a further means of articulation wherein the posterior end of a transverse ridge on the dorsal surface of its ear slots into a left valve resilifer which has been modified into an oblique groove (Jeletzky, 1963, pl. 21, figs. 1F and 2F; Crame, 1983*a*, fig. 2d). This transverse ridge appears to be a modified anterior border to the resilifer and may also be present in the genera *Arctotis*, *Meleagrinella* and *Aucellina* (Jeletzky 1963, p. 157; see e.g. Bodylevsky, 1960, pl. 7, figs. 2a, b).

The ligament area on the buchiid right valve has a narrow, elongate-triangular form very similar to that of the left valve (Figs. 1a, b). A central triangular resilifer is usually clearly visible beneath the beak and this too is bounded anteriorly by a narrow, transverse ridge. The ligament area may continue in front of this ridge onto the base of the ear, but it obviously does not extend for any great distance along its dorsal surface (Figs. 1b, c). Whereas the ligament area of the left valve is approximately parallel to the plane of commissure, that of the right is usually orientated perpendicular, or at a steep angle, to it. This means that the ligament was often external for at least part of its length. A similar, although somewhat broader, alivincular ligament arrangement is present on the oxytomid right valve. The principal difference between the two groups is that in the latter it extends considerably further forward and it is evident that the anterior ear acted as a major structural support for the ligament (e.g. Pompeckj, 1901; Woods, 1905; Cox, 1969; Begg and Campbell, in press;Figs. 1e, f). The attitude of this ligament plate varies from approximately normal to the plane of commissure to an acute angle towards it. In those forms where the blade-like ear dips steeply inwards, the corresponding left valve ligament area is curved forwards to directly overhang it (e.g. Etheridge, Jr., 1902, pl. 1, fig. 8; Zakharov, 1966, pl. IV, fig. 3b); presumably, this arrangement maintained articulation between the valves and reduced the area of exposed ligament. The byssal notch beneath the anterior ear is generally slightly longer and wider in oxytomids than in buchiids. In this group it may or may not be flanked by a true ctenolium (Kauffman, 1976; Jones and Plafker, 1976; Waller, 1978).

In buchiids, concentric ribs and fine radial striae are present on both valves. Radial ornament is much more strongly developed in oxytomids, sometimes in combination with concentric ornament (to form a distinctive cancellate pattern), and sometimes in its complete absence. These radial ribs usually exhibit several orders of strength and may be markedly wavey in their course. On many oxytomids, only the left valve bears strong ornament (Cox, 1969).

Although monotids such as *Monotis* (*Monotis*), *Monotis* (*Entomonotis*) and *Otapiria* are usually readily distinguishable by the density of their radial ornament and small size of the right anterior ear, it is apparent that their outline and valve form closely resembles both buchiids and oxytomids. Similarities to the former of these groups are enhanced by the slightly folded and oblique right anterior ear, as well as narrow triangular ligament areas situated entirely behind the beaks (e.g. Marwick 1935, pl. 35, figs. 15–24). On the other hand, similarities to oxytomids are suggested by the wavey nature of the radial ribs in many species and the narrow left valve hinge area which sometimes bears a distinct bulge at the anterior end of the resilifer and a shallow sulcus directly in front of this (e.g. Marwick, 1935, pl. 36, figs. 31, 34 and 35; Begg and Campbell, in press). Zakharov (1981, p. 42 and fig. 24) has postulated that *Otapiria* may be the direct ancestor of *Buchia*.

It is concluded that the only Southern Hemisphere late Mesozoic genera which can be confidently assigned to the Buchiidae are *Buchia* (which here includes *Australobuchia* of Zakharov, 1981) and, probably, *Jeletzkiella* Jones and Plafker (1976, p. 847, pl. 2, figs. 1–7, 9, 12–15). *Malayomaorica*, *Arctotis*, *Aucellina*, *Maccoyella* and *Pseudavicula* are all regarded as belonging to the Oxytomidae, and *Otapiria*, which has recently been recognized in the Antarctic Jurassic–Cretaceous boundary succession (Crame, 1984), is provisionally retained within the Monotidae (*sensu* Imlay 1967; Covacevich and Escobar, 1979; Begg and Campbell, in press). Of these assignments, the most contentious is probably that of *Malayomaorica* to the Oxytomidae rather than the Buchiidae. Although this is a matter which perhaps cannot yet be fully resolved, it would appear that the right anterior ear of this genus is typically a large blade-like feature which partially supports the ligament and fits snugly into the pre-umbonal part of the left valve's ligament plate (e.g. Wandel, 1936, pl. XVII, fig. 4c). This feature, together with the general form of the valves and ornament pattern (which are fully described in Jeletzky (1963) and Crame (1983*a*)), suggest greater allegiance to the Oxytomidae than any other available family.

Distinguishing Features of *Arctotis*

Arctotis is known almost exclusively from its occurrences in Lias (undifferentiated) to Hauterivian strata of northern Siberia. A single left valve has been described from the Middle-Upper Volgian beds in eastern England (Kelly, 1984) and the genus may possibly be present in Canada and DSDP material from both the Manihiki and Falkland plateaux (Jeletzky, 1963, 1983; Kauffman, 1976). However, our knowledge of both its external and internal features is based almost entirely on Russian material (e.g. Lahusen, 1886; Borissiak, 1915; Petrova, 1947; Bodylevsky, 1958, 1960; Koshelkina, 1963; Zakharov, 1966).

From small to very large (for an oxytomid), *Arctotis* is nearly always strongly inequivalve; the left valve has a more convex profile than the right and is usually slightly longer than it too (Figs, 2a–f). The left valve has a rounded-oval outline and many species tend to be bilaterally symmetrical about a line passing from the umbo to the mid-point on the ventral margin. Anterior and posterior wings are generally poorly differentiated, although in some forms a triangular posterior wing is delineated by a shallow radial furrow (e.g. Borissiak, 1915,pl. 11, fig. 12; Bodylevsky, 1958, pl. XV, fig. 2; Bodylevsky, 1960, fig. 17; Fig. 2a). The outline of this wing is usually accentuated by a shallow concave sinus at the point where the radial furrow meets the posterior margin. From the inside, the left valve can be seen to possess a comparatively long hingeline (at least half as long as the shell) and a broad rectangular ligament area (Fig. 2c, e). The subcentral resilifer is deeply impressed and varies in outline from broad and irregularly rounded (e.g. Bodylevsky, 1960; Jeletzky, 1963; Begg and Campbell, in press) to a somewhat narrower, slanting-triangular form (e.g. Zakharov, 1966; Kauffman, 1976). In many adult specimens the ligament area tilts inwards until it forms almost a right-angle with the plane of commissure. In this position it directly overhangs the dorsally projecting ligament surface on the right valve (e.g. Bodylevsky, 1960; pl. 7, fig. 1a; Zakharov, 1966, pl. IV. fig. 3b; Figs. 2c–f).

