

Invertebrates from the Low Head Member (Polonez Cove Formation, Oligocene) at Vauréal Peak, King George Island, West Antarctica

FERNANDA QUAGLIO¹*, LUIZ E. ANELLI¹, PAULO R. DOS SANTOS¹, JOSÉ A. DE J. PERINOTTO² and ANTONIO C. ROCHA-CAMPOS¹

¹Instituto de Geociências, Universidade de São Paulo, Rua do Lago 562, 05508-080, Cidade Universitária, São Paulo, SP, Brazil

²Instituto de Geociências e Ciências Exatas, Universidade Estadual Paulista, Avenida 24-A, 1515, 13506-900, Rio Claro, SP, Brazil

*quaglio@usp.br

Abstract: Eight taxa of marine invertebrates, including two new bivalve species, are described from the Low Head Member of the Polonez Cove Formation (latest early Oligocene) cropping out in the Vauréal Peak area, King George Island, West Antarctica. The fossil assemblage includes representatives of Brachiopoda (genera *Neothyris* sp. and *Liothyrella* sp.), Bivalvia (*Adamussium auristriatum* sp. nov., ?*Adamussium* cf. *A. alanbeui* Jonkers, and *Limatula (Antarctolima) ferraziana* sp. nov.), Bryozoa, Polychaeta (serpulid tubes) and Echinodermata. Specimens occur in debris flows deposits of the Low Head Member, as part of a fan delta setting in a high energy, shallow marine environment. *Liothyrella* sp., *Adamussium auristriatum* sp. nov. and *Limatula ferraziana* sp. nov. are among the oldest records for these genera in King George Island. In spite of their restrict number and diversification, bivalves and brachiopods from this study display an overall dispersal pattern that roughly fits in the clockwise circulation of marine currents around Antarctica accomplished in two steps. The first followed the opening of the Tasmanian Gateway at the Eocene/Oligocene boundary, along the eastern margin of Antarctica, and the second took place in post-Palaeogene time, following the Drake Passage opening between Antarctic Peninsula and South America, along the western margin of Antarctica.

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Introduction

The Polonez Cove Formation, cropping out at King George Island (KGI), West Antarctica (Fig. 1), preserves a diverse Cenozoic marine biota that has been subject of numerous papers dealing with coccoliths (Gazdzicka & Gazdzicki 1985), foraminifers, ostracods (Blaszyk 1987), brachiopods (Bitner & Pisera 1984, Bitner & Thomson 1999), polychaete worms, bryozoans, gastropods, bivalves (Gazdzicki & Pugaczewska 1984), scaphopods (Pugaczewska 1984), and echinoderms (Jesionek-Szymanska 1984). The Low Head Member of the Polonez Cove Formation is a richly fossiliferous unit (Bitner & Thomson 1999), and crops out at various sites along the eastern coast of KGI. Most of the stratigraphic and palaeontological studies of the Polonez Cove Formation available in the literature refer to the type-section of the formation exposed from Lions Rump to Low Head along the southern coastal of KGI (Fig. 1). Although briefly described by Birkenmajer (1982), Porebski & Gradzinski (1987) and Troedson & Riding (2002), Cenozoic sediments cropping out at Vauréal Peak, on the northern margin of Admiralty Bay, had never been palaeontologically studied or correlated with the Polonez Cove Formation, perhaps due to the limited exposure at this site.

The new taxonomic data here presented, allied to previous studies on fossil invertebrates from Antarctic regions, are

essential for establishing the palaeontological affinities of KGI fossils with other Cenozoic faunas from Antarctic peripheral southern continents. These data bear on the identification of migratory routes of marine faunas from northern warmer waters into Antarctica, and on the understanding of palaeobiogeographical patterns established during the glacial history of West Antarctica at the time of its separation from South America at the end of Palaeogene (e.g. Zinsmeister 1982, Crame 1999, Briggs 2003).

The present paper is a part of a series aiming to describe the marine invertebrate faunas from Cenozoic deposits of KGI (Anelli *et al.* 2006), evaluating their taxonomic affinities in order to recognize dispersal routes that shaped their composition, and interpreting their palaeoenvironment in the context of their depositional history.

Geological setting, age and palaeontology

Fossil invertebrates described herein were collected from outcrop assigned to the Low Head Member of the Polonez Cove Formation at Vauréal Peak, Admiralty Bay, KGI, West Antarctica (Fig. 1), in the summer of 2004, during the Operação Antártica XXII of the Brazilian Antarctic Program (PROANTAR). Other exposures of the Polonez Cove Formation occur on a cliff along the eastern coast of

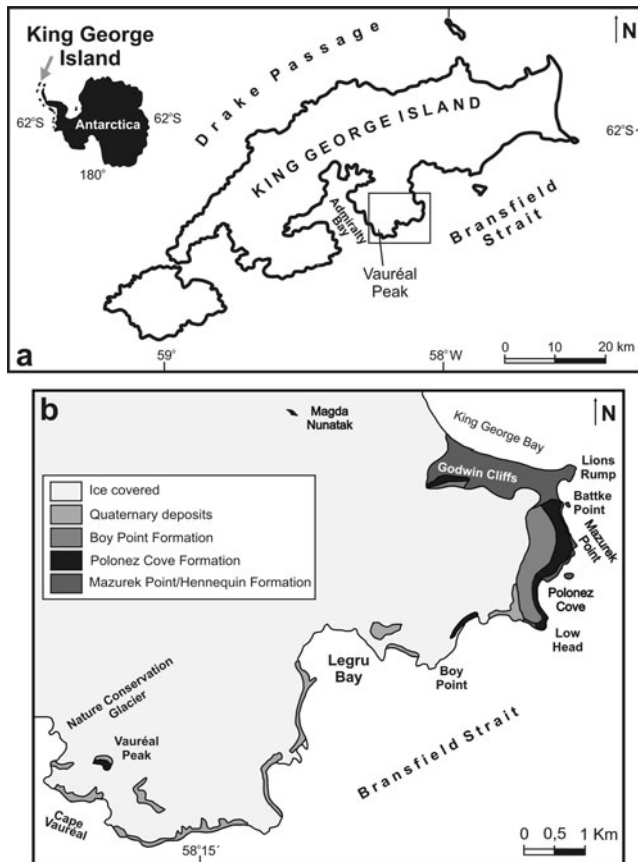


Fig. 1. Location maps of the Polonez Cove Formation exposures and other related units. **a.** location of Vauréal Peak, Admiralty Bay, King George Island, Antarctica; the area inside the square corresponds to Cenozoic glacial sediments detailed in **b.** **b.** Occurrence of the Polonez Cove Formation and associated stratigraphic units (adapted from Birkenmajer 2001 and Troedson & Smellie 2002).

the island, between Lions Rump and Low Head, King George Bay (type-area of the unit, Birkenmajer 1982), at Three Sisters Point, as well as inland at Godwin Cliffs and Magda Nunatak (Porebski & Gradzinski 1987, Birkenmajer 2001, Troedson & Smellie 2002). (Fig. 1b.)

In its type-area, the Polonez Cove Formation is represented by a sequence of diamictites and fossiliferous basaltic conglomerates and sandstones. The main characteristic of the formation is the presence of conglomerate facies containing faceted and striated pebble- to boulder-sized clasts of local and continental Antarctic provenance, assigned to the Krakowiak Glacier Member (Birkenmajer 2001, 2003). A detailed description of the stratigraphy, facies and depositional environment of the Polonez Cove Formation appears in Porebski & Gradzinski (1987, 1990), Santos *et al.* (1990), and Troedson & Smellie (2002).

The Polonez Cove Formation sequence cropping out at Vauréal Peak starts with diamictite, up to 5 m thick,

correlated to the Krakowiak Glacier Member, which passes upwards to lenticular beds of matrix or clast-supported, massive gravel and grainy to pebbly sandstone, 6 m thick, of the Low Head Member (Fig. 2).

The Low Head Member facies described in this paper can be correlated to the LH3 facies (*sensu* Birkenmajer 1994, 1995) and to the L2 facies (*sensu* Troedson & Smellie 2002) of the Low Head Member (Table I).

As shown on the 7 m thick stratigraphic section measured at Vauréal Peak (Fig. 2, Table I), at least four gravelly sandstone beds, around 1–1.5 m thick occur, normally graded, with erosive base and lenticular geometry at outcrop scale. Beds are composed, from base to top, of massive matrix (Gmm) or clast-supported (Gmc) gravels, that grade upward into massive sandstones with sparse granules and pebbles (Sm).

Invertebrate fossils occur in the lower portions of the section. None of the specimens was found in life position; all of them occur randomly distributed in the matrix. All brachiopods are articulated, lacking the anterior portion of the shell and most of all bivalves are articulated. Most invertebrate specimens (brachiopods and particularly serpulid tubes, bryozoans and echinoderms) are fragmentary, but with no features of prolonged reworking, such as roundness or selection. These characteristics suggest that these are allochthonous fossil assemblages (Brett & Baird 1986, Kidwell *et al.* 1986). The occurrence of pyrite framboids in some fossils (Fig. 3) indicates a period of low oxygen conditions (reducing environment) after deposition and none or very low reworking until lithification of the sediments (Brett & Baird 1986). No evidence of ichnofossils was found, that also suggests a probable reducing environment and absence of reworking by bioturbators (Speyer & Brett 1991).

We interpret these deposits as products of episodic sedimentation from cohesive and non-cohesive debris flows, originated by slumping or even from the action of bottom traction currents, followed by aggradational deposition of sediments by deceleration of high-energy episodic flows. This facies association is interpreted as deposited in a fan delta setting, in high- to medium-energy, shallow marine environment (Eyles & Eyles 1992). Regionally, this facies association and arrangement conform to available sedimentary models of a marine transgressive phase, following a retreating grounded ice margin (Porebski & Gradzinski 1987, Santos *et al.* 1990, Birkenmajer 2001, 2003).

The so called “pecten conglomerate” of the Low Head Member (Adie 1962, Barton 1965, discussed in Birkenmajer & Gazdzicki 1986, and Birkenmajer 2001) in the type-area, is the most fossiliferous component of the Polonez Cove Formation. It contains marine macro- and microfossils, including coccoliths, diatoms, foraminifers, polychaete worms, bryozoans, brachiopods, gastropods, scaphopods and echinoderms (Bitner & Pisera 1984, Gazdzicki & Pugaczewska 1984, Jesionek-Szymanska 1984). Some taxa described herein are comparable with fossils previously

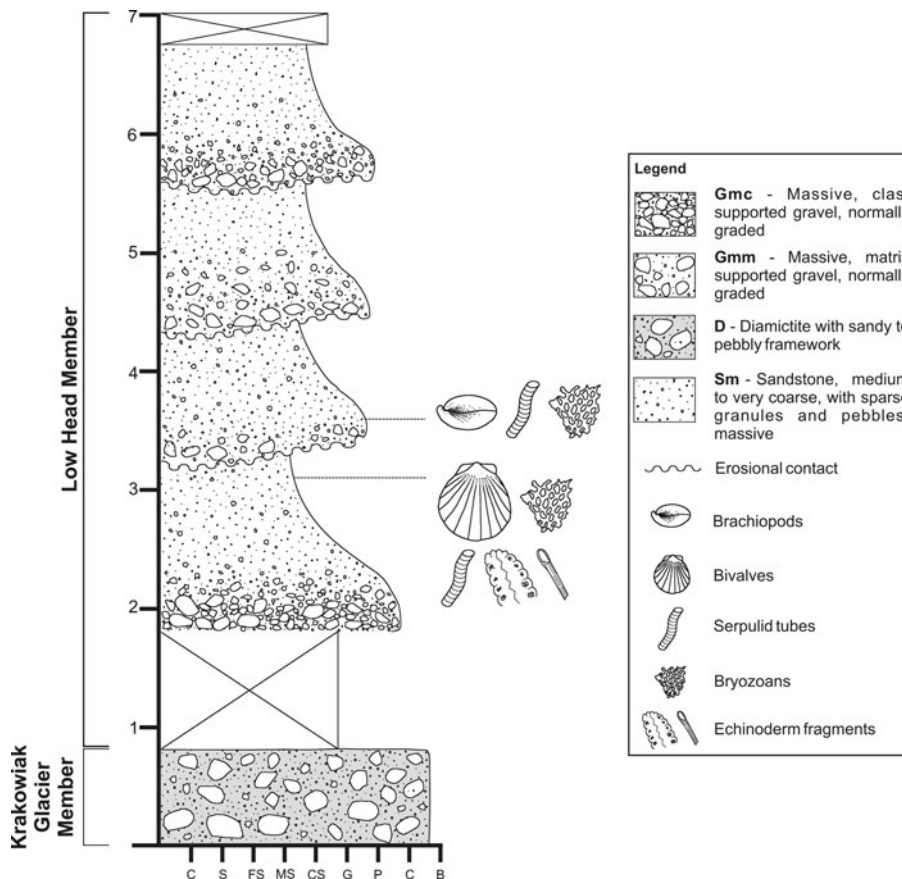


Fig. 2. Stratigraphic column of the Polonez Cove Formation measured at Vauréal Peak.

described from the “pecten conglomerate”; others are for the first time described for the Polonez Cove Formation or even for KGI.

