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The bivalve *Aulacomyella* from the Early Tithonian (Late Jurassic) of Antarctica

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Abstract: The bivalve *Aulacomyella* is described formally from Tithonian deposits of the Antarctic Peninsula region for the first time. Two species are recognized. *A. willeyi* Kelly sp. nov. was collected *in situ* from the Nordenskjöld Formation, Longing Gap on the east coast of Graham Land, and in clasts reworked into Cretaceous glide block deposits on James Ross Island. *A.* cf. *problematica* Furlani is recorded from the Himalia Ridge Formation, Fossil Bluff Group, Alexander Island. These Antarctic records are the first published systematic descriptions of the genus from the Southern Hemisphere. Together with Mexican and Turkish records, they represent the last known occurrences of this genus. Globally the genus is particularly abundant during the Kimmeridgian and Early Tithonian stages and is therefore of value as a biostratigraphic indicator. It was almost certainly an epibyssate suspension feeder, although the precise palaeoecological setting for *Aulacomyella* is uncertain. It normally occurs in black shales or mudstones. The most likely life habits were either living epifaunally on the sea floor, where it bloomed under episodic dysaerobic conditions in an otherwise anaerobic environment, or pseudoplanktonically infesting floating sea weeds etc. Of these hypotheses the former is preferred here.

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Key Words: *Aulacomyella*, bivalvia, black shales, Jurassic, palaeoecology, palaeogeography.

Introduction

Hitherto, the late Jurassic "paper pecten" bivalve *Aulacomyella* has been recorded solely from the Northern Hemisphere. Although the genus is infrequently recorded, when it appears it is normally abundant and occurs usually in black shale facies of Tethyan regions and the southern borders of the Boreal Realm. In the present article recently discovered Tithonian specimens from localities in the Antarctic Peninsula region (Fig. 1) are described: *Aulacomyella willeyi* Kelly sp. nov. and *A.* cf. *problematica* Furlani. These new records are again from black shale and mudstone facies, and are from shell pavements where individual valves are locally abundant.

The systematic part of this work is the sole responsibility of the senior author. The relevant stratigraphy of the area is summarized in Fig. 2, based on Butterworth *et al.* (1988) for Alexander Island and on Whitham & Doyle (1989) for Graham Land and James Ross Island.

In Antarctica the genus *Aulacomyella* was first recognized by Willey (1972) from specimens collected by M.H. Elliott in 1969 on Himalia Ridge (Fig. 1), Alexander Island. This material, from a horizon within the Himalia Ridge Formation, Fossil Bluff Group, has been re-examined and identified as *A.* cf. *problematica* Furlani (see below). Further specimens were collected recently from the Nordenskjöld Formation, Longing Gap, near Cape Longing, Graham Land and from a glide block of the same formation but located within Cretaceous strata, James Ross Island. All the Nordenskjöld Formation material is referred to *A. willeyi* sp. nov.

Aulacomyella is a Middle to Late Jurassic homeomorph of Triassic *Halobia* and *Daonella*. All these genera have similar equivalve, thin shells. They all occupied principally black shale environments. Reappearances of taxa within a generic group have been described by Jablonski (1986) as "Lazarus" taxa. Strictly, *Aulacomyella* cannot be regarded as such a taxon, because it is not the re-appearance of a previous genus. The precise generic relationships between *Aulacomyella* and the Triassic genera awaits further study, and so it is not yet certain even that they all belong within a single species group.

The nature of the shell and shape of *Halobia*, *Daonella* and *Aulacomyella* has given rise to the name "paper pecten" (e.g. Wignall 1990a). Although placed provisionally in the family Posidoniidae, following Cox & Newell (1969), the precise ancestoral history of *Aulacomyella* is still not known. One main problem is that hinge line structure remains unknown.

The sudden appearance of *Aulacomyella* in large numbers in the Late Jurassic suggests considerable biostratigraphic potential. The first records of *Aulacomyella* sp. were of Callovian/Oxfordian age from the Philippines (Andal *et al.* 1968, p. 193). The poorly preserved specimens were identified by Hayami (1968) as *A.* sp. aff. *A. neogeae* Imlay.

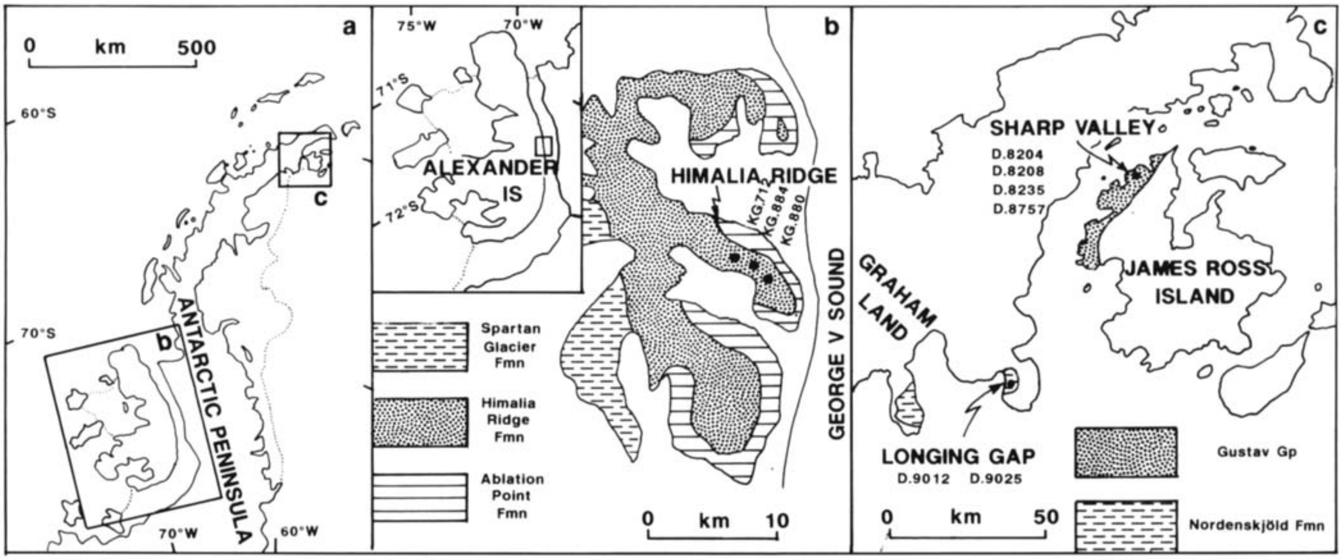

Fig. 1. Localities in the Antarctic Peninsula region from which *Aulacomyella* has been obtained. **a**, the Antarctic Peninsula area; **b**, detail of Himalia Ridge, Alexander Island (*A.* cf. *problematica* Furlani) (after Howlett 1989); **c**, detail of Longing Gap, Graham Land, and Sharp Valley, James Ross Island (*A. willeyi* Kelly sp. nov.) (after Ineson *et al.* 1986).