The presence of a triangular postero-dorsal wing, blunt protruding anterior region and large flat ear give the right valve a profile very similar to that seen in a number of aviculopectinid genera (such as the Triassic *Eumorphotis*; see, e.g. Cox, 1969, fig. C60.6b). Nevertheless, the hingeline is somewhat shorter than in the latter group and there is a much more prominent ligament area and resilifer (Figs. 2b, f; e.g. Bodylevsky, 1960; Koshelkina, 1963; Zakharov, 1966). It is obvious that the ligament area, which varies in attitude from steeply dipping to perpendicular (with respect to the plane of commissure), extends anteriorly onto the dorsal (or uppermost) surface of the anterior ear. Although somewhat variable in length, the ear is always

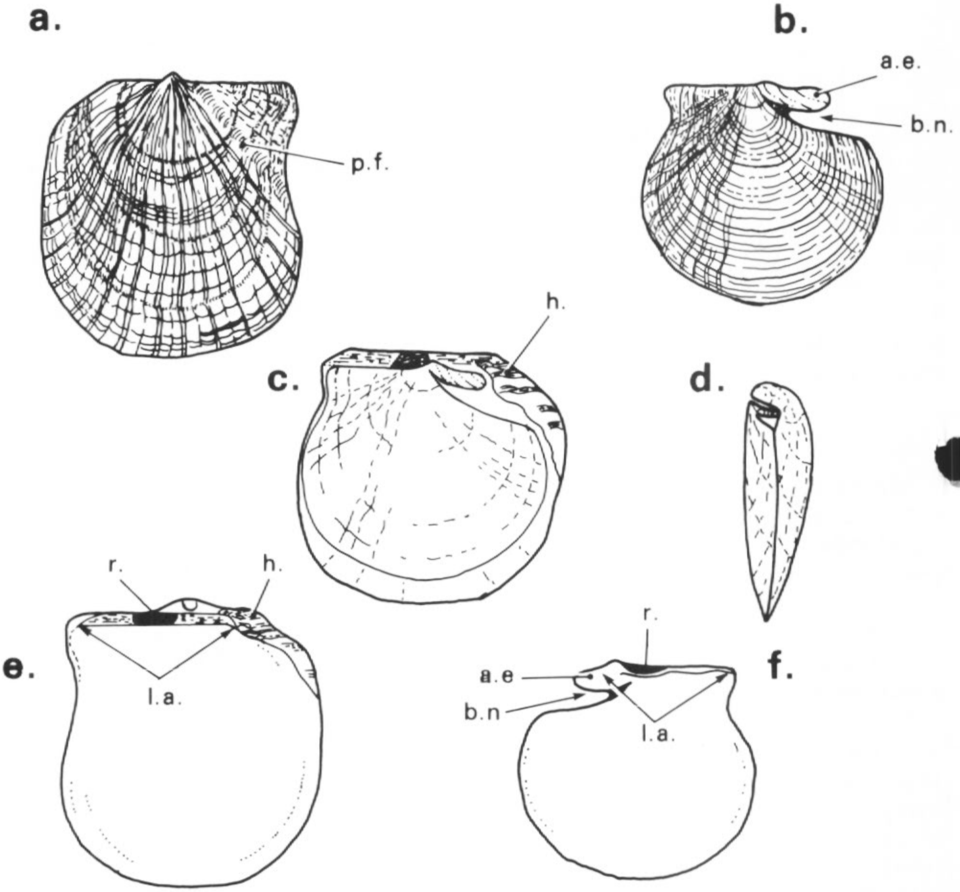

Fig. 2. Principal features of *Arctotis*. a. external view LV, b. external view RV, c. partially articulated specimen viewed from right side, d. anterior view of articulated specimen, e. internal view LV, f. internal view RV. Key: a.e. anterior ear, b.n. byssal notch, h. hood-like projection, l.a. ligament area, p.f. posterior furrow, r. resilifer.

comparatively broad and tilted moderately to strongly inwards; it may curve gently towards the left valve but it is never significantly bent upwards (Figs, 2b–d, f). It is uncertain whether the dorsal and inner surfaces of the anterior ear bear any projections which may have articulated with socket-like depressions in the ligament area of the left valve. Jeletzky (1963, p. 157) believed that a transverse ridge, similar to that seen in *Malayomaorica*, was present in at least some species (e.g. *A. intermedia*; Bodylevsky, 1960, pl. 7, figs. 2a, b; Zakharov, 1966, pl. III, figs. 12a, b), but it has yet to be shown that this feature occurs consistently throughout the genus. One particular problem would seem to be the nature of the left valve resilifer, which does not appear to have been modified for the reception of the right ear's transverse ridge, as in *Malayomaorica*.

Begg and Campbell (in press) detected the presence of a bulging tooth on the postero-ventral flank of the ear of *A. anabarensis* and suggested that this may have been accommodated in a corresponding recess in the left valve anterior ear. However, this too, may be a feature which is only sporadically developed in the genus and it is interesting to note that in a corresponding position near the base of the ear in *A. intermedia*, Bodylevsky (1960) found evidence of a well-defined pit (? the site of

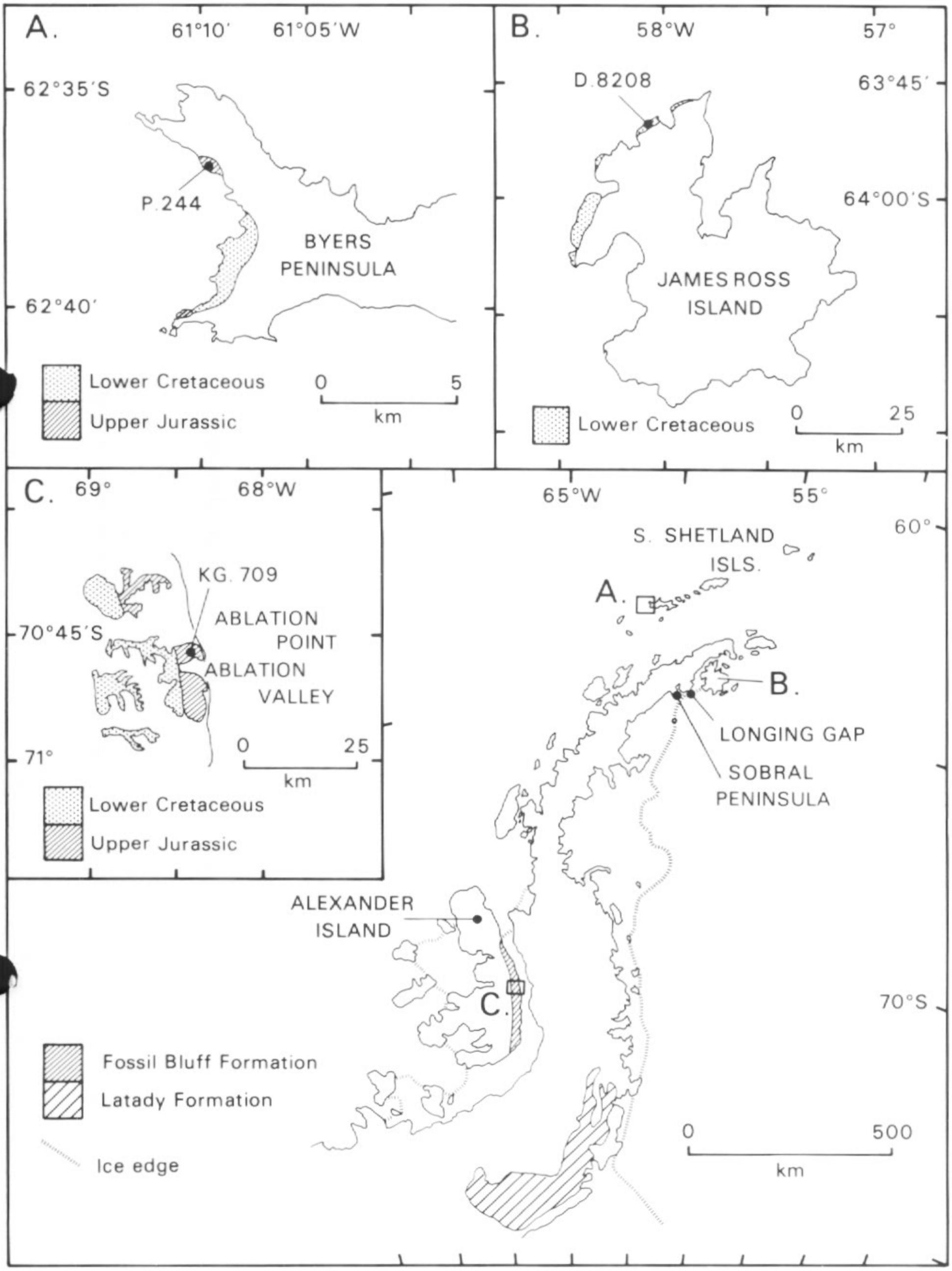

Fig. 3. Locality map for the Antarctic Peninsula region showing marine strata with late Jurassic oxytomids. Insets: A. Byers Peninsula, western Livingston Island, South Shetland Islands, B. James Ross Island, north-east Antarctic Peninsula, C. Ablation Point, central Alexander Island. Key: P.244, D8208 and KG.709 – bivalve localities.