The age of the Low Head Member is still controversial. Available K–Ar dates, Sr-isotope dating and palaeontological data from the type-area indicate a latest early Oligocene age (late Rupelian) for this member (Birkenmajer & Gazdzicki 1986, Dingle *et al.* 1997, Dingle & Lavelle 1998, see Fig. 4). So the “pecten conglomerate” of KGI is probably a unit distinct from the Pliocene “pecten conglomerate” (Cockburn Island Formation; Jonkers 1998, 2003) originally described from Cockburn Island, in the western Weddell Sea.

Taxonomy

Material and methods

Brachiopods were measured with reference to the anterior-posterior axis of the shell (Fig. 5a & b), according to the “landmarks 1 and 9” of Krause (2004, p. 462). Bivalves were measured with reference to the hinge line of the shell. The length, height and width of the bivalve shell correspond to the greatest measured lines parallel, perpendicular and orthogonal to the hinge line, respectively (Fig. 5c & d). Elongation and obesity indexes were calculated according to Stanley (1970). Symbols in tables

are as follows: D = dorsal valve, V = ventral valve, R = right valve, L = left valve, D/V or R/L = articulated valves, * = specimen incomplete, AOL = length of the anterior outer ligament, POL = length of the posterior outer ligament, AVH = anterior dorsal valve height, PVH = posterior dorsal valve height.

Taxonomy above the genus level applied to the brachiopods is based on the classification of Williams *et al.* (2006); suprageneric names utilized for the bivalves are based on the synoptical classification proposed by Amler (1999); systematics of serpulids, bryozoans and echinoderms follows the classification of Howell (1962), Boardman *et al.* (1983) and Durham *et al.* (1966), respectively.

The stratigraphic distribution of taxa is shown on Fig. 2. All material is from a single locality at Vauréal Peak, and, therefore, data on locality and stratigraphy are not repeated below.

All specimens are housed in the scientific collection of the Laboratório de Paleontologia Sistemática of the Departamento de Geologia Sedimentar e Ambiental, Instituto de Geociências, Universidade de São Paulo, under prefix GP/1E.

Systematic palaeontology by Quaglio & Anelli

Phylum BRACHIOPODA Duméril, 1806

Class ARTICULATA Huxley, 1869

Table I. Sedimentary facies of the Polonez Cove Formation at Vauréal Peak area.

Member	Code	Facies	Description	Interpretation	Fossils
	Sm	Sandstone, medium to very coarse, with sparse granules and pebbles, massive	Metre-scale lenticular beds, laterally discontinuous, composed of coarse massive sandstone containing granules and dispersed pebbles. Poor granular selection, medium to low roundness and subspherical grains with irregular surfaces. Overlaps Gmm and Gmc facies, corresponding to the final portion of ascendant grading.	Deceleration of high energy episodic flows originated fromslumping, cohesive debris flows or even the action of bottom tractive currents	serpulid tubes, brachiopods, bivalves, bryozoans, echinoderm fragments
Low Head	Gmc	Massive, clast supported gravel, normally graded	Lenticular beds or with channelized base, of metre-scale thickness and lateral extension, composed of clast-supported massive gravel of grey colour. Commonly the beds include erosive contact at the base and are somewhat normally graded, with the clasts un-oriented and varying from blocks to cobbles at the base grading to pebbles to granules toward the top. The clasts are of medium sphericity and varied roundness, with basaltic and rarely acid volcanic composition. The matrix is mostly of medium to coarse sand, with granule composition usually the same of the clasts.	Product of episodic sedimentation fromuncohesive debris flows, occasionally reworking by traction currents	-
	Gmm	Massive, matrix supported gravel, normally graded	Discontinuous lenticular beds in outcrop scale, of metric thickness. Composed of matrix-supported massive gravel of grey colour. Like the Gmc facies, Gmm is normally graded, characterized by larger clasts at the base (abundance of blocks to cobbles) and the minor ones toward the top (blocks to pebbles). The clast roundness and sphericity, as well clast and matrix lithology are the same as for Gmc facies.	Deposited by slumping or cohesive debris flows	-
Krakowiak Glacier	D	Diamictite	Black-grey diamictite, massive, with sandy to pebbly framework, which is composed predominantly of granitic and quartzitic pebbles (5–20 mm), occasionally showing striated faces. Pebbles up to 5–50 mm occur rarely. Interbedded lenses of coarse sandstone with 5–15 mm pebbles occur locally.	Melt-out and glaciogenic debris flows (according to Troedson & Smellie 2002)	-

Order TEREBRATULIDA Waagen, 1883
 Suborder TEREBRATULIDINA Waagen, 1883
 Superfamily TEREBRATULOIDEA Gray, 1840
 Family TEREBRATULIDAE Gray, 1840
 Subfamily TEREBRATULINAE Gray, 1840
 Genus *Liothyrella* Thomson, 1916

usually large; teeth narrow; low myophragm; outer hinge plates attached near dorsal edge of crural bases [here called crural plates].

Liothyrella sp.
 Fig. 6, Table II

Type-species. Terebratula uva Broderip

Material. Internal mould of articulated valves, with anterior part missing (5465).

Remarks. The specimen found at Vauréal Peak shows some of diagnostic characters of the genus *Liothyrella* pointed out by Lee & Smirnova (2006, p. 2056–2057), which are: shell large to very large, elongate oval to subcircular; foramen

Description. Shell of medium size, lateral margins rounded; ventral valve apparently more convex than dorsal valve; lateral commissures straight, anterior not preserved. Beak short and erect; foramen large, circular; crural plates

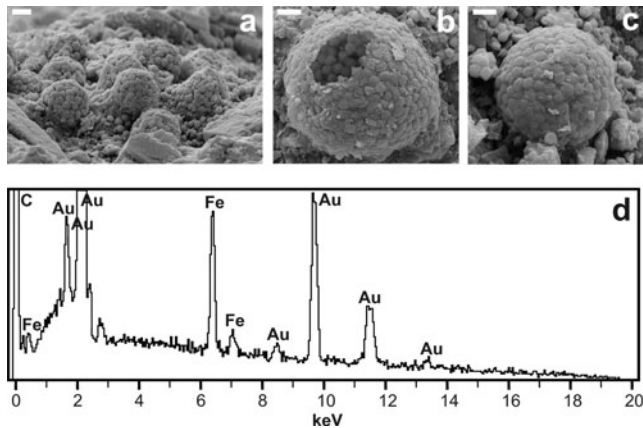


Fig. 3. Pyrite framboids occurring in bryozoan specimen 5352.
a. framboids photographed by SEM (scale bar = 2 µm). **b.** EDS granules composition.

triangular, extending along margin of outer hinge plates; hinge teeth narrow, sulcus constricted. Adductor scars of dorsal valve very broad, with myophragma evident; elongate furrows posteriorly in dorsal valve, close to the umbonal region, are possibly related to the muscular field; two sets of several marks of circular shape laterally to the adductors in the posterior region of both valves, possibly correspond to genital scars.

Comparison. *Liothyrella* sp. from Vauréal Peak differs from *Liothyrella* sp. from Cape Melville Formation (Lower Miocene) at Melville Peninsula (Bitner & Crame 2002) in its greater size, more circular shape and higher convexity of the dorsal valve. It is impossible to compare other features of the two taxa because only external characters of the Miocene *Liothyrella* sp. are known, while the Oligocene *Liothyrella* sp. is known only as an internal mould. The *Liothyrella* specimens from the Eocene La Meseta Formation (Bitner 1996) are larger and more elongate. Although Bitner (1997) illustrated a specimen of *Liothyrella* sp. from the Low Head Member of the Polonez Cove Formation at Mazurek Point (p. 26, fig. 4A–C), it is not described or commented on in a taxonomic approach. The shell from Mazurek Point is smaller and more elongate than *Liothyrella* sp. from Vauréal Peak, but it is apparently distorted (compressed) and poorly preserved.

Remarks. *Liothyrella* sp. from Vauréal Peak is the oldest record of the genus from KGI together with the specimen from the Low Head Member at Mazurek Point (illustrated by Bitner 1997, p. 26, fig. 4A–C).

Suborder TEREBRATELLIDINA Muir-Wood, 1955
 Superfamily TEREBRATELLOIDEA King, 1850
 Family TEREBRATELLIDAE King, 1850

Period	Epoch	Formation	Member	Age
Paleogene	Oligocene	Boy Point		>23.6 ⁷
		Polonez Cove	Low Head	? 28.5 ⁶ 29.4 ⁵ 29.8 ⁴
	Eocene	Mazurek Point / Hennequin		? 34.4 ³ 42.0 ²
Cretaceous	Late			74.0 ¹

Fig. 4. Stratigraphic position of Cenozoic units at Vauréal Peak (plotted ages after studies in other locations in which these units also occur). 1 = K–Ar dating of basaltic lava at Polonez Cove (Birkenmajer & Gazdzicki 1986), 2 = K–Ar dating of andesitic lava at Turret Point (Birkenmajer *et al.* 1989), 3 = K–Ar dating of andesitic lava at Lions Rump (Smellie *et al.* 1984), 4 = Strontium-isotope dating of bivalve shells from Krakowiak Glacier Member tillites at Polonez Cove (Dingle & Lavelle 1998), 5 = Strontium-isotope dating of bivalve shells from Low Head Member conglomerates at Low Head, Polonez Cove and Lions Rump (Dingle *et al.* 1997), 6 = Strontium-isotope dating of bivalve and brachiopod shells from basal tillites at Magda Nunatak (Dingle & Lavelle 1998), 7 = K–Ar minimum age from andesite–dacite lavas at Polonez Cove and Boy Point (Birkenmajer & Gazdzicki 1986).

Subfamily TEREBRATELLINAE King, 1850
 Genus *Neothyris* Douvillé, 1879

Type-species. *Terebratula lenticularis* Deshayes, 1839

Discussion. Characters attributed to the genus *Neothyris* by MacKinnon & Lee (2006, p. 2231, 2233) shared by specimens from the Polonez Cove Formation at Vauréal Peak are shell large, smooth; with beak incurved; strong posterior shell thickening; median septum short; crura rather short; loop teloform.