Aulacomyella? sp., of possible Oxfordian/Kimmeridgian age, has been recorded from the Soma Group, Japan (Tamura 1960).

Of the abundant material from the Late Jurassic, there appear to be three principal species or species groups, although there are at least thirteen names available. Stratigraphically the earliest species is *A. similis* (Münster), the type of which came from the Early Kimmeridgian of Bavaria. In the course of studies for this paper it has now been recognized from Scotland and the Russian Platform. A second, stratigraphically younger, species is *A. problematica* (Furlani 1910) from the Late Kimmeridgian of Yugoslavia. Closely related, if not identical, species have been figured from strata of mid- to late Kimmeridgian and Early Tithonian age from localities in several countries including Mexico (Imlay 1940, Cantú Chapa 1984), Louisiana, U.S.A. (Imlay 1945), Portugal (Freneix & Quesné 1985), Moldavia, U.S.S.R. (Romanov 1976), Crimea, U.S.S.R. (Kiparisova 1967) and Somalia (Cox 1935). The third species group is represented by *A. willeyi* sp. nov., described herein.

Stratigraphy

Although *Aulacomyella* has, hitherto, been little used as a biostratigraphic indicator, it has already been shown to be of value by Cantú Chapa (1984), who identified a zone of *Virgatosphinctes mexicanus* and *Aulacomyella neogeae* in the Early Tithonian of Mexico. The material described below from the Antarctic Peninsula can be correlated with this zone.

The Kimmeridgian stage is used here *sensu gallico*, that is divided into Early and Late Kimmeridgian substages (*e.g.* Hantzpergue 1979).

Alexander Island

The specimens of *Aulacomyella* were found at sites along Himalia Ridge at levels estimated at about 200–400m above the base of the Himalia Ridge Formation of the Fossil Bluff Group (Fig. 2). The lithostratigraphy used in the present work follows the revision by Butterworth *et al.* (1988), and the biostratigraphy by Crame & Howlett (1988). The specimens are preserved in indurated mudstones, which are typical of the lower part of the Himalia Ridge Formation. This compares with unit AV.1 of Howlett (1988), who described the fauna as sparse but including the bivalve, *Otapiria*, the belemnite, *Hibolithes argentinus* Feruglio, and the trace fossil *Chondrites*. Thomson (1979) recorded the ammonites *Aulacosphinctoides* and *Virgatosphinctes* near this level. The occurrence is placed here in either the *Hibolithes belligerundi* belemnite biozone or the *Virgatosphinctes* ammonite biozone of Howlett (1989) and therefore is of Early Tithonian age,

Crame (1984) reviewed the Jurassic-Cretaceous boundary bivalves of the Antarctic Peninsula and their zonation. *Aulacomyella* was not discussed, but in Alexander Island it occurs below the *Australobuchia blanfordiana/spitiensis* and *Otapiria* sp. nov. groups which Crame regarded as Tithonian.

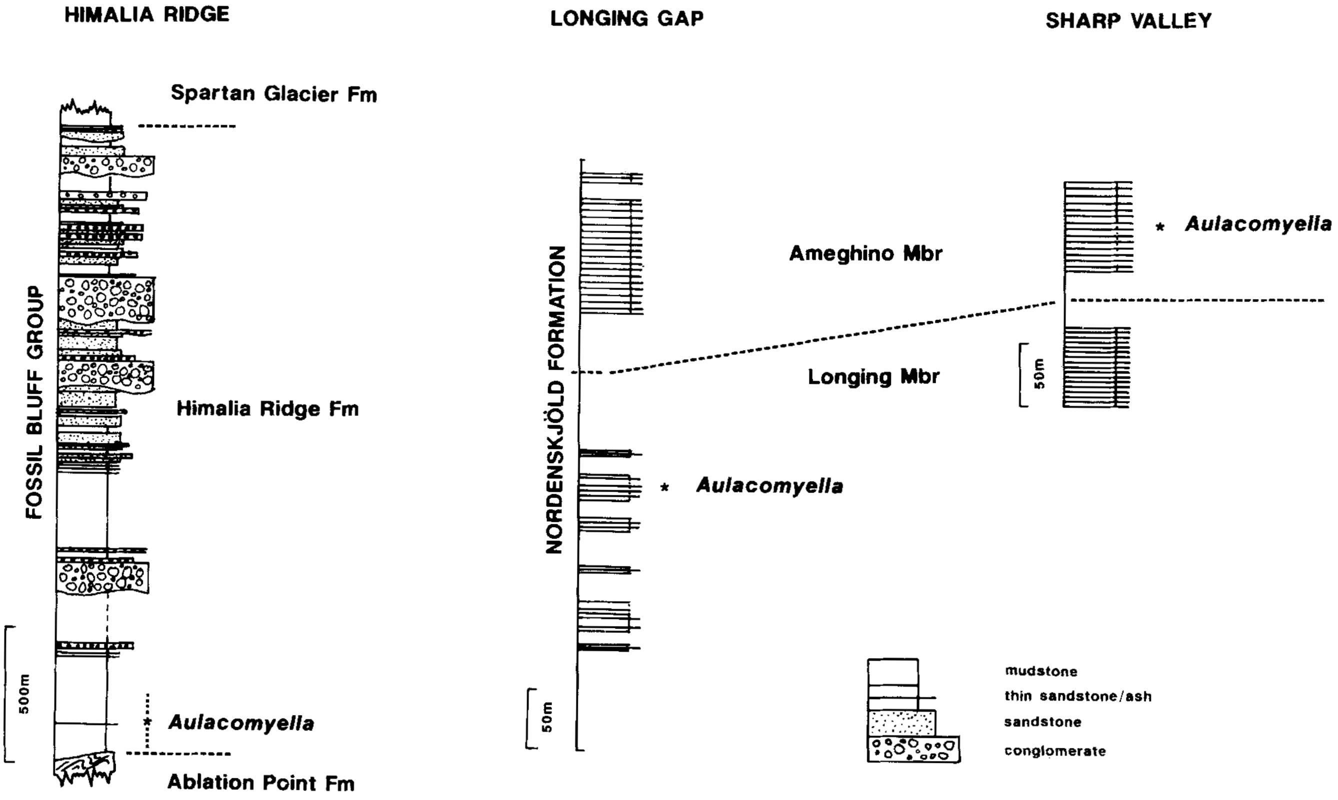

Fig. 2. Comparative stratigraphic sections of Himalia Ridge Formation at Himalia Ridge, Alexander Island (after Butterworth *et al.* 1988), and of the Nordenskjöld Formation at Longing Gap, Graham Land and the Sharp Valley glide block, James Ross Island (after Whitham & Doyle 1989).