insertion of the pedal-byssal musculature). Beneath the anterior ear there is a long, narrow, triangular byssal notch which merges dorsally (i.e. towards the beak) with a thin furrow.

In *Arctotis anabarensis* the anterior ear and byssal notch of the right valve is partly enclosed by a hood-like projection of the antero-dorsal margin of the left valve (Zakharov, 1966, pl. IV, figs. 3b and 4a). This projection is in some respects analogous to the antero-dorsal swelling (or callus) present in the left valve of some specimens of *Malayomaorica* (e.g. Jeletzky, 1963, pl. 21, fig. 2F; Crame, 1983*a*, fig. 2d) but it should be emphasized that there is no evidence that it is flanked (on the umbonal side) by an articulation groove (*Gelenkgrube*).

Up to three orders of radial ribs may be present on the left valve of *Arctotis*. These are typically narrow, acute to moderately well rounded in cross-section and of greater prominence than the concentrics (e.g. Borissiak, 1915, pl. 11, figs. 5, 6 and 12; Bodylevsky, 1958, pl. XV, fig. 2; Koshelkina, 1963, pl. III, fig. 12; Fig. 2a). In some instances, when the radial and concentric components are of almost equal strength, a cancellate ornament pattern is produced; this may be either fine- or coarse-grained (e.g. Bodylevsky, 1960, pl. 7, fig. 1b; Koshelkina, 1963, pl. III, fig. 1b; Zakharov, 1966, pl. III, figs. 7–10, pl. IV, figs 3a and 5). At the point of intersection of a radial and concentric rib a small spinule or tubercle is usually produced. A further distinctive feature of nearly all left valves is the presence of a series (generally between 3 and 6 in number) of prominent concentric wrinkles which represent pauses in shell growth. It is noticeable how the course of the radial ribs is often deflected over these concentric depressions, thus giving them a distinctly wavey appearance (Fig. 2a; e.g. Borissiak, 1915, pl. 11, fig. 6; Zakharov, 1966, pl. IV, fig. 5). Although the ornament on the right valve is significantly reduced in many species, in the Tithonian (Volgian) *A. intermedia* it is just as strong as on the left (e.g. Bodylevsky, 1960, pl. 7, figs. 1a and 2a; Zakharov, 1966, pl. III, figs. 11 and 12a).

Smaller specimens of *Arctotis* can easily be confused with the common Jurassic oxytomid, *Meleagrinella*, Whitfield, 1885 (see e.g. Koshelkina, 1963, pl. II, figs. 1–3; Zakharov, 1966, pl. III, figs. 1–6). Nevertheless, the latter genus is usually distinguishable externally by its denser radial ribbing, pointed postero-dorsal wing and much smaller anterior ear on the right valve. In addition, the ligament area of the left valve is considerably thinner and bears a distinct tooth-like protuberance immediately in front of the resilifer (e.g. Zakharov, 1966, pl. III, fig. 6; Duff, 1978, text-fig. 18a). Some forms of the Lower Cretaceous genera *Aucellina* and *Maccoyella* closely resemble *Arctotis*, the former through its blade-like anterior ear on the right valve and the latter through its general form and strong radial ornament (see, e.g. Jeletzky, 1963; Cox, 1969; Kauffman, 1976). Even though *Aucellina* is usually identified by the form of its left valve and much finer ornament, and *Maccoyella* by its thickened hinge and ligament area, the similarities between these three genera are such as to suggest that they may be closely related.

SYSTEMATIC PALAEONTOLOGY

Class BIVALVIA Linné, 1758
Subclass AUTOBRANCHIA Grobben, 1894
Superorder PTERIOMORPHIA Beurlen, 1944
Order OSTREOIDA Ferrusac, 1822
Suborder PECTININA Waller, 1978
Superfamily BUCHIACEA Waller, 1978
Family OXYTOMIDAE Ichikawa, 1958
Genus *Arctotis* Bodylevsky, 1960

Type species. Hinnites lenaensis Lahusen, 1886, from the Middle Jurassic of the Lena River, northern Siberia; by original designation (Bodylevsky, 1960, p. 44).

Arctotis australis sp.nov.
Figs. 4–8

Type material. Holotype: P.244.8 (int.m., LV) from the Mudstone member of the Byers Formation, western Livingston Island, South Shetland Islands (62° 36′ 20″ S; 61° 09′ 10″ W) (Fig. 3). Paratypes: P.244.9 (ext. m., RV; same locality as holotype); D.8208.10a, 10b, 34, 45, 73, 80, 81, 147, 148, 160, 161 (all int. m. LV, with varying amounts of shell material); D.8208.70 (ext. m. LV); D.8208.29, 36, 39, 42, 53, 102, 103, 114, 148b (all int. m. RV, with varying amounts of shell material); D.8208.8, 41, 101, 148a (ext. m., RV). Locality D.8208 is a 200 m section through a giant slide block of late Jurassic Nordenskjöld Formation lying concordantly within Lower Cretaceous (Albian) sediments, Sharp Valley, NW James Ross Island (Ineson, 1985, Fig. 2) (Fig. 3) (63° 51′ 30″ S; 58° 04′ 30″ W). (Abbreviations: LV – left valve, RV – right valve, int.m. – internal mould, ext.m. – external mould).

Diagnosis. Small-medium; LV almost bilaterally symmetrical and bearing at least two distinct orders of radial ribs; RV with small to large, gently curving anterior ear which becomes almost horizontal in adult specimens; RV almost smooth.

Derivation of name. australis: belonging to the south, southern; referring to the occurrence of *Arctotis* in the Southern Hemisphere.

Description. Although small buchiacean-type bivalves are numerous in the Nordenskjöld Formation (and its stratigraphic equivalents), they are not easily identified. This is partly due to the fact that most specimens are juveniles (with many spat falls having preferentially colonized small hard substrate 'islands'; Farquharson, 1983, p. 13 and fig. 12) and partly to poor preservation. Most specimens show at least some degree of postmortem compaction and the outer shell layer (which bears most of the ornament) has frequently been dissolved away. The best-preserved material comes from the Mudstone member of the Byers Formation, Livingston Island (two specimens from loc. P.244, Fig. 3) and a giant exotic block of Nordenskjöld Formation contained within Lower Cretaceous conglomerates in Sharp Valley, NW James Ross Island (many specimens from loc. D. 8208, Fig. 3; see also Ineson, 1985, fig. 2).