Neothyris sp.
 Figs 7 & 8, Table III

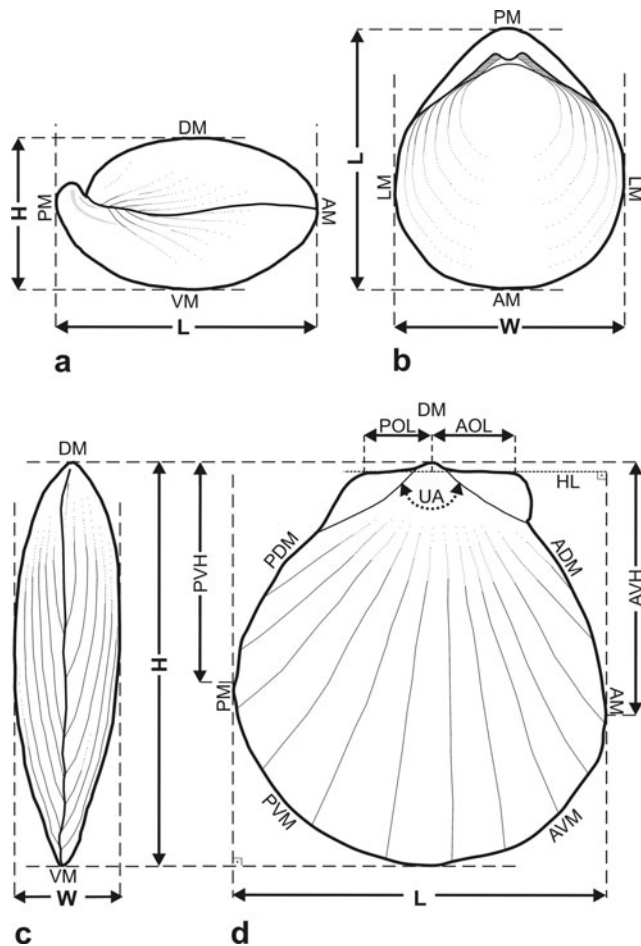


Fig. 5. Orientation and characters measured. **a–b.** Brachiopod, **c–d.** bivalve. **a.** lateral view, **b.** dorsal view, **c.** anterior view, **d.** lateral view of RV. ADM = anterior dorsal margin, AM = anterior margin, AOL = length of the anterior outer ligament, AVH = anterior dorsal valve height, AVM = anterior ventral margin, DM = dorsal margin, H = height, HL = hinge line, L = length, LM = lateral margin, PDM = posterior dorsal margin, PM = posterior margin, POL = length of the posterior outer ligament, PVH = posterior dorsal valve height, PVM = posterior ventral margin, T = thickness, UA = umbonal angle, VM = ventral margin, W = width.

Material. Articulated valves lacking anterior margin (5374c, 5594a); posterior region of articulated valves (5374e, 5438f, 5438g, 5438i, 5464); dorsal valve (5462); posterior region of dorsal valve (5461, 5594b).

Description. Shell of medium size, trigonal to ovoid in outline, ventral valve more convex than dorsal, lateral margins rounded, with greatest width at anterior mid-length; lateral commissure straight, anterior region apparently rounded (in specimen 5594a), posterior region of ventral valve very thick. Shell surface with well defined growth lines. Beak curved, well developed; foramen not observable. Crura and septum reaching around 30% of

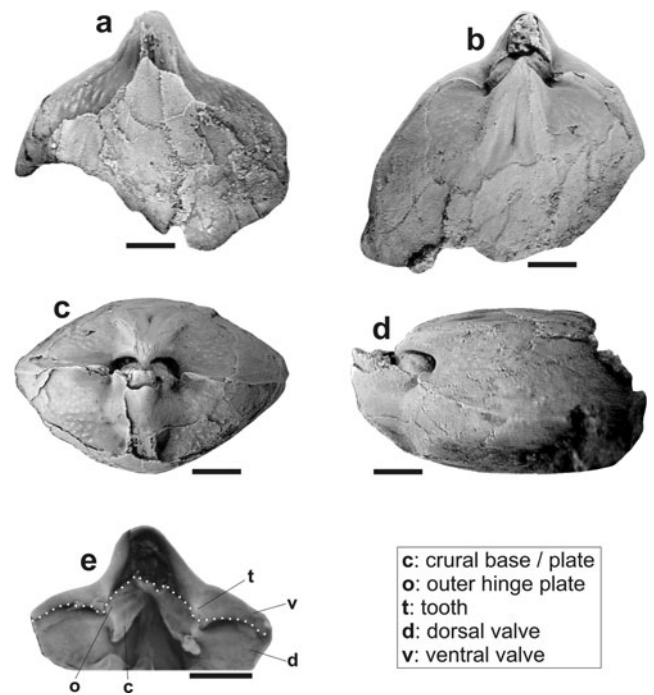


Fig. 6. *Liothyrella* sp. **a–d.** specimen 5465, internal mould of articulated pair; **a.** ventral view, **b.** dorsal view, **c.** posterior view, **d.** lateral view. **e.** latex cast of anterior region of 5465, dotted line marks the limit between ventral (upper) and dorsal (lower) valves (all bars = 5 mm).

shell length; loop teloform (see Fig. 8). Adductor scars of dorsal valve broad, with myophragm weakly developed; myophragm of ventral valve well developed. Shell microstructure composed of thin primary layer, mosaic structure observed in the second layer; punctae large.

Comparison. Specimens from Vauréal Peak locality are similar to *Neothyris* sp. identified from Lions Rump by Bitner & Pisera (1984), both from Low Head Member of the Polonez Cove Formation. They differ in the smaller size, more ovoid shape and more developed beak of the Vauréal Peak specimens. *Neothyris* sp. from Vauréal Peak resembles *Neothyris* sp. from the Destruction Bay Formation at Melville Peninsula (Biernat *et al.* 1985) in general shape and beak, but is smaller. The differences could be due to ecological factors, but internal characters of the specimens cannot be compared.

Remarks. Neall (1972) pointed out that the anterior region of the *Neothyris* shell is thin and fragile, and the posterior part is the most commonly preserved. All of our specimens preserved only the posterior region of the shell. The lack of preservation of the foramen presents the greater difficulty for the identification of our specimens. However, other characters above described point to the genus *Neothyris*. Besides, the occurrence of *Neothyris* at Vauréal Peak is

Table II. Dimensions in millimetres and character values of specimen of *Liothyrella* sp.

Specimen	Valve	Length	Thickness	Width	Elongation	Obesity
5465	D/V	27.3*	14.7	25	1.8	0.58

possible because this genus is common in other Cenozoic deposits of KGI (Bitner & Pisera 1984, Biernat *et al.* 1985, Bitner 1997, Bitner & Crame 2002).

Class BIVALVIA Linné, 1758 (Buonanni, 1641)
 Subclass PTERIOMORPHIA Beurlen, 1944
 Order PTERIOIDA Newell, 1965
 Suborder PTERIINA Newell, 1965
 Superfamily PECTINACEA Rafinesque, 1815
 Family PECTINIDAE Rafinesque, 1815
 Genus *Adamussium* Thiele, 1934

Type-species. *Pecten colbecki* Smith, 1902

Remarks. Jonkers (2003, p. 67) proposed several diagnostic characters of the genus *Adamussium*. Among these, the material from Vauréal Peak presents: shell smooth or with low costae formed by simple crenulation of the disc; very wide umbonal angle; hinge straight or with dorsal projections; anterior auricle of the left valve curved outward, anterior auricle of the right valve with a shallow arcuate to relatively deep and acute byssal notch; and a functional ctenolium may be present in adults.

Adamussium auristriatum sp. nov.
 Fig. 9, Table IV

Material. Holotype, internal mould of articulated valves (5457b), external mould of right valve (5457a). Paratypes, internal moulds of articulated valves (5458b); internal moulds of right valve (5301a, 5361, 5405); external moulds of right valve (5301b, 5394, 5458a); external mould of left valve (5428).

Etymology. From Latin *auris* = ear and *striatum* = striated, referring to the radial costae on the anterior auricle.

Diagnosis. Umbonal angle around 130°; commarginal sculpture of lirae, weakly marked, almost equally and widely spaced down the entire shell; RV auricles almost symmetrical, posterior and anterior with well defined commarginal lines, anterior auricle with radial costae.

Description. Shell varying from moderate to small in size, subcircular; dorsal margin short, ventral margin wide and rounded; equant; very compressed, with moderately convex valves; beaks orthogyrate; umbonal angle wide (around 130°); valves slightly opisthocline (mean AVH/PVH = 1.10); radial sculpture of around 10–15 main plicae, intercalated with lower and less developed plicae; commarginal sculpture of lirae, weakly marked, almost

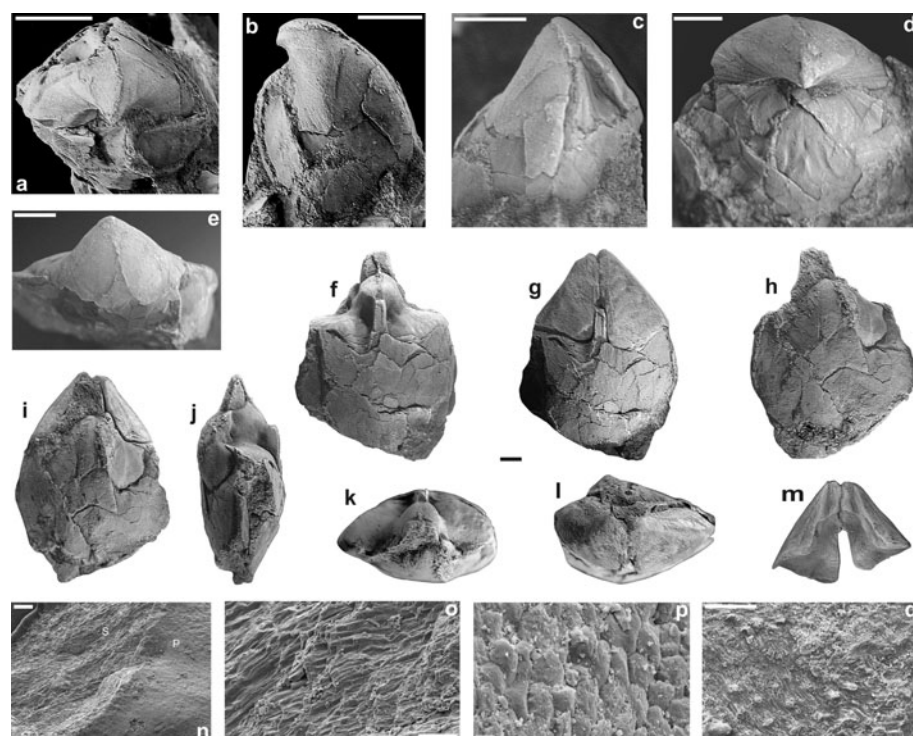


Fig. 7. *Neothyris* sp. **a–c.** Specimen 5374c, articulated pair; **a.** posterior view, **b.** lateral view, **c.** ventral view. **d–e.** Specimen 5374e, articulated pair lacking anterior part; **d.** posterior view, **e.** ventral view. **f–m.** Specimen 5594a–b, posterior part of shell and internal mould of articulated valves of same individual; **f.** ventral view of internal mould, **g.** the same with posterior part added, **h.** dorsal view of internal mould, **i.** the same with posterior part added, **j.** lateral view, **k.** posterior view of internal mould, **l.** the same with posterior part added, **m.** internal view of posterior part (all bars = 5 mm). **n–q.** Microstructure photographed by SEM, **n–p.** specimen 5300, **n.** primary (p) and secondary (s) calcitic layers (scale bar = 200 µm), **o.** detail of **n**, showing secondary layer only (scale bar = 100 µm), **p.** mosaic arrangement of secondary layer (scale bar = 10 µm), **q.** specimen 5438, showing punctae (scale bar = 100 µm).

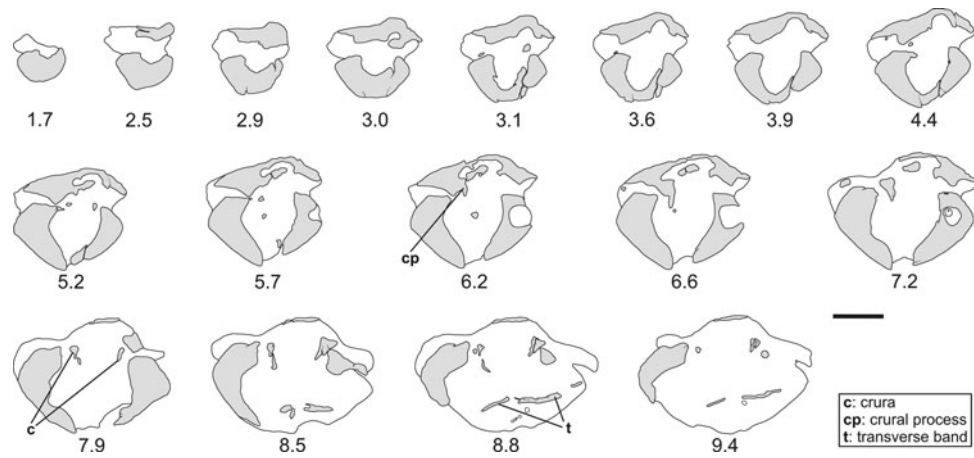


Fig. 8. Serial sections of *Neothyris* sp. Numbers represent distance (mm) from ventral beak; dorsal valve is upward; filled areas correspond to calcitic shell; first appearance of some structures is indicated. Length of specimen around 25 mm (scale bar = 5 mm).

equally and widely spaced down the entire shell; microsculpture of narrow antimarginal ridgelets; hinge line almost straight; RV auricles highly symmetrical (mean AOL/POL = 1.04), posterior and anterior with well defined commarginal lines, anterior auricle rounded, with 4–6 radial costae; byssal notch acute, ctenolium with six byssal teeth (in 5457b).