Graham Land

At Longing Gap, *A. willeyi* occurs in thin shell pavements at about 120m above the exposed base of the type locality of the Nordenskjöld Formation, towards the top of the Longing Member. The stratigraphy of the formation (Fig. 2) follows Farquharson (1982, 1983) with revisions by Whitham & Doyle (1989). The lithology is shaley mudstones with subordinate ash fall horizons. The specimens associated with *Aulacomyella* include other bivalves such as *Anopaea*, *Australobuchia*, and *Otapiria*, and the ammonites *Virgatosphinctes* and *Lithacoceras*. The age of this fauna is Early Tithonian (Whitham & Doyle 1989).

James Ross Island

An extremely large (200 x 800 m) glide block of Nordenskjöld Formation occurs within Aptian-Albian Cretaceous rocks of the Kotick Point Formation, Gustav Group, in Sharp Valley, about 2 km east of Stoneley Point. This and other glide blocks were identified by Ineson (1985) and the Cretaceous stratigraphy described by Ineson *et al.* (1986). Whitham & Doyle (1989) identified lithologies characteristic of both the Longing and Ameghino members within the glide block. *Aulacomyella* was collected in association with *Otapiria*, *Anopaea*, *Australobuchia* and virgatosphinctid ammonites in the Ameghino Member, about 140 m above the base of the section. *Virgatosphinctes* was also recognized near this level, indicating a Tithonian age. However, the occurrence of *Spiticeras* at a slightly higher level suggests the proximity of the Jurassic-Cretaceous boundary. Thus the *Aulacomyella* may be of Late Tithonian age, and if so are the last known representatives of the genus world-wide.

Systematics

The synonymic annotations used by Matthews (1973) and Bengtson (1988) are followed here. The specimens described below are stored in the British Antarctic Survey Palaeontological Collections, housed in Cambridge. These collections are curated jointly by the Natural History Museum in London, and are allocated additional acquisition numbers for that museum, see Appendix.

All specimens were coated with ammonium chloride before photography. Orientations of dimensions and shell terminology used are given in Fig. 4.

Family POSIDONIIDAE Frech, 1909

(= Halobiidae Kittl, 1912

(*nom. transl.* Cox & Newell, 1969)

ex Posidoniinae Frech, 1909)

Subfamily AULACOMYELLINAE Ichikawa, 1958

In the present work, the Aulacomyellinae is placed as a subfamily of the Posidoniidae, following Ichikawa (1958), although it is noted that Romanov (1976) preferred to place both *Posidonia* and *Aulacomyella* within the Rhombopteriidae (Korobkov 1960). Further studies based on hinge and shell structure are needed on these groups before their precise relationships can be established. The present material is not sufficiently well preserved for such studies. *Aulacomyella* is differentiated from both *Halobia* and *Daonella* by its much shorter hinge line. Its lateral profile is more circular to slightly taller than the usually more elongate halobiids and daonellids. *Aulacomyella* differs from other posidoniids. *Posidonia* and *Bositra* lack radial ornament. *Pseudodidymotis* and *Veldinella* are more prosocline, and *Amonotis* and *Diotis* have dorsally convergent dorsal margins (in *Aulacomyella* the dorsal margins are straight to ventrally convergent). In *Daonella* and *Enteropleura* two internal ridges radiate from the beak (no such ridges are present in *Aulacomyella*).

Genus *Aulacomyella* Furlani, 1910

(=*Posidoniella* Furlani, 1910, *non* de Koninck, 1885)

(=*Aulacomiella* Romanov, 1976)

Type species: *Posidoniella problematica* Furlani (1910), by monotypy; Lemes Schichten, Late Kimmeridgian, Lemes Passe, Yugoslavia.

Diagnosis: Sub-orbicular to ovoid commissural outline; equivalve and thin shelled; anterior of shell slightly differentiated into auricle and with weak byssal gape; ornament of fine radial riblets; hinge structure unknown.

Remarks: Left and right valves of *Aulacomyella* are particularly difficult to differentiate from each other. The assumption is made here that the shell is byssate, and the slightly straighter anterior margin is where the supposed byssal gape is situated (Fig. 4). The orientation adopted here usually depends on the differentiated anterior area being clear. In *A. similis* Münster this anterior portion is relatively smooth and free of radial ribbing in contrast to the main flank. In the species described below ribbing exists all over the shell, and the anterior region is less clearly demarcated, but can be distinguished by the slightly straighter anterior margin and the slightly more prominent antero-dorsal margin.

The following species, recognized from published figures and museum collections, probably belong in the genus:

A. abadiensis Freneix & Quesné (1985), Late Kimmeridgian, Portugal.

A. farquharsoni Cox (1935), Late Kimmeridgian, Somalia.

A. aff. *farquharsoni* Cox (Wignall & Clausen 1990), Early Kimmeridgian, England.

A. heimi Burckhardt (*in* Heim 1926) *nom. nud.*, Late Kimmeridgian, Mexico.

A. lata Burckhardt (*in* Heim 1926) *nom. nud.*, Late Kimmeridgian, Mexico.

A. leeana (Waterston 1951), Early Kimmeridgian, Scotland.

A. lacunosae (Quenstedt 1852), Kimmeridgian, Bavaria, Germany.

A. neogeae Imlay (1945), Late Kimmeridgian, Mexico.

A. neogeae Imlay subsp. *taurica* Kiparisova 1967, Late Kimmeridgian, Crimea, U.S.S.R.

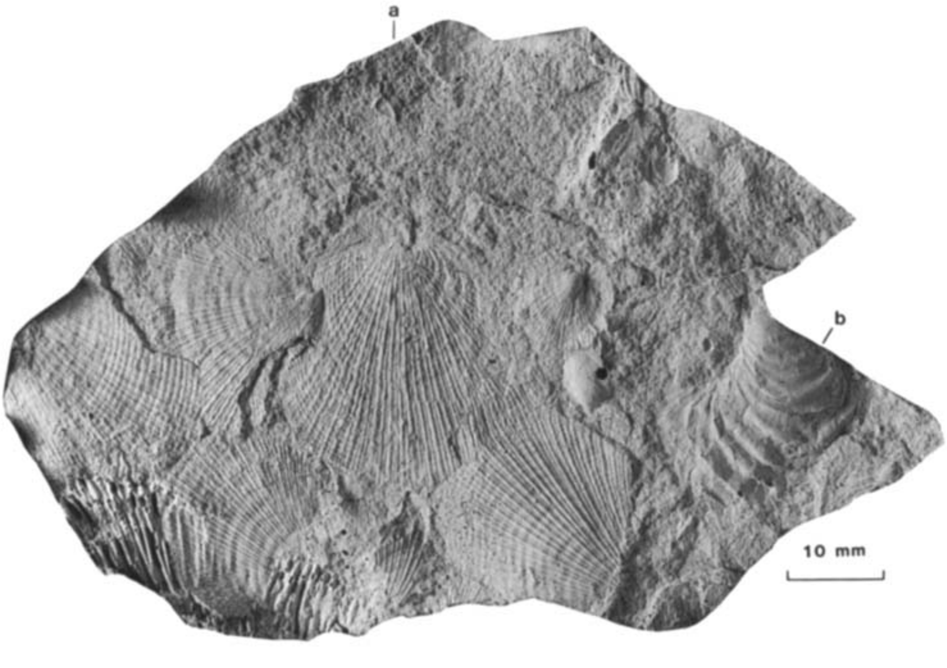

Fig. 3. Latex cast of a slab showing a typical death assemblge of *Aulacomyella willeyi* Kelly sp. nov., D.8757.31c, including the holotype (arrowed, a), and *Anopaea* (arrowed, b); glide block of Ameghino Member, Nordenskjöld Formation, Tithonian (?Late) within Early Cretaceous, Kotick Point Formation, Gustav Group, Sharp Valley, James Ross Island.

A. nummulina (Blake 1875), Early Kimmeridgian, England.
A. ovata Romanov (1976), Late Kimmeridgian, Moldavia, U.S.S.R.
A. problematica (Furlani 1910), Late Kimmeridgian, Yugoslavia
A. similis (Münster 1833), Kimmeridgian, Bavaria, Germany.
A. subtilis (Gerasimov 1955), Early Kimmeridgian, Russian Platform, U.S.S.R.
A. willeyi Kelly sp. nov., Early Tithonian, Antarctic Peninsula.

Distribution: ?Callovian/Oxfordian, Philippines; Oxfordian/ Kimmeridgian, Japan; Early Kimmeridgian, British Isles, Germany (south), USSR (Central Russian Platform); Late Kimmeridgian, Greece, Portugal, Somalia, USA (Louisiana), USSR (Crimea, Moldavia), Yugoslavia; Late Kimmeridgian-Early Tithonian, Mexico; Early Tithonian, Turkey, west Antarctica.

Aulacomyella willeyi Kelly sp. nov.

Figs 3–5

v. *1989* *Aulacomyella* sp.; Whitham & Doyle, p. 376 [Nordenskjöld Formation, Tithonian, Longing Gap, Graham Land]

v. in press *Aulacomyella* sp.; Doyle & Whitham [See Whitham & Doyle 1989]

Holotype: D.8757.31c, specimen on slab (Fig. 3; Fig. 5j), collected by A.G. Whitham, 1985/6, Ameghino Member, Nordenskjöld Formation, Tithonian (?Late); within glide block in the Kotick Point Formation, Gustav Group, of Aptian-Albian age, Sharp Valley, northern James Ross Island.

Paratypes: D.8204.10,11, D.8208.174, D.8235.4,5,7, collected by J.A. Crame, 1981/1982, as for holotype; D.8757.31a,31b,31c,31d, as for holotype; D.9010.3, D.9012.138,141,142,143,144, D.9025.28, collected by P. Doyle 1987/8, Longing Member, Nordenskjöld Formation, Early Tithonian, Longing Gap, Graham Land.

Description: Shell small to medium size, usually slightly taller than wide, with maximum length 22mm and maximum height 23.5mm; equivalve; weakly inflated as adult, but degree of inflation decreases with size; very thin shelled; commissural outline subcircular to subovoid; short straight hinge line merging gradually with posterior margin and which continues evenly rounded to the anterior margin; anterior margin slightly flattened but curves onto the anterior end of the hinge line; the beaks are subcentral, orthogyrate and small; umbones orthogyrate, rounded and very slightly projecting; flank ornament of fine rounded radial riblets which maintain a density of about 20 ribs per 10 mm by intercalation; radial ribs are reflected on the shell interior, but disappear slightly towards the umbo (slightly obscured because of preservation as composite moulds); anterior portion of flank not differentiated, but ribbed like rest of flank; radial ribs towards the anterior and posterior, especially in larger specimens, show tendency towards being regularly weakly tuberculate at junctions with commarginal ornament; coarser commarginal folds are usually present across most of the flank, but show up most conspicuously nearer the dorsal margins; commarginal growth lines are most conspicuous towards the ventral margin; byssal gape, hinge structure and muscle scars not observed.