The largest LV is the holotype (P.244.8; Fig. 4a), which has a length (L) and width (W) of 40 mm. Although these dimensions suggest a circular outline, the LV is typically more oval or elongate-rounded ($\bar{x}L = 22.17$, $\bar{x}W = 19.50$, $\bar{x}W/L = 0.91$, $N = 12$; Figs. 4a–i). Juveniles (e.g. D.8208.80; Fig. 4i) consistently have rounded outlines, but thereafter length usually exceeds width. There are a few squatter forms with rounded-quadrate profiles (e.g. D.8208.10b; Fig. 4f) and it is uncertain at present whether these represent genuine varieties or are distortions produced by compaction. The subcentral to central, pointed umbo is flanked by straight to slightly convex antero- and postero-dorsal margins which typically slope gently downwards to the anterior and posterior margins (e.g. Figs. 4a–e). The latter vary from almost straight to convex and lead into a well-rounded ventral margin. The LV is typically moderately inflated in the umbonal and central regions and almost flat towards the margins (Figs. 4a–i).

One LV bears traces of a distinct posterior furrow (D.8208.73; Fig. 4h); this can be traced from the umbo to the postero-ventral margin and is clearly imprinted on the inner shell layers. Specimen D.8208.160 (Fig. 4b), a somewhat distorted large LV, bears a distinct sinus in the posterior margin and it is thought this may mark the exit

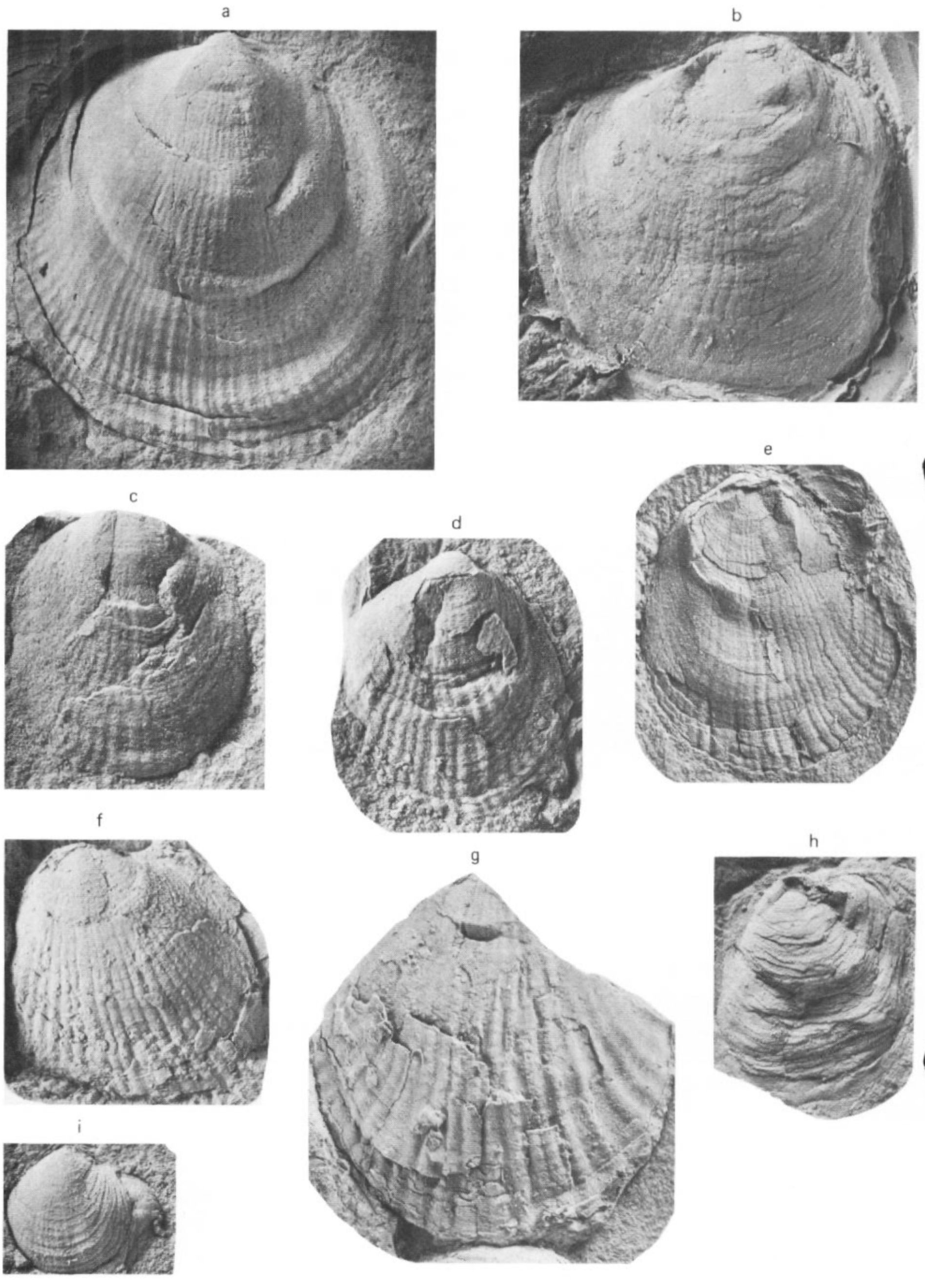

Fig. 4. *Arctotis australis* sp.nov. – left valves. a. the holotype, P.244.8 (× 1.5). b. large specimen showing posterior sinus, D.8208.160 (× 1.5). c. D.8208.34 (× 2). d. D.8208.45 (× 2). e. D8208.81 (× 2). f. D.8208.10b (× 2). g. incomplete specimen, D.8208.10a (× 1.5). h. D8208.73 (× 2). i. juvenile, D.8208.80 (× 2). Specimens a-h are internal moulds bearing varying amounts of shell material; specimen i has a complete outer shell layer. Locality P.244 is on Byers Peninsula, western Livingston Island, South Shetland Islands and D.8208 is on the NW coast of James Ross Island.