Comparison. *Adamussium auristriatum* sp. nov. differs from the Pleistocene–Recent *A. colbecki colbecki* in its smaller size, its equally convex valves, its narrower umbonal angle, its more equally spaced and weaker commarginal sculpture, and the presence of radial costae on the RV anterior auricle. *Adamussium auristriatum* sp. nov. differs from *A. colbecki cockburnensis* from the Late Pliocene Cockburn Island Formation (Jonkers 2003) in its opisthocline valves, narrower umbonal angle, more symmetrical auricles, weaker commarginal sculpture and the presence of radial costae on the RV anterior auricle. The auricles and umbonal angle of *A. alanbeui* Jonkers, 2003 are very distinct from those of *A. auristriatum* sp. nov., which contains commarginal sculpture and symmetric auricles. However, the pattern of antimarginal microsculpture is very similar in the two. The specimens of *A. alanbeui* from the type-area of Polonez Cove Formation (initially identified as *Eburneopecten* sp. by Gazdzicki & Pugaczewska 1984) are poorly preserved, but the sculpture pattern is very unlike *A. auristriatum* sp. nov. Comparison with other *Adamussium* species is presented in the Table V.

Remarks. *Adamussium colbecki colbecki* is known from Pliocene and Pleistocene deposits of West Antarctica, and from the Recent of the Southern Ocean (Jonkers 2003). *Adamussium colbecki cockburnensis* is recorded only from Late Pliocene Cockburn Island Formation (Jonkers 2003). One specimen of *A. alanbeui* from the Polonez Cove Formation, presumably from the Low Head Member, at Godwin Cliffs, Lions Rump area, was identified and illustrated by Jonkers (2003). This species differs from other species of *Adamussium* in lacking radial costation and commarginal lirae (Jonkers 2003). Together with *A. alanbeui*, *A. auristriatum* sp. nov. is the oldest record of the genus and probably represents a closer relative to the Recent *A. c. colbecki* than *A. colbecki cockburnensis* and *A. alanbeui* do. Despite the resemblance of the Oligocene *A. auristriatum* sp. nov. to the Recent *A. colbecki colbecki* and the Pliocene *A. colbecki cockburnensis*, it is reasonable that they comprise three distinct, but closely related taxa.

?*Adamussium* cf. *A. alanbeui* Jonkers 2003
Fig. 10, Table VI

Material. Internal mould of articulated valves (5354b); fragment of external mould of left valve (5354a).

Description. Shell small; equant; very compressed; valves orthocline, moderately convex; external sculpture of very thin commarginal growth lines and very faint antimarginal riblets. In right valve, dorsal margin of posterior auricle short; anterior auricle apparently fragmented.

Table III. Dimensions in millimetres and character values of representative specimens of *Neothyris* sp.

Specimen	Valve	Length	Thickness	Width	Elongation	Obesity
5462	V	19.2*	12*	18.2	1.6	0.65
5438i	D/V	—	11.9	18.5	—	0.64

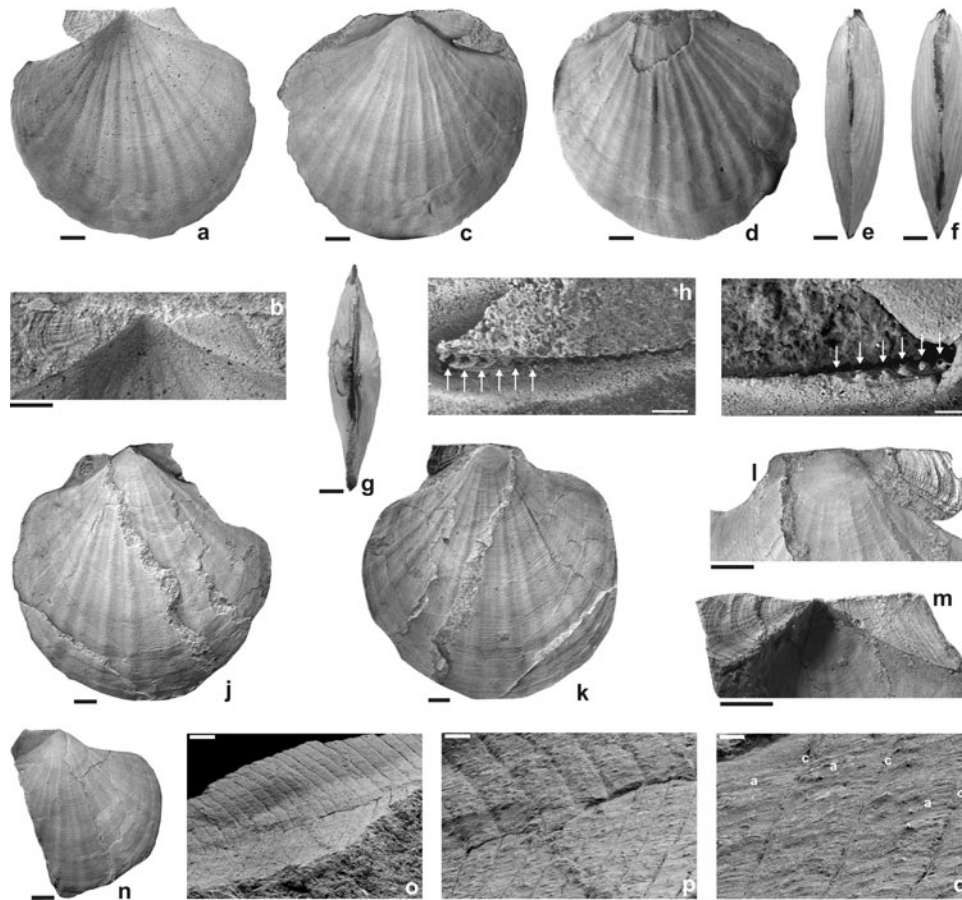


Fig. 9. *Adamussium auristriatum* sp. nov. **a–h.** Holotype 5457a–b, **a–b.** (5457a), external mould of RV, **b.** detail of auricles, **c–h.** (5457b), internal mould of articulated pair; **c.** right view, **d.** left view, **e.** anterior view, **f.** posterior view, **g.** dorsal view, **h.** detail of ctenolium, showing teeth sockets (arrows). **i.** Latex cast of ctenolium of 5457b, showing teeth (arrows). **j–k.** Paratype 5394–5405, RV, **j** (5405), internal mould, **k.** (5394) external mould. **l.** Latex cast of 5394. **m–n.** Paratype 5458a–b, **m.** (5458a) RV auricles of external mould (all bars = 5 mm), **n.** (5458b) right view of internal mould of articulated pair. **o–q.** Paratype 5301b, commarginal frills (c) and antimarginal microsculpture (a) in SEM micrographs of central region of external mould of RV (umbo to the left) (scale bars of **o** = 1 mm, **p** = 300 µm and **q** = 100 µm).

Remarks. Jonkers (2003) pointed out that *A. alanbeui* is distinguished from *A. colbecki* by its smaller size, its lower convexity, and the lack of radial costation and commarginal lirae. *A. alanbeui* (previously identified as *Eburneopecten* sp. by Gazdzicki & Pugaczewska 1984) occurs in Oligocene strata of McMurdo Sound region, in the type-area of the Polonez Cove Formation, KGI, and in Oligocene–Miocene Cape Melville Formation at Melville Peninsula, KGI (Jonkers 2003).

Comparison. The specimen collected from Vauréal Peak resembles *A. alanbeui* erected by Jonkers (2003) mainly in the absence of radial macrosculpture, presence of narrow

antimarginal sculpture, and shape and size of the anterior right valve auricle (see Table V). Although the specimen from Vauréal Peak is poorly preserved, it is a plausible record because *A. alanbeui* is recorded from the Low Head Member at Lions Rump (Jonkers 2003, p. 70).

Superfamily LIMACEA Rafinesque, 1815

Family LIMIDAE Rafinesque, 1815

Genus *Limatula* Wood, 1839

Type-species. *Pecten subauriculata* Montagu, 1808

Table IV. Dimensions in millimetres and character values of representative specimens of *Adamussium auristriatum* sp. nov.

Specimen	Valve	Length	Height	Width	Elongation	Obesity	AOL	POL	AOL/POL	AVH/PVH
5301a	R	44	48	13*	0.91	3.69	10.1	10	1.01	1.16
5394	R	63.1	60.9	15	1.03	4.06	14.3	13.5	1.03	1.02
5457b	R/L	53.5	48.2	13	1.10	3.70	12.8	11.8	1.08	1.13

Table V. Comparative features of *Adamussium colbecki colbecki*, *A. colbecki cockburnensis*, *A. alanbeui* and *A. auristriatum* sp. nov.

Features	<i>A. colbecki colbecki</i> ¹	<i>A. colbecki cockburnensis</i> ¹	<i>A. alanbeui</i> ¹	? <i>A. cf. alanbeui</i> ²	<i>A. auristriatum</i> sp. nov. ²
Size	Moderate (mean H = 70 mm)	Moderate (mean H = 56 mm)	Small (mean H < 50 mm)	Small (H = 42 mm)	Moderate (mean M = 52)
Valves	Slightly opisthocline (AVH/PVH = 0.96)	Opisthocline (AVH/PVH = 0.91)	Acline	—	Opisthocline (mean AVH/PVH = 1.10)
Convexity	Moderate	Weak	Weak	—	Moderate
Greater convexity	LV	LV	LV	—	Equal
Umbonal angle	Very wide (138°)	Wide (134°)	Narrow (110–120°)	Very narrow (105°)	Wide (130°)
Radial sculpture	20 broadly undulating with intercalated low plicae	15 broadly undulating with intercalated low plicae	No	No	10–15 main plicae with intercalated low plicae
Commarginal sculpture	Distinct lirae, with groups differently spaced	Lirae regularly and widely spaced	No	No	Lirae, weakly marked, regularly and widely spaced
Microsculpture	Wide to narrow antimarginal ridges	Narrow antimarginal ridges	Narrow antimarginal ridgelets	—	Narrow antimarginal ridgelets
Auricles symmetry	Highly symmetrical (AOL/POL = 1.02)	Highly asymmetrical (AOL/POL = 1.4)	Slightly asymmetrical (AOL/POL = 1.1–1.3)	—	Highly symmetrical (AOL/POL = 1.01–1.08)
Auricles sculpture	No	No	No	—	Anterior auricle with radial costae
Byssal notch	Very deep (arcuate or acute)	Deep	Very shallow	—	Very deep (acute)
Number of byssal teeth	Very variable (mean = 2.5)	—	—	—	6

Notes: ¹according to Jonkers 2003, ²specimens from the Low Head Member of the Polonez Cove Formation at Vauréal Peak, - = not observable.

Remarks. Fleming (1978, p. 17) characterized *Limatula* as having “tall, narrow, cylindrical and equilateral shell, almost circular in cross-section when the paired valves are closed, radial ornament, sometimes restricted or best developed in a median zone, flanked by almost smooth anterior and

posterior submargins, and having a median structure consisting of a central riblet slightly more prominent than its fellows, reflected internally by a central groove flanked by costellae that are the most prominent internal structure”. However, Fleming (1978) stated that the pattern of radial

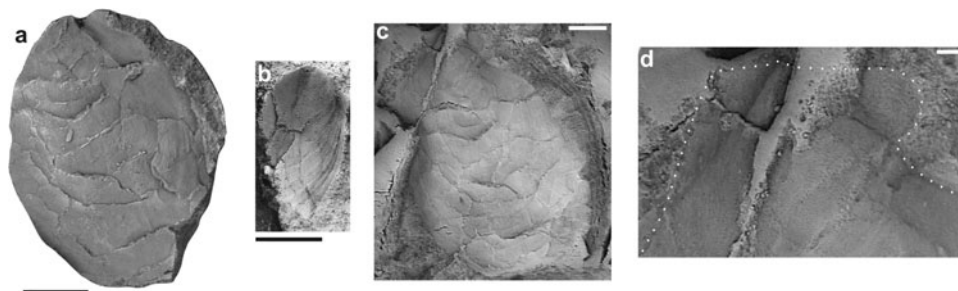


Fig. 10. ?*Adamussium* cf. *A. alanbeui*. **a–b.** Specimen 5354a–b, **a.** internal mould of articulated pair, right view, **b.** fragment of external mould of LV. **c–d.** latex mould of external mould of RV, **d.** detail of auricles of **c**, dotted line indicates dorsal margin (all bars = 5 mm).