Measurements:

Specimen	Left/Right valve	Total Length	Total Height
D.8757.31c	R	22.0	23.5
D.9012.142	?	10.0	11.5
D.9012.144	?R	14.5	19.5
D.9012.144	?R	9.0	11.0
D.9012.144	?L	-	21.5
D.9012.144	?	14.5	14.5
D.9012.144	?	14.5	15.0
D.9025.37	?	15.0	14.5

Remarks: *A. willeyi* is distinguished from all other species of *Aulacomyella* by its particularly distinctive development of weak swellings on the radial ribs where they are traversed by the weaker commarginal ornament. This feature, which is particularly pronounced on the anterior and posterior portions of the flank, has not been identified in other species. Most specimens are usually slightly taller than long, which

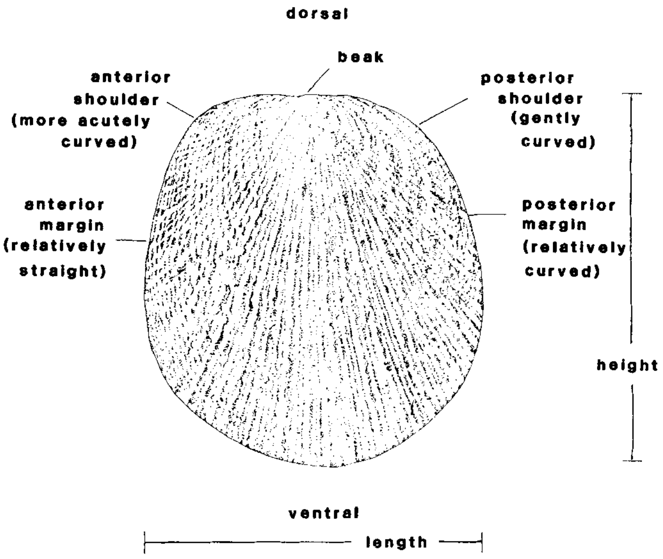

Fig 4. General shell exterior morphology in the left valve of *Aulacomyella willeyi* Kelly sp. nov., showing morphology and orientation of dimensions.

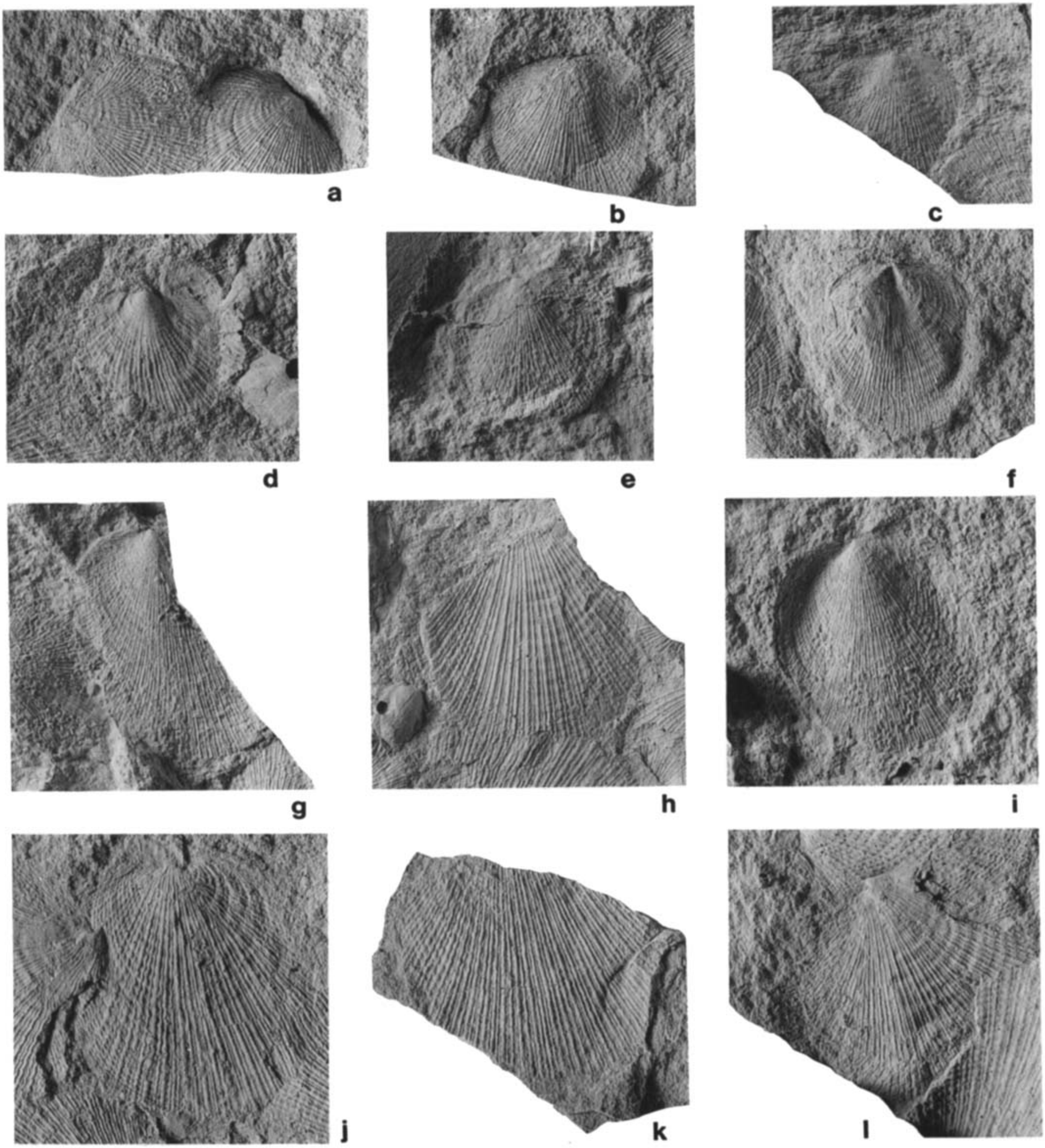

Fig. 5. *Aulacomyella willeyi* Kelly sp. nov., Longing Member, Nordenskjöld Formation, Early Tithonian; **a-c**, **e-g**, **i**, Gap Longing, Graham Land (**a-c**, **f**, D.9012.142; **e**, **g**, **i**, D.9012.144); **d**, **h**, **j**-**l**, Ameghino Member, Sharp Valley glide block, northern James Ross Island (**d**, **h**, **j**, **l**, D.8757.31c; **k**, D.8204.11). Figs **a**,**b** and **k** are composite moulds, the rest are latex casts; Fig. **j**, holotype; Figs **a-i**, **k-l** paratypes. Magnifications: Figs **a-c**, **e-l** x1.8, **d** x3.