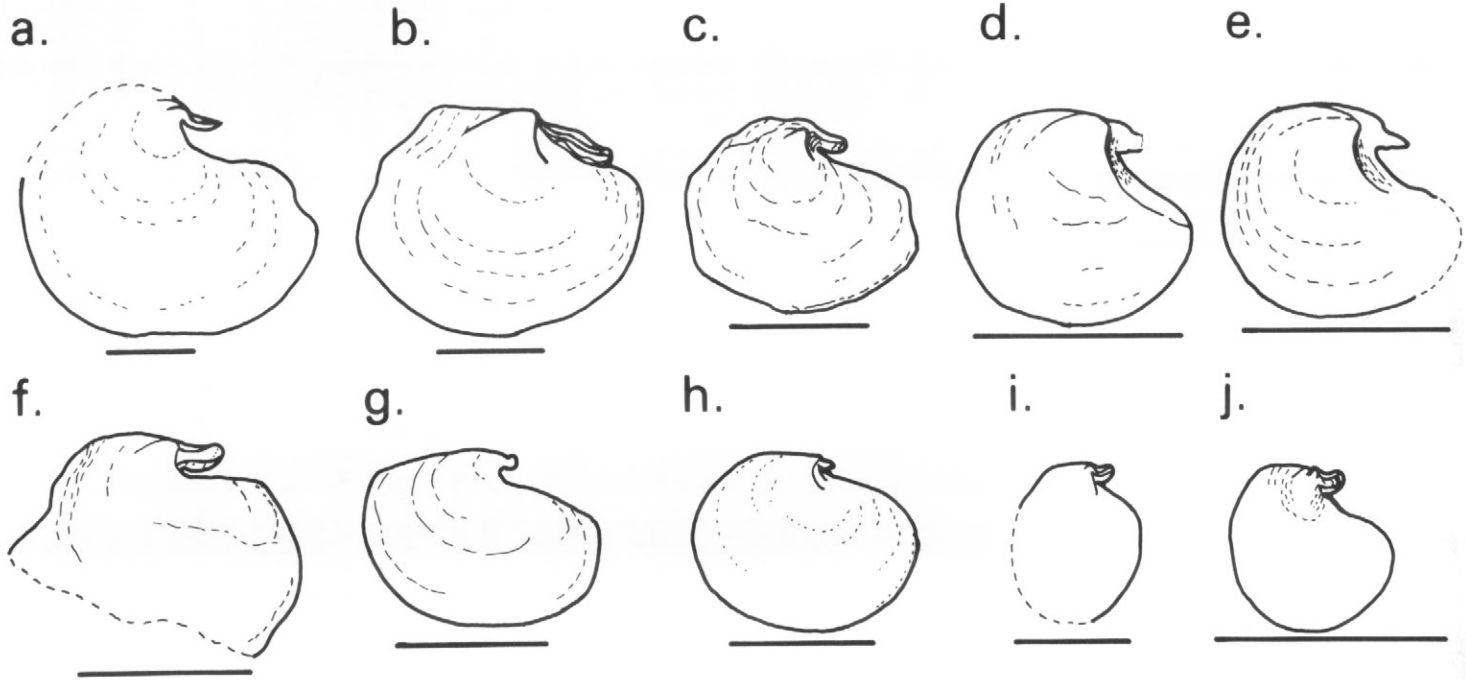

Fig. 5. *Arctotis australis* sp.nov. – right valve outlines. a. P.244.9, b. D.8208.29, c. D.8208.53, d. D.8208.39, e. D.8208.41, f. D.8208.42, g. D.8208.101, h. D.8208.103, i. D8208.80, j. D.8208.8. 1 cm scale bar beneath each specimen.

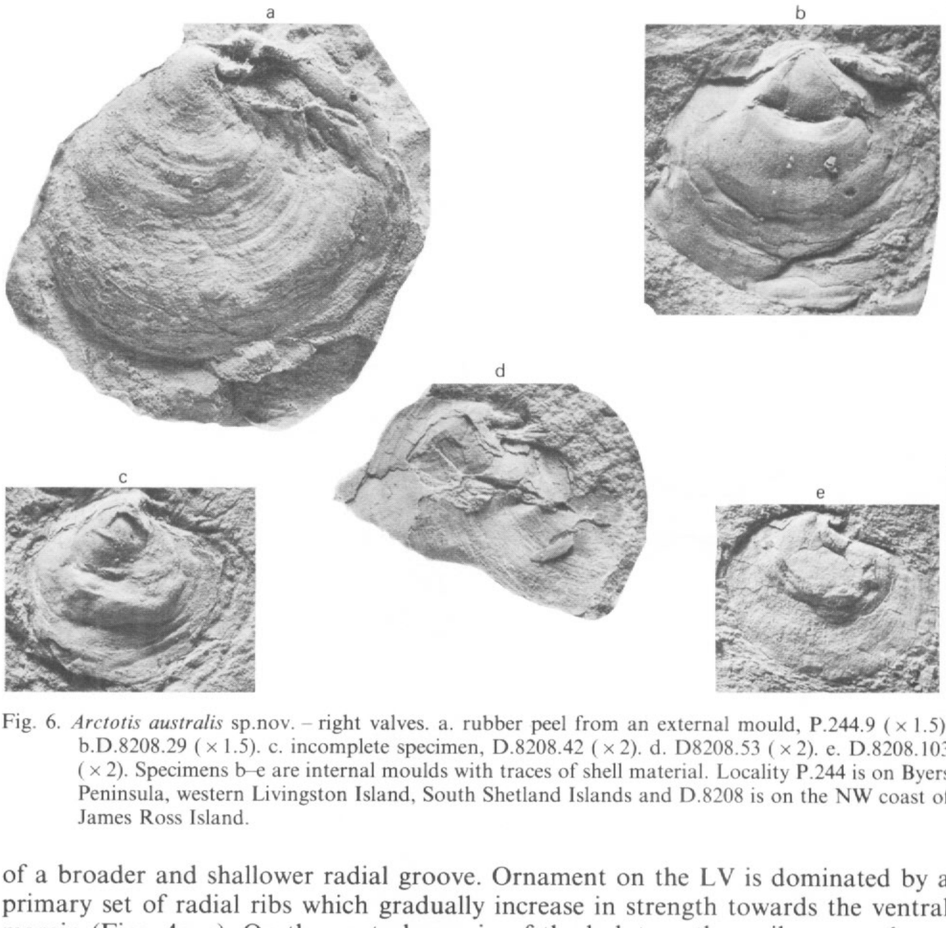

Fig. 6. *Arctotis australis* sp.nov. – right valves. a. rubber peel from an external mould, P.244.9 (× 1.5). b.D.8208.29 (× 1.5). c. incomplete specimen, D.8208.42 (× 2). d. D8208.53 (× 2). e. D.8208.103 (× 2). Specimens b–e are internal moulds with traces of shell material. Locality P.244 is on Byers Peninsula, western Livingston Island, South Shetland Islands and D.8208 is on the NW coast of James Ross Island.

of a broader and shallower radial groove. Ornament on the LV is dominated by a primary set of radial ribs which gradually increase in strength towards the ventral margin (Figs. 4a–g). On the ventral margin of the holotype these ribs are < 1 mm in width and occur in the frequency of approximately 9 per cm. They are slightly thicker on a number of other specimens (Figs. 4d–f) and on D.8208.10a (Fig. 4g) they reach over 1.5 cm across. There are traces of very fine intercalated secondary radials on the holotype (Fig. 4a) but in general the narrow interspaces between the primaries appear to be smooth. The ribs have a low, rounded cross-profile but on the coarsely ribbed specimen, D.8208.10a (Fig. 4g), some of the primaries in the centre of the valve have acute summits. Disruption of the course of the radial ribs by prominent concentric wrinkles is most obvious on the holotype (Fig. 4a), but also occurs to some extent on all other specimens (Figs. 4b–g). Fine concentric growth lines slightly distort the line of the radials in some instances (e.g. D.8208.81; Fig. 4e), and in others form tiny tubercles at their point of intersection (e.g. P.244.8, D.8208.10a; Figs. 4a and g). Where the concentric lines are most prominent, a faint cancellate pattern is produced.

There is a pronounced change from the oval or sub-circular outlines of juvenile right valves (i.e. $L < 10$ mm; Figs. 5i and j) to the rounded-rectangular form of adults in which the width clearly exceeds the length ($\bar{x}L = 15.33$, $\bar{x}W = 17.55$, $\bar{x}W/L = 1.14$, $N = 9$; Figs. 5a–h). All the adult right valves are characterized by a high postero-dorsal region, comprising an indistinctly recessed triangular to sub-rounded wing, and a correspondingly lower antero-ventral region, comprising an elongate, rounded pro-