Table VI. Dimensions in millimetres and character values of specimen of ?*Adamussium* cf. *A. alanbeui*.

Specimen	Valve	Length	Height	Width	Elongation	Obesity
5354b	R/L	34.3	42	0.77*	0.82	54.5

sculpture is variable among *Limatula* species, with some having radial costellae restricted to an ornamented band in the median part of the disc, others with the ribs persisting on the auricles or persisting but becoming weaker toward the auricles area, and some species having riblets on the ears. Some Recent (Dell 1990, Narchi *et al.* 2002) and fossil species of *Limatula* (Fleming 1978, Beu & Maxwell 1990) have a more trigonal than ovoid shape. All characters proposed by Fleming (1978) as diagnostic of *Limatula* are present in the specimens described here.

Subgenus *Limatula* (*Antarctolima*) Habe, 1977

Type-species. *Lima* (*Limatula*) *hodgsoni* Smith, 1907

Remarks. Fleming (1978) erected the subgenus *Squamilima* just after Habe (1977) erected *Antarctolima*; both authors based it on the same type-species. Thus, we use the name *Antarctolima* here, despite the fact that Fleming (1978, p. 81) have described the subgenus more accurately. This author pointed out that this *Limatula* group has “medium-sized shell of trigonal to broadly pyriform outline, height about 1.25 times length, with weak auricular sinuses and weak median structure, represented internally by a square-cut sulcus bordered by costellae slightly more prominent than the rest; ornament of regularly spaced, numerous, crowded ribs separated by narrow deep sulci, decussated by incremental lirae or rugae that may form prominent cusplike scales on the ribs; radials continuing to the auricles or fading on submargins”. All these features are observed in *Limatula* specimens from Vauréal Peak.

Limatula (*Antarctolima*) *ferraziana* sp. nov.

Fig. 11, Table VII

Material. Holotype, internal and external moulds (53322, 5324). Paratypes, internal moulds (5360a, 5451, 5452, 5453), external moulds (5309, 5346, 5360b).

Etymology. Referring to the Brazilian Antarctic Station Comandante Ferraz, located at Admiralty Bay, King George Island, West Antarctica.

Diagnosis. Shell pyriform, umbones prominent, sharp; radial sculpture almost reaching auricle area; median ridge more prominent than others, reflected internally as a

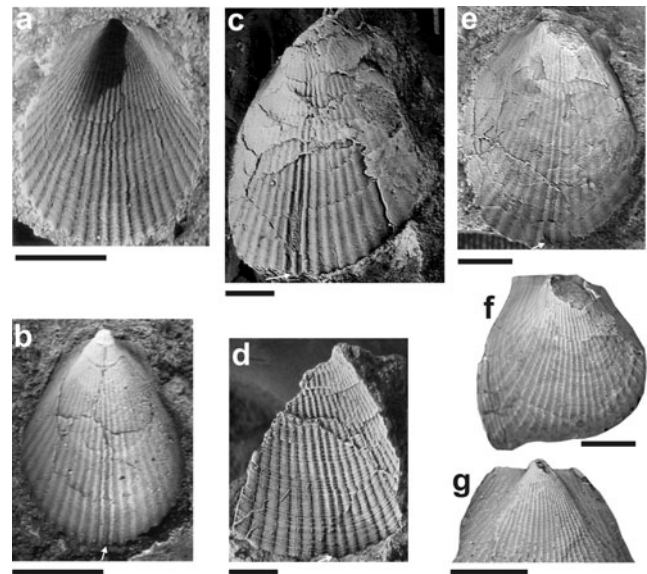


Fig. 11. *Limatula* (*Antarctolima*) *ferraziana*. **a–b.** Holotype 5322/5324, LV, **a.** (5324), external mould, **b.** (5322), internal mould. **c–d.** Paratype 5360a–b, LV, **c.** internal mould, **d.** fragment of external mould. **e–f.** Paratype 5451/5309, RV, **e.** internal mould, **f.** latex cast of external mould. **g.** Paratype 5346, LV, latex cast. Arrows indicate “median structure” of the shells (all bars = 5 mm).

groove, adjacent ridges to the median more constricted, acute in transverse section; commarginal sculpture more conspicuous when intersecting radial sculpture, with scaly appearance weaker than in *L. (A.) hodgsoni*; auricles small, almost symmetrical, posterior auricle slightly larger than anterior.

Description. Shell varying in height from 12.5 to 27.4 mm; equilateral in smaller specimens, slightly inequilateral in larger specimens; pyriform, equant, moderately inflated; umbones prominent, sharp; radial sculpture of 28–30 well developed ribs, almost reaching auricle area, and reflected internally, median ridge (14–15th) more prominent than others, reflected internally as a groove, adjacent ridges more constricted, with acute margin when observed in transverse section; commarginal sculpture of numerous regularly spaced growth lines, extending to auricle area, raised into scale-like ridges when intersecting radial sculpture; dorsal margin short; ventral margin longer, rounded and slightly crenulated; hinge line almost straight,

Table VII. Dimensions in millimetres and character values of representative specimens of *Limatula ferraziana* sp. nov.

Specimen	Valve	Length	Height	Width	Elongation	Obesity
5322	R	9.7	12.3	6.1*	0.78	1.9
5451	R	18.2	22	12.8*	0.82	1.7
5452	L	16.3*	21*	12.8*	0.77	1.6
5453	R	15.9	17.8	12*	0.89	1.4
5360	L	21.8*	25*	13*	0.87	1.9

hinge edentulous; auricles small, almost symmetrical, posterior auricle slightly larger than anterior.

Comparison. Gazdzicki & Pugaczewska (1984) identified *Limopsis* (*Pectunculina*) cf. *insolita* from the Low Head Member (Polonez Cove Formation) at Lions Rump. Their shells are quite similar to the material from Vauréal Peak and we consider that both represent the same species. The size, general shape, ornamentation and auricles are quite similar in both materials. The description by Gazdzicki & Pugaczewska (1984) included features that disagree with the diagnosis provided by Newell (1969, p. 248) for the Order Arcoida (which Limopsidae belongs to), and we consider that Gazdzicki & Pugaczewska (1984) misidentified their specimens.

Limatula (*Antarctolima*) *ferraziana* sp. nov. is similar to the Recent species *Limatula* (*Antarctolima*) *hodgsoni*, which is common in continental and peninsular Antarctica (Fleming 1978, Dell 1990, Absher & Feijó 1998, Narchi *et al.* 2002). It differs from the Recent species in being smaller, and in having smaller auricles and weaker scaly sculpture on the radial ornamentation. Page & Linse (2002)

considered *L. (A.) hodgsoni* to be the basal group of Antarctic *Limatula* (which includes *L. hodgsoni*, *L. ovalis* and *L. pygmaea*) and estimated the minimal speciation time of *L. (A.) pygmaea* and *L. (A.) ovalis* to be around 19 Ma. Hence, as the age of the Low Head Member is estimated at 29.8 Ma (Dingle *et al.* 1997), it is not surprising that *L. (A.) ferraziana* sp. nov. is more closely related to *L. (A.) hodgsoni* than to the other Antarctic *Limatula* (*Antarctolima*) species.

Phylum ANNELIDA Lamarck, 1809

Class POLYCHAETA Grube, 1850

Order ERRANTIDA Audouin & Milne-Edwards, 1832

Family SERPULIDAE Burmeister, 1837

Fig. 12a–d

Material. Several fragmentary calcareous tubes (5288a–d, 5316, 5344, 5349a–c).

Description. The tubes are calcareous, cylindrical, thin, straight, or with some curved in to “L” and “C” shapes; size varying from 3 to 35 mm long and 1 to 2 mm wide

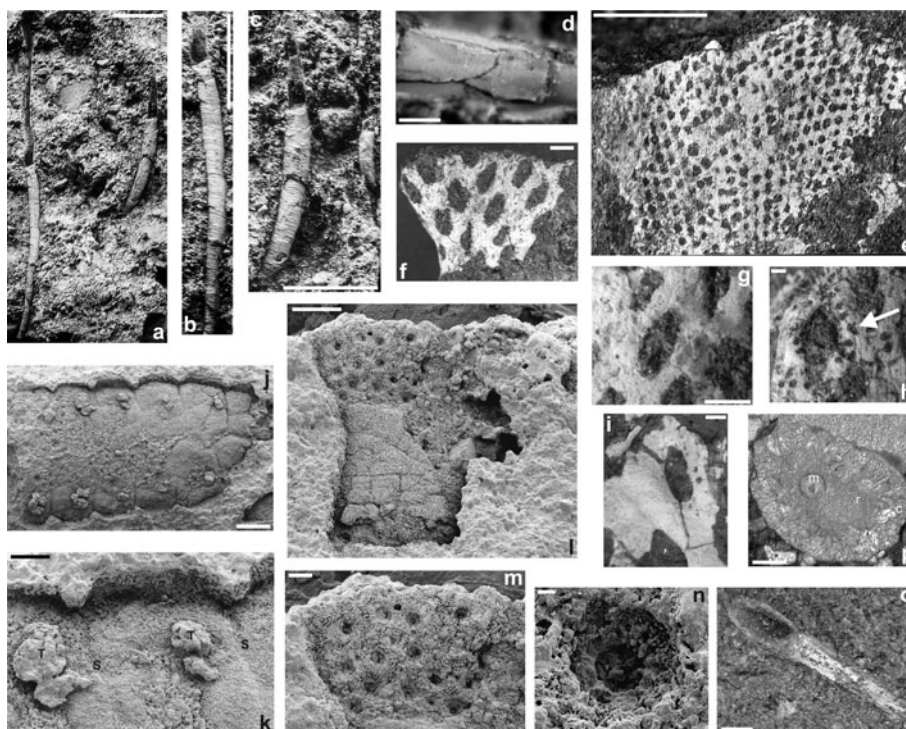


Fig. 12. Miscellaneous. **a–d.** Serpulidae, **a–c.** specimen 5349c, **a.** two fragmented tubes, **b–c.** the same specimens magnified, showing the external ornamentation (scale bars = 5 mm), **d.** specimen 5316, smooth aspect of the tube internally (scale bar = 500 µm). **e–i.** Bryozoa, **e.** specimen 5318b, general aspect of a fragment (scale bar = 5 mm), **f–g.** specimen 5349, **f.** general aspect of a fragment (scale bar = 1 mm), **g.** the same specimen magnified (scale bar = 1 mm), **h.** specimen 5352b, showing poorly preserved zooids (arrow) (scale bar = 300 µm), **i.** specimen 5352a (scale bar = 500 µm). **j–p.** Echinoidea, **j–n.** specimen 5328a, **j.** internal mould of interambulacrum (scale bar = 1 mm), **k.** the same specimen magnified (scale bar = 300 µm), showing the location of tubercles (t) and the adradial suture (s), **l.** external mould of a fragment of ambulacral plate (scale bar = 1 mm), **m.** the same specimen magnified (scale bar = 300 µm), **n.** miliary tubercule (scale bar = 300 µm), **o–p.** specimen 5339, fragment of primary spine, **o.** external aspect (scale bar = 100 µm), **p.** transverse section showing medulla (m), radiating (r) and cortex (c) layers (scale bar = 20 µm).

(diameter), most tubes having the same width along their entire length, but some tapering at the tips (possibly due to preservation conditions). Transverse section cylindrical. External ornamentation of 2–3 primary and 6–8 secondary transverse ridges per mm; smooth internally.

Comparison. Tubes from Vauréal Peak are quite similar to those found in Miocene deposits of CRP-1 (Jonkers & Taviani 1998, Cape Roberts Science Team 1998) and early Oligocene CRP-3 (Taviani & Beu 2001) cores at Cape Roberts, Victoria Land Basin. The external ornamentation of tubes from Vauréal Peak is also similar to that reported from the type-area of the Low Head Member (Gazdzicki & Pugaczewska 1984).