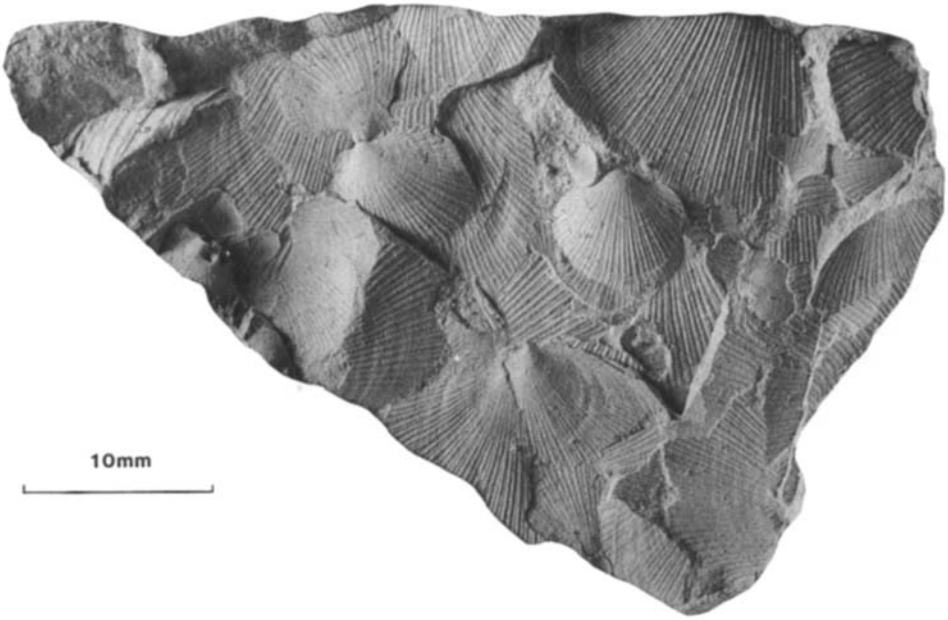

Fig. 6. Latex cast of *Aulacomyella* cf. *problematica* Furlani, KG.712.139, Himalia Ridge Formation, Fossil Bluff Group, Early Tithonian; Himalia Ridge, eastern Alexander Island.

differentiates internal moulds more readily from most specimens of the *A. problematica* group such as *A. neogeae* Imlay. *A. similis* (Münster) is characterized by a more strongly differentiated anterior wing which is almost smooth.

Distribution: Early Tithonian (? Late Tithonian) of the northern Antarctic Peninsula.

A. cf. *problematica* Furlani, 1910

Fig. 6.

v. 1972 *Aulacomyella* sp.; Willey, p. 55, fig. 41 [Fossil Bluff Group, Himalia Ridge Formation, Tithonian, Himalia Ridge, Alexander Island].

For full synonomy of *A. problematica* see Romanov (1976).

Material: KG.712.139, KG.880.3, KG.884.2. Collected by M.H.Elliott, 1969, from the Himalia Ridge Formation, Fossil Bluff Group, Himalia Ridge, eastern Alexander Island. Note: the figured specimen of Willey (1972, fig. 41) is KG.712.139, and *not* KG.703.02 as stated on figure 41 caption. A cast of this specimen is refigured here (Fig. 6).

Description: (based on incomplete specimens) up to at least 15mm length; shell thin, moderately inflated in juveniles and weakly inflated in adults; commissural outline subovate; beaks small, subcentral; umbones not projecting; fine smooth radial ribs over whole flank; new ribs inserted by intercalation; feeble commarginal folds present on ?posterior; anterior and posterior auricles not differentiated.

Remarks: Willey (1972) noted the similarity of his specimens to those from Mexico described as *A. neogeae* Imlay (1940). However, that species is placed here in the species group of *A. problematica*. *A. neogeae*, together with *A. neogeae taurica* subspecies nov. from the Crimea (Kiparisova 1967) and *A. farquharsoni* Cox (1935) from Somalia, were all included by Romanov (1976) in synonymy with *A. problematica* specimens from Moldavia. *A. ovata* Romanov, also placed in the group of *A. problematica* here, is a relatively short species, which lacks the weakly tuberculate ornament of *A. willeyi*. The Early Kimmeridgian species *A. similis* (Münster 1833) from central and northern Europe is distinguished from *A. willeyi* by a much more clearly differentiated anterior auricle; this auricle is usually smooth as opposed to radially ribbed.

All other Early Tithonian records of *Aulacomyella* appear to belong to the species group of *A. problematica*. *A. neogeae* Imlay was figured from Mexico (Cantú Chapa 1984), from the zones of *Virgatosphinctes mexicanus* and *Aulacomyella neogeae* of the Taman Formation. *A.* cf. *farquharsoni* Cox was identified from Turkey by Enay *et al.* (1971), but was not figured.

Palaeoecology

At present there are only limited studies of the palaeoecology of *Aulacomyella*. Wignall (1990b) recorded the mode of life as an epifaunal, byssate, suspension feeder. From his study of the Late Kimmeridgian of Mexico, Schumann (1988) concluded that *Aulacomyella* lived byssally attached and pendent, probably growing on floating seaweed or driftwood. This conclusion was based on the presence of *Aulacomyella* in anoxic sediments with a general absence of benthos and its association only with nekto-pelagic organisms, principally ammonites. Doyle & Whitham (in press) preferred a benthic mode of life for *Aulacomyella* from the Late Jurassic black shales of the Nordenskjöld Formation at Longing Gap. They suggested that it represented an opportunistic species, developing as benthic 'blooms' during episodically dysaerobic conditions. Wignall & Simms (1990) showed that it was possible for benthic organisms, including pterioid bivalves, to survive successfully for short periods within an otherwise hostile black shale environment.

Aulacomyella occurs in moderate abundance in the Longing Member of the Nordenskjöld Formation, forming local shell pavements, and is not usually found as single isolated examples. The valves appear to be largely disarticulated and most are crushed, often being preserved as flattened composite moulds. The shell pavements are largely monospecific and are interbedded with barren shales with no benthos or bioturbation (Doyle & Whitham, in press). This is similar to pavements of *Daonella* in the Botneheia Formation of Svalbard (Kelly field observations, 1985). *Australobuchia* (="*Buchia*" of Doyle & Whitham, in press) is sometimes found associated with *Aulacomyella* in groups byssally attached in life position upon an *Aulacomyella* pavement. Doyle and Whitham described this as their *Aulacomyella-Buchia* assemblage, implying a contemporaneous occurrence, although it seems more likely that this assemblage represents successive colonisation episodes. This is because the *Australobuchia* specimens can be seen to be overlying, and therefore post-dating the *Aulacomyella* shell pavement (Fig. 7). The only other benthic elements recorded from this assemblage are isolated and infrequent specimens of the inoceramid *Anopaea* and the oxytomid *Arctotis*. Oxytomids, including *Arctotis*, were found closely attached to floating ammonites and wood elsewhere in the Longing Member (Doyle & Whitham, in press) and are assumed to have been byssally attached.