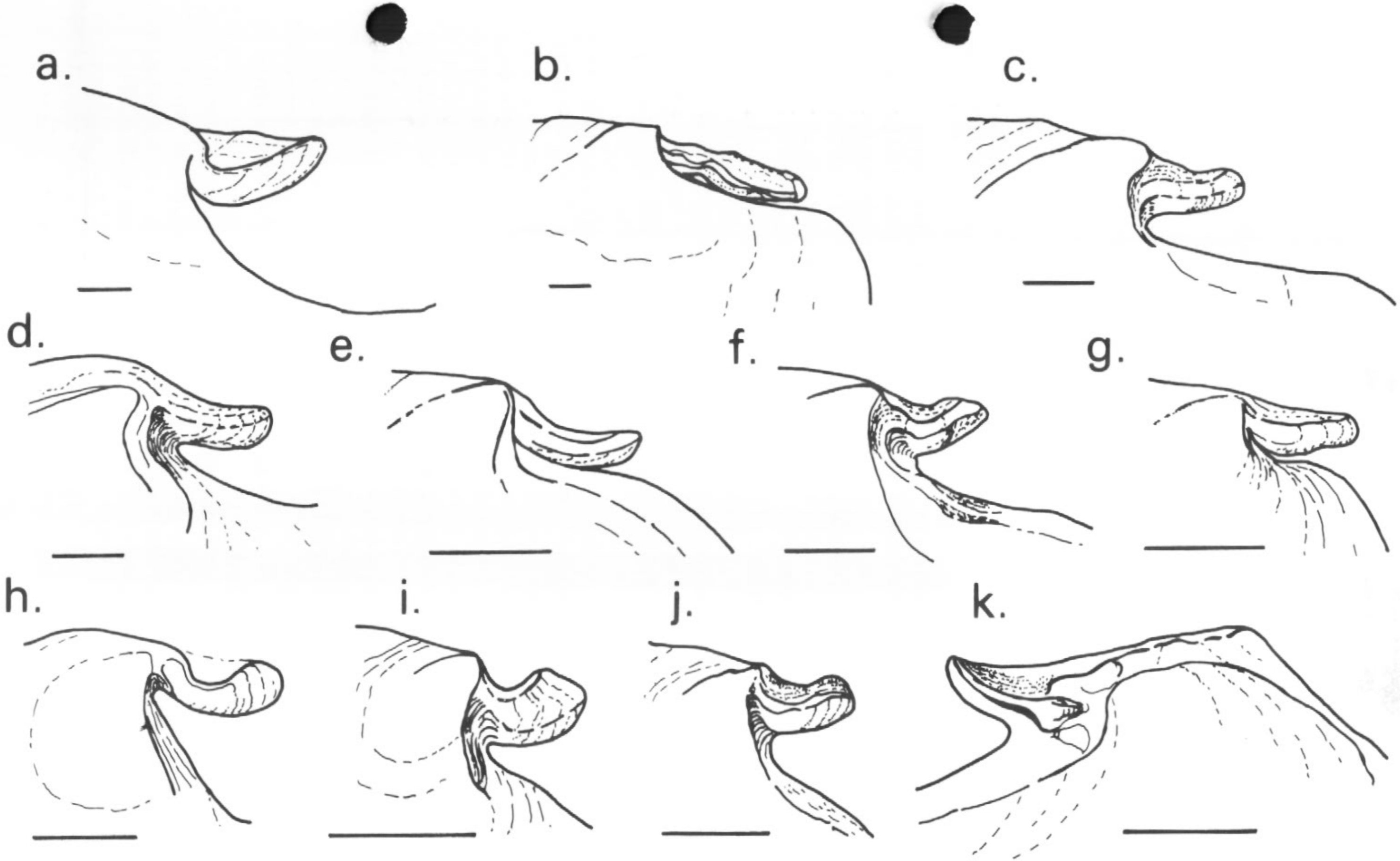

Fig. 7. *Arctotis australis* sp.nov. – enlargements of the right anterior ear and byssal notch. a. P.244.9, b. D.8208.29 c. D.8208.42, d. D.8208.53, e. D.8208.88, f. D.8208.103, g. D.8208.36, h. D.8208.148 i. D.8208.8, j. D.8208.80, k. D.8208.41. All specimens are external views except for k, which is an internal. 2 mm scale bar beneath each specimen.

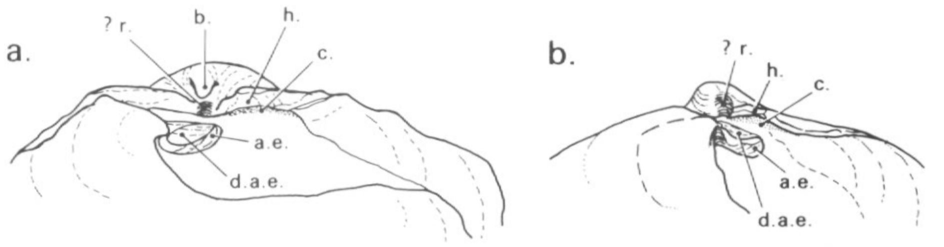

Fig. 8. *Arctotis australis* sp.nov. – exploded views of the hinge region of two partially articulated specimens. a. P.244.9 (× 2.5), b. D.8208.148 (× 7.5), a.e. anterior ear, b. beak, c. cavity, d.a.e. dorsal surface of the anterior ear, h. hood-like projection, ?r. ?resilifier.

jection (the so-called 'aviculopectinid' profile; Figs, 5a–h; 6a–e). The RV is almost smooth, exhibiting only sporadic concentric wrinkles and very faint patches of radial ribbing (Figs. 6a–e).

The most distinctive feature of the RV is the anterior ear. This has the form of a rounded blade which is gently flexed (so that it has a convex outer surface) and projects slightly to strongly upwards (Figs. 6a–e; 7a–j). However, it should be emphasized that the ear does not project above the hingeline and that its flat to concave dorsal surface is a continuation of the RV ligament area. Whereas in juvenile specimens the ear tends to be comparatively short and stubby, and more strongly upturned (Figs. 7i and j), in adults it is longer and straighter (Figs. 7a–h). From specimens P.244.9 and D.8208.29 (Figs. 6a and b; 7a and b) it is apparent that, as well as increasing in length, the ear also changes its alignment from almost parallel to the plane of commissure (juveniles) to almost perpendicular to it (adults). That on D.8208.29 (Fig. 6b and 7b) appears to have collapsed, but on P.244.9 (Figs. 6a and 7a) the ear is gently upturned and so strongly tilted inwards that its dorsal surface forms a broad platform (> 1.5 mm across) which actually dips slightly outwards (i.e. towards the observer). The notch beneath the ear is narrow to moderately broad and tapers rapidly inwards towards the umbo.

Although the convex outer surface of the RV anterior ear curves slightly inwards, there is no indication that its tip ever crosses the plane of commissure to articulate with a socket (*Gelenkgrube*) in the LV. Details of the LV hinge and ligament area are scarce, but two partially articulated specimens show the probable relationships between the anterior regions of the valves (P.244.9, D.8208.148; Figs. 8a and b). On the larger of these (P.244.9), it would appear that the prominent shelf-like dorsal surface of the ear rested within a shallow cavity formed beneath a hood-like projection on the anterior section of the LV hinge (Figs. 6a and 8a). A similar arrangement, on a somewhat smaller scale, is evident on D.8208.148 (Fig. 8b). On some specimens, such as D.8208.41 (Fig. 7k). there are indications of a tooth-like bulge on the inner surface of the ear, close to its base. However, it is unclear at present whether such a projection would actually have articulated with the LV hinge or merely rested beneath it. On both P.244.9 and D.8208.148 there are indications of a shallow concave depression immediately posterior to the hood-like projection (Figs. 8a and b), but it is thought more likely that this represents the traces of a sub-central resilifer. The strong inward tilt of the RV ear, together with its partial accommodation within a hood-like projection, means that the RV ligament area lies as much beneath the LV area as it does against it. In fact, the latter is curved strongly forwards so that it directly overlies the RV area and this results, in adult specimens, in the whole LV umbonal region towering over that of the RV (Figs. 6a and 8a). In small specimens and juveniles, the RV ear appears to simply rest against the LV ligament area.