Remarks. The elongate form, cylindrical transverse section, smooth inner surface and calcareous composition are characteristic features of serpulid tubes (see Schweitzer *et al.* 2005 for features of this and other Polychaeta families). Besides, there are several records of polychaete tubes from Palaeogene and Neogene deposits of Antarctica (Jonkers & Taviani 1998, Taviani & Beu 2001, Schweitzer *et al.* 2005), including the type-area of Low Head Member of Polonez Cove Formation at KGI (Gazdzicki & Pugaczewska 1984). Also, Recent polychaetes are common in several regions of Antarctic (e.g. Cantone 1995, Ramos & San Martín 1999). All these points make the presence of polychaete tubes at Low Head Member of the Polonez Cove Formation at Vauréal Peak plausible.

Phylum BRYOZOA Ehrenberg, 1831

Fig. 12e–i

Material. Several fragments (5300, 5310, 5318a–d, 5318f, 5337, 5349, 5352, 5293).

Remarks. Several taxa of bryozoans are recorded from Oligocene deposits of KGI, including the type-area of the Polonez Cove Formation (Gazdzicki & Pugaczewska 1984). Specimens from Low Head Member at Vauréal Peak are fragments, lacking critical features for taxonomic analysis (e.g. zooids), and some with recrystallized calcite, preventing refined taxonomic identification within the phylum.

Phylum ECHINODERMATA Klein, 1734

Subphylum ECHINOZOA Haeckel in Zittel, 1895

Class ECHINOIDEA Leske, 1778

Echinoidea *incertae sedis*

Fig. 12j–p

Material. Internal mould of interambulacrum and external mould of ambulacral plate fragment (5328a), fragment of primary spine (5339).

Description. Specimen 5328a (Fig. 12j–n) corresponds to an interambulacrum and an ambulacral plate. The interambulacrum is 9.1 mm × 3.6 mm, composed of two columns of six alternating plates; primary tubercles not preserved, instead, the locations of each tubercle next to the adradial suture; miliary tubercles are preserved on the fragment of an ambulacral plate. Specimen 5339 (Fig. 12o & p) corresponds to a spine 27 mm long and 0.8 mm in diameter; thickness is the same along the length, enlarging at one tip which possibly corresponds to the shaft; external ornamentation of fine longitudinal striations; transverse section cylindrical, internal microstructure composed of narrow medulla; radiating layer occupying most of the area of the section; cortex layer relatively thick.

Remarks. There are several records of echinoderms from Palaeogene and Neogene deposits of KGI (Jesionek-Szymanska 1984, 1987, Meyer 1993, Blake & Aronson 1998); the commonest records, including those from the type-area of the Low Head Member (Jesionek-Szymanska 1984), are assigned to the Order Cidaroida. Representatives of this order have enlarged primary tubercles and conspicuous aureolae. Our specimens, however, comprise two minor fragments (whose primary tubercles are not preserved) and a fragment of spine, which is too thin comparatively to cidaroid spines. These conditions do not allow their assignment to lower taxonomic categories.

Comparative (palaeo)ecology

All genera from the Polonez Cove Formation at Vauréal Peak have modern representatives whose environmental preferences and geographical distribution can be used in order to interpret a hypothetical palaeoenvironmental scenario for the fossil assemblage in the context of the depositional pattern of the formation.

Liothyrella is a pedunculate, suspension feeder brachiopod occurring from Central America to Antarctica and New Zealand (Foster 1989). The species *Liothyrella uva* Broderip, very common in southern South America and Antarctica, is found at depths up to 1500 m (Foster 1974, 1989, Bitner 1996), in clumps attached to hard substrata and in such cryptic environments as cracks, crevices, and fjords, where turbulence is reduced (Barnes & Clarke 1995, Peck 1996, Peck *et al.* 1997). Specimens of *Liothyrella neozelanica* Thomson from New Zealand, collected at depths of 9–22 m, have thicker and larger shells than specimens from depths of 101 m (Foster 1989). Regardless of the fact that physiological adaptation of the brachiopod *L. uva* to polar Antarctic conditions is not well corroborated (Peck & Robinson 1994, Peck 1996, Peck *et al.* 1997), it is only found in cool waters. So, *Liothyrella* sp. from the Polonez Cove Formation may have lived in cool shallow waters, somewhat protected from wave

currents, as its modern South American and Antarctic representatives.

Recent *Neothyris* is a free-lying, suspension feeder brachiopod, commonly found in Southern Hemisphere cool shelf waters, mostly in sub-Antarctic islands and New Zealand (Neall 1970). The species *N. lenticularis* occurs in subtropical waters from New Zealand to the external boundary of the Circum-Antarctic Current, being absent in Antarctica (Neall 1970). According to this author (Neall 1970) the genus is indicative of mean annual surface water temperature of 8–11°C. Similarly to *Liothyrella* sp., the presence of the genus *Neothyris* in the Polonez Cove Formation corroborates the idea that cool temperate conditions were present in West Antarctica around early Oligocene (Zachos *et al.* 1994, Dmitrenko 2004). *Neothyris* larvae attach at shell fragments or granules, loosing totally or partially their pedicles during adult phase (Neall 1970). This may be the case of *Neothyris* from the Polonez Cove Formation, as indicated by the apparently absence of the foramen. Modern forms are found in sandy, shelly and/or pebbly sediments and may tolerate some turbulence (Neall 1970), which also agrees with the depositional framework proposed to the Polonez Cove Formation (Troedson & Smellie 2002; this work).

The Antarctic endemic *Adamussium colbecki* is a suspension feeder bivalve with circumpolar distribution (Chiantore *et al.* 2000). During its earlier stages, the species is found attached by byssus to living adult shells or to hard substrata, while adults are commonly found free-lying (Nicol 1966). Abundant populations are found living at depths above 100 m (Chiantore *et al.* 2000), but isolated specimens are also reported from depths of 594 m (Hedley 1916) or even 1500 m (Dell 1990). It seems that the water energy is more critical than the nature of the substrate, as *A. colbecki* is found also in hard, gravel, fine sand or silty substrates (Jonkers 2003). Nigro (1993) suggested that strong wave action occurring after sea-ice melting, and the prevalence of rocky substrate might inhibit the presence of *A. colbecki* at depths of 10–15 m in Terra Nova Bay. Berkman *et al.* (2004) concluded that *A. colbecki* prefers low-energy deep water environments or coastal areas under sea ice, while Nigro (1993) supposed that first growth stages may occur in deeper areas and that adults move later towards shallow waters. However, as some adults may live continuously attached by byssus, some water current typical of shallow waters may be tolerable. The presence of deep byssal notch and asymmetric auricles in modern species corroborates this life style (Jonkers 2003). Besides, considering the morphology of the fossil species *A. auristriatum*, it is acceptable that, during the deposition of the Polonez Cove Formation, it might live attached by byssus in pebbles, below wave base environments, or even protected under the sea ice.

Limatula is a free-lying suspension feeder bivalve with worldwide distribution (Allen 2004), including tropical and

polar regions, living from shallow to deep waters (Fleming 1978). Living representatives of *Antarctolima* subgenus occur at depths of 1180 m, but higher densities of this brachiopod were found in the Ross Sea from 6–695 m (but often in quite shallow water), on hard substrata, gravel or even on the surface mat of sponge spicules (Nicol 1966, Dell 1990). Accordingly, the Oligocene *L. (Antarctolima) ferraziana* sp. nov. may have preferred shallow depths and gravel substrata conditions, as indicated by the inferred depositional pattern of the Polonez Cove Formation.

Palaeobiogeography

Figure 13 shows the occurrences of genera *Liothyrella*, *Neothyris*, *Adamussium* and *Limatula* in the latest Cretaceous, late Eocene, early Oligocene, early Miocene and Recent. In spite of the restrict number and diversification, known spatial and stratigraphical distributions of these taxa allow some interesting views on their possible dispersal pattern during the Cenozoic.

Liothyrella, recorded from the Maastrichtian to the Recent, is restricted to the Southern Hemisphere and is more common in Palaeogene than in Neogene deposits (Owen 1980, Craig 2000, Bitner & Crame 2002), mainly in Australia and New Zealand. In Antarctica, *Liothyrella* has been recorded from the Eocene La Meseta Formation, Seymour Island, Western Weddell Sea (Bitner 1996). Another record is from the Low Head Member of the Polonez Cove Formation in Mazurek Point (Bitner 1997). According to the palaeontological record (Fig. 13a–e), the genus originated during the Maastrichtian in south-western margin of Australia and possibly migrated during Palaeogene along the opening sea way between Australia and Antarctica (Tasmanian Gateway) towards the Antarctic Peninsula (Craig 2000) and southern South America (Fig. 13f). After the middle Eocene *Liothyrella* reached the western edge of Antarctica and southern South America. This is suggested by the presence of Recent *L. uva* in those regions, with five subspecies described by Foster (1989) as evolved clines from South America towards Antarctica.

Neothyris is recorded from the Neogene to the Recent (MacKinnon & Lee 2006) and living species are restricted to New Zealand, Australian (Craig 1999) and sub-Antarctic (Neall 1972) waters. Fossil records in Antarctica were previously recognized in the Low Head Member of the Polonez Cove Formation at Lions Rump (Bitner & Pisera 1984), and in the late Oligocene Destruction Bay Formation at Melville Peninsula (Biernat *et al.* 1985). Cohen *et al.* (1998) estimated the divergence time of *Neothyris* from its stem lineage as around 47–63 Ma (early Paleocene to early Eocene). There is no record of *Neothyris* prior to latest early Oligocene (Fig. 13c–e), which does not exclude the possibility of *Neothyris* occurring in West Antarctica during the Eocene. The