The *Aulacomyella-Buchia* [*Australobuchia*] assemblage of the Longing Member gives no unequivocal indication of the mode of life of *Aulacomyella*. It is certain that *Australobuchia* was truly benthic, attached to the *Aulacomyella*

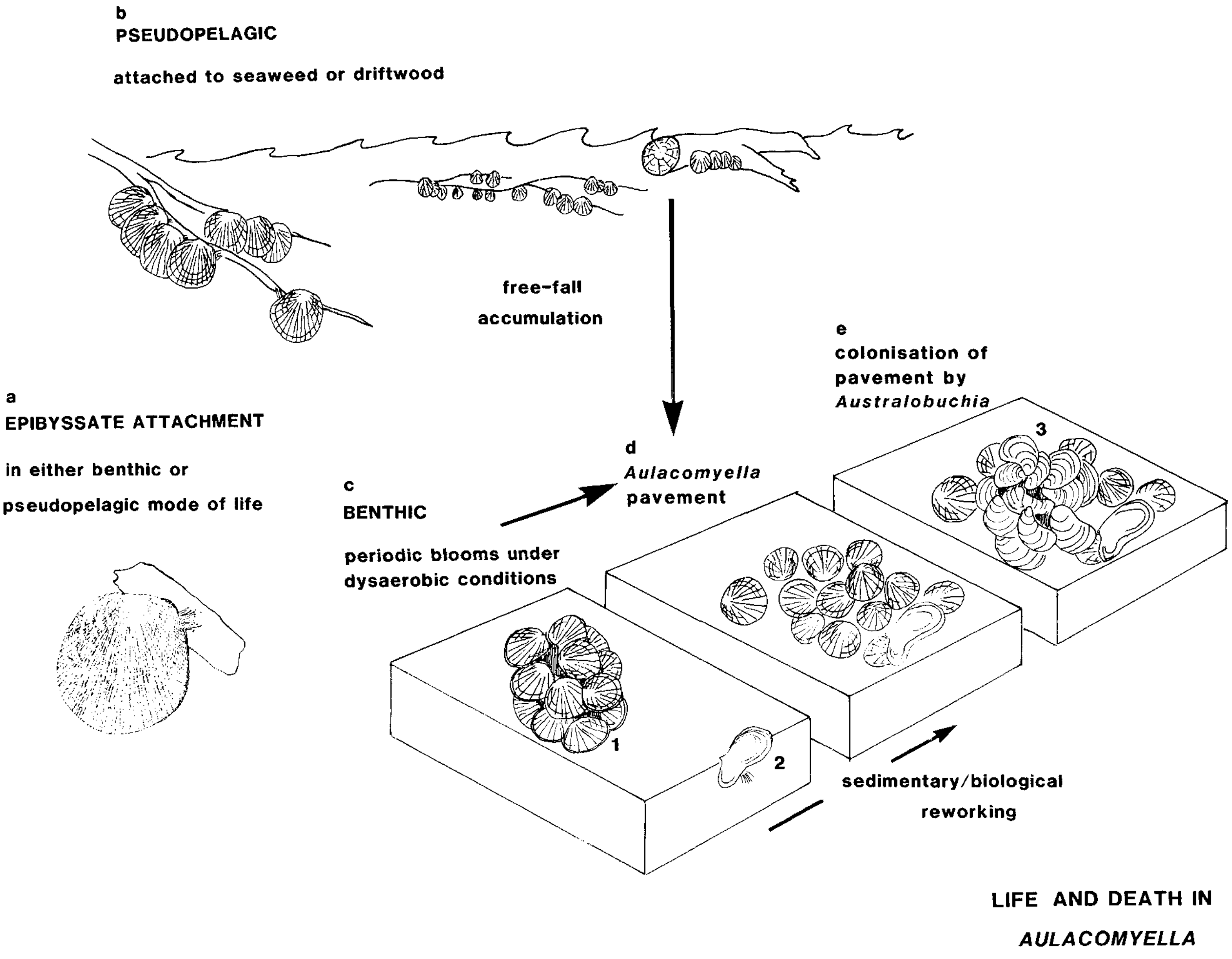

Fig.7. Palaeoecology of *Aulacomyella*. **a**, Reconstructed autecology showing byssal attachment to substrate. There are two possible modes of life, either **b**, living pseudoplanktonically attached to floating sea-weeds or drift wood (after Schumann, 1988), or **c**, living as part of a dysaerobic benthic community (1=*Aulacomyella*) with *Anopaea* (2) and *Australobuchia* (3). The figure shows the two possible pathways leading to the death assemblages; the latter (c-d-e) is preferred in this study.

shell pavement. The disarticulated nature of the shells forming the pavement would seem to suggest some form of transport or post-mortal rearrangement. Current activity within the Nordenskjöld Formation is thought to have been weak, based on sedimentological observations (Doyle & Whitham, in press; A.G. Whitham, personal communication 1990), and thus disarticulation could suggest possible derivation from the water column. Certainly other "paper pectens" such as *Halobia* and *Daonella*, regarded as benthic by Wignall (1990a), are found articulated, often in the "butterfly" position (*e.g.* Kiparisova *et al.* 1966, pl. 3, fig. 2; pl. 5, fig. 13), as one might expect in quiet water conditions. A pseudoplanktonic mode of life is a possible hypothesis, given the lack of oxygenation of the bottom waters indicated by the paucity of benthos and endobenthos in the Longing Member.

Paucispecific shell pavements are a common feature of black shales (e.g. Hallam 1987, Wignall & Myers 1988) and have recently been associated with the development of episodically dysaerobic conditions. However, derived pseudoplanktonic molluscs generally occur as scattered specimens, classically as isolated shells which have been dropped into otherwise anaerobic sediments (e.g. Wignall & Simms 1990), rather than in shell pavements. This appears to be the case lower in the Longing Member where oxytomids are found as isolated examples, and the few *Arctotis* specimens associated with the *Aulacomyella* pavements may similarly represent derived pseudoplanktonic bivalves. The exception to this could be production of shell pavements derived from pseudoplanktonic molluscs where sedimentation proceeds at a slow rate. There is little evidence to suggest that sedimentation was slower during accumulation of the *Aulacomyella*-bearing beds than it was earlier in the Longing Member during the accumulation of those beds with isolated dropped-in oxytomids.