Remarks. At first sight, some of the left valves in this collection could be confused with specimens of the cosmopolitan Jurassic oxytomid, *Meleagrinella*. For example, the Callovian species *M. braamburiensis* (Phillips) has a left valve which can be almost bilaterally symmetrical and bears radial ornament punctuated by occasional concentric growth furrows (e.g. Duff, 1978, pl. 4, figs. 26c and 27c). In addition, some forms of the same species have faintly costulate radial ribs and others are weakly to strongly cancellate (e.g. Duff, 1978, text-figs, 19b and c, pl. 4, figs. 20, 28 and 31). A further species, *M. sinuata* (Teichert) from the Bajocian of Western Australia, has a prominent posterior sulcus which gives some left valves an *Arctotis*-like appearance (e.g. Teichert, 1940, pl. 1, fig. 8; Skwarko 1974, pl. 32, fig. 9). Nevertheless, it would seem that the left valve is significantly smaller than that of *Arctotis*, bears thinner and more continuous (i.e. straighter) radial ribs and frequently has a distinct postero-dorsal wing. From the inside, the left valve ligament area of *Meleagrinella* can be seen to be broadly similar to that of *Arctotis* but it is distinguished by the presence of an anterior tooth-like protuberance which projects ventrally into the shell cavity (e.g. Duff, 1978, text-fig. 18a). Right valves of *Meleagrinella* are readily identified by their rounded outline, prominent postero-dorsal wing and tiny anterior ear (e.g. Cox, 1940; Duff, 1978, pl. 4, fig. 32).

Malayomaorica can also have an almost bilaterally symmetrical left valve (e.g. Crame, 1983*a*, figs, 3h and k), but it is never as strongly radially ornamented as the specimens described here and its left valve ligament area is unique amongst oxytomids (Jeletzky, 1963; Crame, 1983*a*). The significant differences between the right valves of *Malayomaorica* and *Arctotis* are discussed below.

In conclusion, the following features suggest that the Antarctic specimens are closer to *Arctotis* than to any other known oxytomid genus: LV – comparatively large size, approximately bilaterally symmetrical, posterior sulcus, strong wavey radial ribs, ligament area towers over that of RV; RV – aviculopectinid outline, prominent blade-like ear which dips strongly inwards, lack of radial ornament; both valves – prominent concentric growth furrows.

Small left valves within the Antarctic collection, such as D.8208.34 and 45 (Figs. 4c and d), show some resemblances to small specimens of *A. intermedia* Bodylevsky (e.g. Bodylevsky, 1960, pl. 7, fig. 1b) from the Lower-Upper Volgian (= Tithonian) of northern Siberia and eastern England (NB this range may be extended to include the Volgian-Ryazanian of NE USSR too; Kelly, 1984, p. 64). However, the left valve of this species is readily distinguishable from *A. australis* sp.nov. by its stronger first order radial ornament and the presence of small but distinct antero- and postero-dorsal wings on small and medium-sized specimens (Zakharov, 1966, pl. III, figs. 8–10). A further distinction between the two species is that the right valve of *A. intermedia* is consistently strongly ornamented (Bodylevsky, 1960, pl. 7, figs. 1a and 2a; Zakharov, 1966, pl. III, figs. 11 and 12a). The holotype (P.244.8; Fig. 4a) bears a striking superficial resemblance to left valves of *A. anabarensis* (Petrova), an Upper Berriasian-Lower Hauterivian species from northern Siberia (e.g. Zakharov, 1966, pl. IV, figs 3a and 5). This is a larger species than *A. intermedia*, and has a left valve bearing numerous fine radial ribs that are noticeably deflected over prominent concentric growth pauses. The hinge and ligament areas on both valves are close to those of *A. australis* sp.nov. and it is likely that the means of articulation was very similar; *A. anabarensis* has a strongly projecting hood on the left valve ligament area and this appears to have partially accommodated a sub-horizontal right anterior ear (cf. Figs. 6a and 8a and Zakharov, 1966, pl. IV, figs. 3b and 4a). The right valve of *A. anabarensis* is almost smooth (e.g. Zakharov, 1966, pl. IV, fig. 2b) but it has to be borne in mind that both it and the left valve are characterized by a strongly developed postero-dorsal wing. For this reason, as well as for minor differences in surface ornament, this species is believed to be clearly separable from *A. australis* sp.nov.

Occurrence. Probably restricted to the lower levels of the Nordenskjöld Formation, northern Antarctic Peninsula region; Kimmeridgian-early Tithonian (see discussion section, below).

Genus *Malayomaorica* Jeletzky, 1963

Type species. Aucella malayomaorica Krumbeck, 1923, from the early to middle Kimmeridgian of Indonesia and New Zealand; by original designation (Jeletzky 1963, p. 149).

Malayomaorica sp.nov.?
Figs. 9 and 10

Fig. 9. *Malayomaorica* sp.nov.? a. incomplete left valve, KG.709.11 (× 2). b. right valve, KG.709.7 (× 2). Both specimens are rubber peels from external moulds. Locality KG.709 is on the western face of Ablation Point, Alexander Island.

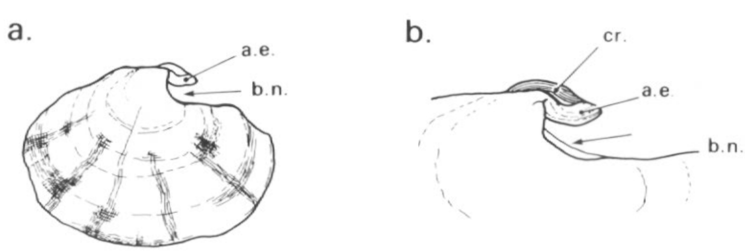

Fig. 10. *Malayomaorica* sp.nov.? a. outline of the right valve, KG.709.7, × 2. b. enlargement (× 10) of the anterior ear and byssal notch on the same specimen. a.e. anterior ear, b.n. byssal notch, cr. crest.

Material. One ext. m. RV (KG.709.7) and one incomplete ext. m. LV (KG.709.11); loose specimens from a moraine derived from the western face of Ablation Point, Alexander Island (70° 47′ 30″ S; 68° 22′ 40″ W) (Fig. 3); Fossil Bluff Formation.

Description. The right valve (KG.709.7, Figs. 9b and 10a) measures approximately 10 mm (L) by 13 mm (W) and has a distinctive rounded-rectangular outline. It has a prominent protruding anterior region similar to that of the right valve of the preceding species of *Arctotis*, but the postero-dorsal region is noticeably lower and only has a very slightly convex profile (Figs. 9b and 10a). In the antero-dorsal region there is a small but sharply defined ear which has a strongly convex outer surface and is gently upturned. Closer inspection reveals that the axis of the ear is essentially parallel to that of the plane of commissure and that its dorsal surface bears a flange-like crest (Figs. 10a and b). Set obliquely to the hingeline, the latter feature has a strongly convex upper surface and bears numerous fine growth lines. Evidently the ligament abutted against its posterior face and it is even possible that it extended right across it. The notch beneath the ear is very deep and has a sub-rectangular profile (Figs. 10a and b).

The weakly inflated right valve bears a delicate cancellate ornament produced by the intersection of numerous concentric growth lines with fine wavey radial ribs. Tiny spine-like projections are frequently produced at the points of intersection and the overall appearance is that of a very fine mesh (Fig. 9b); the continuity of this pattern is broken only by occasional irregular concentric growth pauses. A very similar style of ornament is present on the left valve (KG.709.11, Fig. 9a), which has approximate measurements of 16 mm (L) by 13 mm (W). Even though its anterior region is missing, this specimen would appear to have been slightly obliquely elongated and it is obviously considerably more inflated than the previous one.