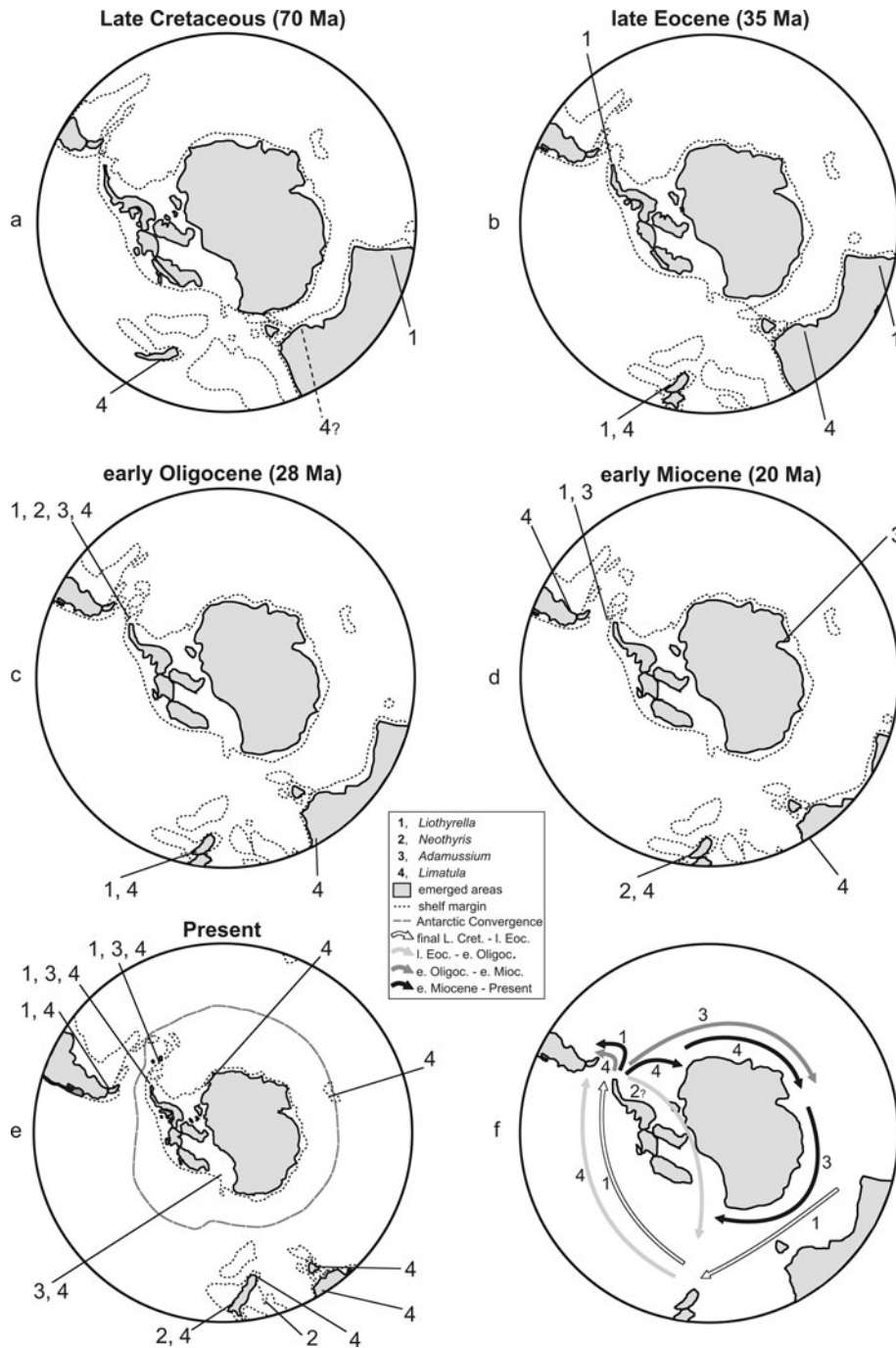


Fig. 13. Occurrences and inferred dispersal patterns of brachiopods and bivalves genera studied in this work for the interval latest Late Cretaceous to Recent. **a.** Late Cretaceous, **b.** late Eocene, **c.** early Oligocene, **d.** early Miocene, **e.** Recent, **f.** dispersal routes suggested by fossil record of *Liothyrella*, *Neothyris*, *Adamussium* and *Limatula* genera in a general paleogeographical base; arrows represent dispersal routes for each taxon. Note dispersal of *Liothyrella* and *Limatula* after the opening of the Tasmanian Gateway, from the end of Late Cretaceous until early Oligocene, and dispersal of *Liothyrella*, *Adamussium* and *Limatula* only after the opening of Drake Passage after early Oligocene (Fossil record according to Ihering 1907, Neall 1972, Buonavito 1977, Fleming 1978, Owen 1980, Bitner & Pisera 1984, Biernat *et al.* 1985, Beu & Dell 1989, Foster 1989, Beu & Maxwell 1990, Bitner 1997, Frassinetti 1998, Craig 2000, Bitner & Crame 2002, Jonkers 1998, 2003, this work. Maps modified from paleogeographical reconstructions kindly provided by Dr Lisa M. Gahagan, from University of Texas, Austin).

modern genera closely related to *Neothyris* (according to Cohen *et al.* 1998) are widely distributed in New Zealand and adjacent waters.

Until recently, *Adamussium* was considered as a genus restricted to the Holocene, being represented by the Recent circum-Antarctic *A. colbecki* (Smith 1902). Fossil records of this genus were firstly reported from Oligocene strata of McMurdo Sound region (Beu & Dell 1989). Further records include specimens from Oligocene/Miocene Cape Melville Formation at Melville Peninsula, KGI (Jonkers 2003); middle Miocene Battye Glacier Formation, East

Antarctica (Stilwell *et al.* 2002); late Pliocene Cockburn Island Formation at Cockburn Island, and Holocene Taylor Formation at New Harbour and Minna Bluff (Jonkers 1998) (see Fig. 13c–e). The origin of *Adamussium* is still unclear, as its hypothetical ancestor seems apparently missing (Dell & Fleming 1975, Canapa *et al.* 2000, Jonkers 2003, Barucca *et al.* 2005). This is possibly due to the unique set of characters of the genus and the relatively unknown phylogenetic relationships among the Pectinidae species (Canapa *et al.* 2000, Barucca *et al.* 2005). Jonkers (2003) listed some “primitive” characters that *Adamussium*

shares with the Oligocene–Recent *Austrochlamys*. It is possible that the evolutionary histories of both genera are restricted to the Southern Ocean - as fossil and living *Adamussium* are so far found only in West Antarctica - with both genera originated from an ancient pectinid lineage which was already established in West Antarctica prior to the Cenozoic. Once *Adamussium* arose in Antarctic Peninsula, it probably dispersed along the eastern margin of the continent during the Neogene (Fig. 13f).

Limatula is recorded from Middle Jurassic to Recent faunas and has worldwide distribution (Fleming 1978, Allen 2004). In the South Pacific, it occurs from the Cretaceous onwards in New Zealand (Beu & Maxwell 1990), from the Eocene in Australia (Buonaiuto 1977), from the Neogene in southern South America (Ihering 1907, Fleming 1978, Frassinetti 1998), and from the Pleistocene in Victoria Land Basin, Antarctica (Taviani *et al.* 1998; Fig. 13b–e). Fleming (1978) stated that *Limatula* (represented by the group of *Limatula corallina*) originated in the Jurassic in Europe, and occupied Africa and India during Mesozoic. At the end of the Late Cretaceous this group would evolved and possibly occupied the Pacific coast of Gondwana. However, the Recent Antarctic *Limatula* would derivate from stocks of *L. crebresquamata*, from upper Oligocene of Victoria, and entered the Southern Ocean from Australia, a scenario considered by Fleming (1978, p. 86) as “an oversimplification of inadequate data”. Indeed, *L. (Antarctolima) ferraziana* seems more closely related to Recent Antarctic and sub-Antarctic *Limatula* species (mainly *L. hodgsoni*), than *L. crebresquamata* or any southern South America fossil *Limatula*. Hence *L. (Antarctolima) ferraziana* is the most adequate group to represent the ancestral stock of *Antarctolima* group. Considering palaeogeographic reconstructions and morphological affinities of Southern Ocean *Limatula* species, it would be more plausible to assume that, in the case *L. (Antarctolima)*, ancient lineages were already present in the Pacific margin of Gondwana during the early Cenozoic.

Figure 13f synthesizes the fossil record of *Liothyrella*, *Adamussium* and *Limatula* represented in Fig. 13a–e. The dispersal pattern roughly fits the onset of the Circum-Antarctic Current - that started close to the Eocene/Oligocene boundary and was completely shaped during the late Oligocene (Pfuhl & McCave 2005) or later, during middle Miocene (Barker & Thomas 2004) - at two steps. In the first step the oldest taxa (*Liothyrella* and *Limatula*) dispersed after Tasmanian Gateway opening (~33 Ma, Exon *et al.* 2001), during early Cenozoic, from Australia and New Zealand towards the Antarctic Peninsula, through cool currents that represent the western portion of Circum-Antarctic Current (Lazarus & Caulet 1993). While the fossil record shows that *Liothyrella* may have dispersed previously than

Tasmanian Gateway opening (Fig. 13), Beu *et al.* (1997) considered larvae dispersal unlikely to have occurred before the development of the Circum-Antarctic Current. Although this cool current initiated later than Eocene/Oligocene boundary, a warmer current flowing from south-east Australia towards southern South America existed during Palaeocene to Eocene (Lazarus & Caulet 1993, p. 165, fig. 18), and may have been responsible for the dispersal of some taxa, as *Liothyrella*, during this interval. The first step of dispersal is in accordance with the context of Weddellian Province proposed by Zinsmeister (1979), as we are considering the faunal distribution regardless proximity of landmasses. In addition, *Neothyris* and *Limatula* dispersal routes extend to the Palaeogene the hypothesis of larvae transporting from New Zealand/Chatham Rise to Antarctic Peninsula proposed by Stilwell (1997).

The second step was accomplished after the Drake Passage opening initiated at 28 Ma or earlier (Barker & Thomas 2004), following development of eastern part of the Circum-Antarctic Current (~24 Ma, Pfuhl & McCave 2005). At the end of Palaeogene, both genera reached South America. At the beginning of the Neogene, intensification of the Circum-Antarctic Current around the eastern margin of Antarctica allowed the dispersal of *Adamussium* and *Limatula* around Antarctica. Considering that the dispersal pattern implies a clockwise route, the presence of *Limatula* in New Zealand at the end of Cretaceous foresees that this genus may be present also in Australia during this time. *Neothyris* lacks a clear dispersal pattern, probably due to its incomplete record. Two possible routes can be assigned to this genus: through currents that would have flowed in a shallow sea that existed between West and East Antarctica during early Oligocene to middle Miocene (Lazarus & Caulet 1993), as indicated in Fig. 13f; or the genus would have followed the second stage of dispersal over eastern margin of Antarctica at the end of Palaeogene.

Tasmanian Gateway and Drake Passage openings are considered “key deep sea ocean gateways” (Crame 1999, p. 4) of the Antarctic geological history and, not surprisingly, affected biotic composition and distribution in Southern Ocean (Beu *et al.* 1997) by changing oceanic circulation during the Cenozoic.

Concluding remarks

Palaeontological results presented here provide new taxonomic information about the diversity of Palaeogene invertebrates in West Antarctica, including new occurrences of brachiopod and bivalve genera - *Neothyris* sp., *Adamussium auristriatum* sp. nov. and *Limatula (Antarctolima) ferraziana* sp. nov. - that may represent some of the oldest lineages of these genera so far recorded in KGI and Antarctica. This new information raises some questions about the

palaeobiogeographical evolution in Southern Ocean, as how the thermal isolation of Antarctica affected evolving biota from Southern Ocean areas. Even though such major questions are not the main scope of this work, some interesting aspects bearing on the theme can be achieved.

Taxa from the Polonez Cove Formation at Vauréal Peak (*Neothyris* sp., *Liothyrella* sp., *Adamussium auristriatum*, *Limatula ferraziana*, serpulid tubes and echinoid fragments) have modern representatives. As discussed above, brachiopods and bivalves have wide bathymetric range. Indeed most Recent bivalves have significantly wide depth ranges in Antarctica (Brey *et al.* 1996), that is interpreted by Barnes *et al.* (2006, p. 124) as a suggestion of the presence of a “past shelf refugia”. Species of wide bathymetric ranges would be favoured after events of expansion and recession of ice sheet grounding line (Barnes *et al.* 2006). Where ice offered some protection these species would be able to persist in shelf areas. So, it is possible that at times of the deposition of Polonez Cove Formation, presence of sea ice offered some protection to the fauna, as also indicated by the environmental preferences of the modern *Adamussium colbecki*.

Considering the depositional model of the Polonez Cove Formation, it is plausible to say that invertebrates at Vauréal Peak lived in a shallow marine environment. This is also indicated by the substrate preferences of modern species, except for *Adamussium colbecki* which may lives in virtually all kinds of substrate. Moreover, apart from the echinoid, all of them are suspension feeders, which means that some water movement for filtering was required. From the taphonomic data it is also probable that the fossil fauna lived below the fair weather wave base, as no reworking features are observed in specimens.

Regardless the fact that we are considering only four taxa from only one locality, the proposed dispersal pattern seems consistent with available models of oceanic circulation during fragmentation of Gondwana, when Australia/Antarctica and Antarctic Peninsula/South America separated (Lazarus & Caulet 1993, Exon *et al.* 2001). For this reason, the dispersal pattern here proposed is considered as a first approach.

Almost all modern representatives of the Vauréal Peak fauna live in Antarctica, including *A. colbecki*, that is distributed only in areas inside the Antarctic Convergence. The exception is *Neothyris*, that occurs in cool temperate water of New Zealand. This suggests that at least part of the modern Antarctic faunal configuration was outlined during latest early Oligocene, even though the cool polar climate as observed today was not present during that period.