Aulacomyella are not known to be associated with floating "substrata" in the Nordenskjöld Formation; this is in contrast to the numerous examples of ammonites and driftwood with epifauna of oxytomids (Doyle & Whitham, in press). However, it may be possible that sea-weeds, presumably with a low preservation potential, could have provided a suitable habitat for *Aulacomyella* as postulated by Schumann (1988). Another possibility is that *Aulacomyella* was free-swimming, as was argued by Jeffries & Minton (1965) for the earlier Jurassic thin shelled, equivalve bivalve *Bositra*. There are marked anterior and posterior gapes in *Bositra*, suitable for the expulsion of water jets, and although the presence of such features cannot be determined on the present *Aulacomyella* specimens, other material from Scotland (Kelly collection) shows only an anterior gape, here interpreted as byssal, as in *Halobia*.

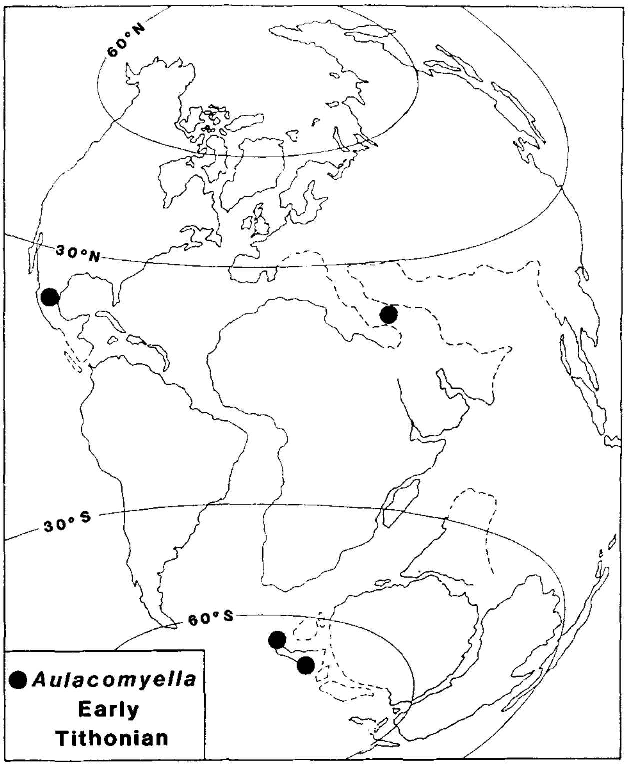

Fig. 8. Palaeobiogeographic distribution of *Aulacomyella* in Early Tithonian deposits of the world. Continental reconstruction based on Smith & Briden (1977, map 48).

Palaeobiogeography

In the Early Tithonian, *Aulacomyella* occurs in Mexico, Turkey and the Antarctic Peninsula (Fig. 8). The precise palaeobiogeographic relationship between the occurrence of *A.* cf. *problematica* in the fore-arc basin of Alexander Island and of *A. willeyi* sp. nov. in the back-arc basin of north-east Antarctic Peninsula is not yet clear. It is unlikely that the peninsula represented a complete land barrier. Certainly there is evidence of benthic fauna, such as *Retroceramus*, in the Late Jurassic common to both sides of the volcanic arc. *A.* cf. *problematica* certainly represents the southernmost occurrence of the genus. *A. willeyi*, although specifically distinct from A. cf. *problematica*, belongs with it in the same group of species, which includes all the other Early Tithonian records from Mexico and Turkey. The distributional pattern can barely be described as bipolar as the northern occurrences are both at about 20°N and the southern ones about 70°S. Almost all Kimmeridgian records of *Aulacomyella* are from the Northern Hemisphere, and only one, *A. farquharsoni* Cox (1935) from Somalia, is approximately equatorial. Prior to the Kimmeridgian all records are from the north-west Pacific. The overall distribution pattern indicates that the genus existed in warm to temperate seas from about 65°S to 40°N.

Conclusions

Of the Antarctic occurrences of *Aulacomyella*, those from

Graham Land and James Ross Island are referred to *A. willeyi* Kelly sp. nov., and those from Alexander Island are referred to *A.* cf. *problematica* Furlani. Together with Mexican and Turkish examples, these are among the latest occurrences of the genus and are of Early Tithonian age. The occurrence in the Ameghino Member on James Ross Island may be the last appearance in the Tithonian, just below the Jurassic-Cretaceous boundary and be of possible Late Tithonian age. The Antarctic occurrences are believed to be the only known records of the genus in the Southern Hemisphere.

There is no conclusive evidence for determining the mode of life of *Aulacomyella*, although the balance of evidence does suggest that it was apparently not free-swimming (at least during its adult stage). What is clear, however, is that it was an epibyssate suspension feeder. *Aulacomyella* periodically bloomed within the Longing Member of the Nordenskjöld Formation, as an opportunist. This is clearly illustrated by discrete shell pavements punctuated by barren intervals which record the ecological response of this bivalve to episodicaly dysaerobic conditions in an otherwise anaerobic environment. Although it is possible that this genus was pseudoplanktonic, the evidence presented here suggests that a benthic mode of life was more likely.

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Appendix

Natural History Museum specimen registration numbers:

B.A.S. Number	B.M.(N.H.) Number
D.8204.10	BAS L.2540
D.8204.11	BAS L.2541
D.8208.174	BAS L.2542
D.8235.4	BAS L.2543
D.8235.5	BAS L.2544
D.8235.7	BAS L.2545
D.8757.31a	BAS L.2546
D.8757.31b	BAS L.2547
D.8757.31c	BAS L.2548
D.8757.31d	BAS L.2549
D.9010.3	BAS L.2550
D.9012.138	BAS L.2551
D.9012.141	BAS L.2552
D.9012.142	BAS L.2553
D.9012.143	BAS L.2554
D.9012.144	BAS L.2555
D.9025.28	BAS L.2556
KG.712.139	BAS L.2557
KG.880.3	BAS L.2558
KG.884.2	BAS L.2559