Remarks. The short blade-like ear with a dorsal crest and deep sub-rectangular notch on the right valve, together with the cancellate ornament on both valves, strongly suggest that these specimens should be assigned to the genus *Malayomaorica*. However, the ornament seems to be intermediate between the relatively coarse-grained pattern characteristic of the widespread Southern Hemisphere Kimmeridgian species, *M. malayomaorica* (Krumbeck) (Jeletzky, 1963; Crame, 1983*a*) and the almost smooth Kimmeridgian-early Tithonian form from the Falkland Plateau, *M. occidentalis* Jeletzky (1983, p. 967, pl. 1, figs. 8 and 13). It is probably closest to that exhibited by *Buchia misolica* (Krumbeck, 1934), p. 454, pl. 15, figs. 10a, b), a poorly known species from the late Jurassic of Indonesia. Fleming (1958, p. 379) indicated that certain 'buchiids' from the early Tithonian of New Zealand may also belong within this species, and that it was, perhaps, a direct descendant of *Buchia* (= *Malayomaorica*) *malayomaorica*. With the latter phylogenetic connection in mind, Jeletzky (1963, p. 159) transferred *B. misolica* to the genus *Malayomaorica* and thus this constitutes a possible taxonomic category for the Antarctic material. Nevertheless, it should be emphasized that neither *B. misolica* nor the New Zealand material referred to *B.*aff. *misolica* (e.g. Stevens, 1978, figs. 4.62, 6 and 7) have yet been conclusively shown to belong within *Malayomaorica*. With taxonomic revisions of both the Indonesian and New Zealand material pending, the Antarctic specimens have been left in open nomenclature.

Occurrence: Imprecisely located near the base of the Fossil Bluff Formation; Kimmeridgian or early Tithonian.

Stratigraphical Discussion

The mudstone member of the Byers Formation, from which the holotype of *Arctotis australis* sp.nov. was obtained, has yielded a suite of fossils with Kimmeridgian-Tithonian affinities. Among these are species of the belemnite genera *Belemnopsis* and *Hibolithes*, a perisphinctid ammonite close to *Subplanites* Spath and a berriasellid resembling *Berriasella behrendsi* Burckhardt (Smellie and others, 1980, p. 58). The

Nordenskjöld Formation, from which the remaining specimens of this species were collected, has a similar age-range; although *in-situ* material from the type locality at Longing Gap indicates a Kimmeridgian-early Tithonian age, further ammonites and bivalves from Sobral Peninsula, plus a series of loose specimens from James Ross Island, are indicative of the late Tithonian or early Berriasian (Farquharson, 1983). As the Mudstone member of Livingston Island is now known to grade upwards into overlying basal Cretaceous conglomerates and sandstones (Smellie and others, 1980; Crame and Farquharson, 1984), the stratigraphic range of the Nordenskjöld Formation and its equivalents is believed to be at least Kimmeridgian–Berriasian.

A 200 m stratigraphic section measured through the giant slide block of Nordenskjöld Formation on James Ross Island (loc. D.8208, Fig. 3) revealed that *Arctotis australis* sp.nov. was restricted to the basal 57 m. Here it is associated with perisphinctid ammonites (which include a form closely resembling *Subplanites*) and belemnopseid belemnites. Higher up in the section, between approximately 144 and 180 m, a further ammonite-bivalve assemblage yielded several berriasellids as well as buchiids that can probably be referred to the *B. blanfordiana* (Stoliczka) group. This assemblage suggests an early to mid-Tithonian age and can be correlated with a similar berriasellid-*Buchia* assemblage known from the lower levels of the Fossil Bluff Formation, Alexander Island (e.g. Crame, 1984, p. 245). The slide block would therefore appear to have a Kimmeridgian to early or mid-Tithonian age-range and this is in broad agreement with an age determination based on a preliminary palynological investigation of the same section (unpublished report held in BAS Earth Sciences Division).

Unfortunately, the loose specimens of *Malayomaorica* sp.nov.? are only imprecisely located on the western face of Ablation Point, Alexander Island (Fig. 3). This means, according to Elliott's (1974, fig. 2) geological map, that they could have originated from either Kimmeridgian or Tithonian strata. No age-diagnostic fossils occur with them, and all that can be said at present is that they come from a level which is probably equivalent to the basal portion of the main Ablation Valley section (e.g. Crame, 1984, fig. 2A).

The Early-Middle Kimmeridgian species, *Malayomaorica malayomaorica*, is thought to be restricted in Antarctica to the Latady Formation (Middle–Upper Jurassic), which crops out on the south-eastern flank of the Antarctic Peninsula (Fig. 3) (Crame, 1983*a*). Although no precise correlations can as yet be given between this unit and the Fossil Bluff Formation, it is likely that it largely predates it (Crame, 1983*a*, fig. 6) and that *M. malayomaorica* occurs stratigraphically beneath *M*. sp.nov.? Even if this does not prove to be the case, there is evidence that the genus *Malayomaorica* persists into the early Tithonian on the Falkland Plateau, where *M. occidentalis* is at least partly of this age (Jeletzky, 1983).

From the foregoing it is concluded that there were at least two distinct lineages of stratigraphically important oxytomid bivalves in the Antarctic Peninsula region during the Kimmeridgian–Tithonian: one is based on the genus *Malayomaorica* and the other on *Arctotis*. The precise nature and extent of these lineages has yet to be fully determined, and in particular it would seem to be important to establish whether either of them is phylogenetically linked to the common Antarctic Lower Cretaceous (Aptian–Albian) oxytomids, *Aucellina* and *Maccoyella*. Although it may be premature to postulate any direct connections at present, it is striking how both *Malayomaorica*, through its thickened hinge and ligament area, and *Arctotis*, through its general shell form and ornament pattern, closely resemble the latter of these genera.

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From the Middle Lias to the Lower Hauterivian, the vast majority of the occurrences of *Arctotis* were in northern Siberia (Zakharov, 1966). Even at the level of the Jurasic-Cretaceous boundary, when there was an expansion in its range to include localities such as Canada and eastern England (Jeletzky, 1973; Kelly, 1984), it is clear that the genus was still restricted to a high palaeolatitude (e.g. Kelly, 1984, text-fig. 42). It is, perhaps, the best bivalve indicator for the Boreal realm and some authorities believe that it can also be used as a reliable guide to cool-temperate sea waters (e.g. Hallam, 1977, p. 65). In the Southern Hemisphere, three new species were tentatively described by Kauffman (1976) from DSDP material recovered from the Manihiki Plateau, south Pacific. However, the status of these identifications is in some doubt as they are based on poorly preserved specimens which could be, in part at least, Lower Albian in age. They are associated with other oxytomid genera such as *Aucellina*, *Pseudavicula* and *Maccoyella* and may, eventually, have to be re-assigned to one of these categories.

The only other known Southern Hemisphere occurrences of *Arctotis* are those described in this paper. Their approximate palaeolatitude (60° S) is equivalent to that of their Northern Hemisphere counterparts and their presence in Antarctica strongly suggests that *Arctotis* had a bi-polar distribution. Similar patterns have recently been established for genera such as *Retroceramus*, *Anopaea* and *Buchia* (e.g. Crame 1982, p. 598) and there is now an increasing volume of evidence to suggest that there was a distinct late Jurassic high-latitude fauna of pteriomorph bivalves in the Southern Hemisphere. The palaeoclimatic implications of this fauna will be discussed elsewhere.

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