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References

- ABSHER, T.M. & FEJÓ, A.R. 1998. Morphology and ecology of bivalve molluscs from Admiralty Bay, King George Island, Antarctica. *Brazilian Archives of Biology and Technology*, **41**, 437–446.
- ADIE, R.J. 1962. The geology of Antarctica. *Geophysical Monographs*, **7**, 23–39.
- ALLEN, J.A. 2004. The Recent species of the genera *Limatula* and *Limea* (Bivalvia, Limacea) present in the Atlantic, with particular reference to those in deep water. *Journal of Natural History*, **38**, 2591–2653.
- AMLER, M.R.W. 1999. Synoptical classification of fossil and Recent Bivalvia. *Geologica et Palaeontologica*, **33**, 237–248.
- ANELLI, L.E., ROCHA-CAMPOS, A.C., DOS SANTOS, P.R., PERINOTTO, J.A.D. & QUAGLIO, F. 2006. Early Miocene bivalves from the Cape Melville Formation, King George Island, West Antarctica. *Alcheringa*, **30**, 111–132.
- BARKER, P.F. & THOMAS, E. 2004. Origin, signature and paleoclimatic influence of the Antarctic Circumpolar Current. *Earth-Science Reviews*, **66**, 143–162.
- BARNES, D.K.A. & CLARKE, A. 1995. Epibiotic communities on sublittoral macroinvertebrates at Signy Island, Antarctica. *Journal of the Marine Biological Association of the United Kingdom*, **75**, 689–703.
- BARNES, D.K.A., HODGSON, D.A., CONVEY, P., ALLEN, C.S. & CLARKE, A. 2006. Incursion and excursion of Antarctic biota: past, present and future. *Global Ecology and Biogeography*, **15**, 121–142.
- BARTON, C.M. 1965. The geology of South Shetland Islands. III. The stratigraphy of King George Island. *British Antarctic Survey Scientific Reports*, No. 44, 1–33.
- BARUCCA, M., OLMO, E., CAPRIGLIONE, T., ODIERNA, G. & CANAPA, A. 2005. Taxonomic considerations on the Antarctic species *Adamussium colbecki* based on molecular data. In LUPORINI, P. & MORBIDONI, M., eds. *Proceedings of the Fifth PNRA Meeting on Antarctic Biology*. Rome: Polarnet Technical Report, 2005/1, 53–57.
- BERKMAN, P.A., CATTANEO-VIETTI, R., CHIANTORE, M. & HOWARD-WILLIAMS, C. 2004. Polar emergence and the influence of increased sea-ice extent on the Cenozoic biogeography of pectinid molluscs in Antarctic coastal areas. *Deep-Sea Research II*, **51**, 1839–1855.
- BEU, A.G. & DELL, R.K. 1989. Mollusca. In BARRET, P.J., ed. *Antarctic Cenozoic history from the CIROS-1 drill-hole, McMurdo Sound*. *DSIR Bulletin*, No. 245, 135–141.
- BEU, A.G. & MAXWELL, P.A. 1990. Cenozoic Mollusca of New Zealand. *New Zealand Geological Survey Paleontological Bulletin*, **58**, 518 pp.
- BEU, A.G., GRIFFIN, M. & MAXWELL, P.A. 1997. Opening of Drake Passage gateway and Late Miocene to Pleistocene cooling reflected in Southern Ocean molluscan dispersal: evidence from New Zealand and Argentina. *Tectonophysics*, **281**, 83–97.
- BIERNAT, G., BIRKENMAJER, K. & POPIEL-BARCZYK, E. 1985. Tertiary brachiopods from the Moby Dick Group of King George Island (South Shetland Islands, Antarctica). *Studia Geologica Polonica*, **81**, 109–141.
- BIRKENMAJER, K. 1982. Pliocene tillite-bearing succession of King George Island (South Shetland Islands, Antarctica). *Studia Geologica Polonica*, **74**, 7–72.
- BIRKENMAJER, K. 1994. Geology of Tertiary glaciogenic deposits and volcanics (Polonia Glacier Group and Chopin Ridge Group) at Lions Rump (SSSI No. 34), King George Island, West Antarctica. *Bulletin of the Polish Academy of Sciences, Earth Sciences*, **42**, 207–221.

- BIRKENMAJER, K. 1995. Basal and intraformation unconformities in Lower Oligocene glaciogenic deposits (Polonez Cove Formation), King George Island, South Shetland Islands (West Antarctica). *Studia Geologica Polonica*, **107**, 93–123.
- BIRKENMAJER, K. 2001. Mesozoic and Cenozoic stratigraphy units in parts of the South Shetland Islands and northern Antarctic Peninsula (as used by the Polish Antarctic programmes). *Studia Geologica Polonica*, **118**, 188 pp.
- BIRKENMAJER, K. 2003. Admiralty Bay, King George Island (South Shetland Island, West Antarctica): a geological monograph. *Studia Geologica Polonica*, **120**, 73 pp.
- BIRKENMAJER, K. & GAZDZICKI, A. 1986. Oligocene age of the *Pecten* Conglomerate on King George Island, West Antarctica. *Bulletin of the Polish Academy of Science, Earth Sciences*, **34**, 219–226.
- BIRKENMAJER, K., SOLIANI JR, E. & KAWASHITA, K. 1989. Geochronology of Tertiary glaciations on King George Island, West Antarctica. *Bulletin of the Polish Academy of Sciences, Earth Sciences*, **37**, 27–48.
- BITNER, M.A. 1996. Brachiopods from the Eocene La Meseta Formation of Seymour Island, Antarctic Peninsula. *Palaeontologia Polonica*, **55**, 65–100.
- BITNER, M.A. 1997. Cenozoic brachiopod fauna of Antarctica. In GLOWACKI, P., ed. *Polish Polar Studies, 24th Polar Symposium*. Warszawa: Institute of Geophysics of the Polish Academy of Sciences, 21–29.
- BITNER, M.A. & CRAME, J.A. 2002. Brachiopods from the Lower Miocene of King George Island, West Antarctica. *Polish Polar Research*, **23**, 75–84.
- BITNER, M.A. & PISERA, A. 1984. Brachiopods from the “*Pecten* conglomerate” (Polonez Cove Formation, Pliocene) of King George Island (South Shetland Islands, Antarctica). *Studia Geologica Polonica*, **79**, 121–124.
- BITNER, M.A. & THOMSON, M.R.A. 1999. Rhynchonellid brachiopods from the Oligocene of King George Island, West Antarctica. *Polish Polar Research*, **20**, 83–88.
- BLASZYK, J. 1987. Ostracods from the Oligocene Polonez Cove Formation of King George Island, West Antarctica. *Palaeontologia Polonica*, **49**, 63–81.
- BLAKE, D.B. & ARONSON, R.B. 1998. Eocene stelleroids (Echinodermata) at Seymour Island, Antarctica Peninsula. *Journal of Paleontology*, **72**, 339–353.
- BOARDMAN, R.S., CHEETHAM, A.H. & COOK, P.L. 1983. Introduction to Bryozoa. In BOARDMAN, R.S. *et al.*, eds. *Treatise on Invertebrate Paleontology, Part G, Bryozoa* (Revised). New York: Geological Society of America, 3–48.
- BRETT, C.E. & BAIRD, G.C. 1986. Comparative taphonomy: a key to paleoenvironmental interpretation based on fossil preservation. *Palaios*, **1**, 207–227.
- BREY, T., DAHM, C., GORNY, M., KLAGES, M., STILLER, M. & ARNTZ, W.E. 1996. Do Antarctic benthic invertebrates show an extended level of eurybathy? *Antarctic Science*, **8**, 3–6.
- BRIGGS, J.C. 2003. Marine centres of origin as evolutionary engines. *Journal of Biogeography*, **30**, 1–18.
- BUONAIUTO, M.F. 1977. Revision of the Australian Tertiary species ascribed to *Limatula* Wood (Mollusca, Bivalvia). *Transactions of the Royal Society of South Australia*, **101**(1), 21–33.
- CANAPA, A., BARUCCA, M., MARINELLI, A. & OLMO, E. 2000. Molecular data from the 16rRNA gene for the phylogeny of Pectinidae (Mollusca: Bivalvia). *Journal of Molecular Evolution*, **50**, 93–97.
- CANTONE, G. 1995. Polychaeta “Sedentaria” of Terra Nova Bay (Ross Sea, Antarctica): Capitellidae to Serpulidae. *Polar Biology*, **15**, 295–302.
- CAPE ROBERTS SCIENCE TEAM. 1998. Miocene strata in CPR-1, Cape Roberts Project, Antarctica. *Terra Antarctica*, **5**, 63–124.
- CHIANTORE, M., CATTANEO-VIETTI, R., POVERO, P. & ALBERTELLI, G. 2000. The population structure and ecology of the Antarctic scallop *Adamussium colbecki* in Terra Nova Bay. In FARANDA, F., GUGLIELMO, L. & IANORA, A., eds. *Ross Sea ecology*. Berlin: Springer, 563–573.
- COHEN, B.L., GAWTHROP, A. & CAVALIER-SMITH, T. 1998. Molecular phylogeny of brachiopods and phoronids based on nuclear-encoded small subunit ribosomal RNA gene sequences. *Philosophical Transactions of the Royal Society of London*, **B353**, 2039–2061.
- CRAIG, R.S. 1999. A new Pliocene terebratulid brachiopod from the Roe Calcarene, Eucla Basin of southern Australia. *Records of the Western Australian Museum*, **19**, 267–275.
- CRAIG, R.S. 2000. The Cenozoic brachiopods of the Carnarvon Basin, Western Australia. *Palaeontology*, **43**, 111–152.
- CRAME, J.A. 1999. An evolutionary perspective on marine faunal connections between southernmost South America and Antarctica. *Scientia Marina*, **63**, suppl.1, 1–14.
- DELL, R.K. 1990. Antarctic Mollusca with special reference to the fauna of the Ross Sea. *Bulletin of the Royal Society of New Zealand*, **27**, 1–311.
- DELL, R.K. & FLEMING, C.A. 1975. Oligocene–Miocene bivalve Mollusca and other macrofossils from sites 270 and 272 (Ross Sea), Deep Sea Drilling Project Leg 28. *Initial Report of the Deep Sea Drilling Project*, **28**, 693–703.
- DINGLE, R.V. & LAVALLE, M. 1998. Late-Cretaceous–Cenozoic climatic variations of the northern Antarctic Peninsula: new geochemical evidence and review. *Palaeogeography, Palaeoclimatology, Palaeoecology*, **141**, 215–232.
- DINGLE, R.V., MCARTHUR, J.M. & VROON, P. 1997. Oligocene and Pliocene interglacial events in the Antarctic Peninsula dated using strontium isotope stratigraphy. *Journal of the Geological Society, London*, **154**, 257–264.
- DMITRENKO, O.B. 2004. Paleoclimatic environment of the Paleogene Southern Ocean by nanofossils. *Oceanology*, **44**, 121–133.
- DURHAM, J.W., FELL, H.B., FISCHER, A.G., KIER, P.M., MELVILLE, R.V., PAWSON, D.L. & WAGNER, C.D. 1966. Systematic descriptions. In MOORE, R.C., ed. *Treatise on Invertebrate Paleontology, Part U, Echinodermata 3*. New York: Geological Society of America, 297–672.
- EXON, N.F., KENNETT, J.P., MALONE, M.J., BRINKHUIS, H., CHAPRONIERE, G.C.H., ENNYU, A., FOTHERGILL, P., FULLER, M.D., GRAUERT, M., HILL, P.J., JANECEK, T.R., KELLY, D.C., LATIMER, J.C., NEES, S., NINNEMANN, U.S., NUERNBERG, D., PEKAR, S.F., PELLATON, C.C., PFUHL, H.A., ROBERT, C.M., ROESSIG, K.L., ROEHL, U., SCHELLENBERG, S.A., SHEVENELL, A.E., STICKLEY, C.E., SUZUKI, N., TOUCHARD, Y., WEI, W. & WHITE, T.S. 2001. The Tasmanian Gateway: Cenozoic climatic and oceanographic development, sites 1168–1172. *Proceedings of the Ocean Drilling Program, Initial Reports*, **189**, 98 pp.
- EYLES, N. & EYLES, C.H. 1992. Glacial depositional systems. In WALKER, R.G. & JAMES, N.P., eds. *Facies models: responses to sea level change*. St. Johns, Newfoundland: Geological Association of Canada, 73–100.
- FLEMING, C.A. 1978. The bivalve mollusc genus *Limatula*: a list of described species and a review of living and fossil species in the Southwest Pacific. *Journal of the Royal Society of New Zealand*, **8**(1), 17–91.
- FOSTER, M.W. 1974. Recent Antarctic and Subantarctic brachiopods. *Antarctic Research Series*, **21**, 1–189.
- FOSTER, M.W. 1989. Brachiopods from the extreme South Pacific and adjacent waters. *Journal of Paleontology*, **63**, 268–301.
- FRASSINETTI, D.C. 1998. Moluscos del Plioceno Superior marino de Isla Guafo, sur de Chile. Parte 1, Bivalvia. *Museo Nacional de Historia Natural, Boletín (Santiago)*, **46**, 55–79.
- GAZDZICKA, E. & GAZDZICKI, A. 1985. Oligocene coccoliths of the *Pecten* conglomerate, West Antarctica. *Neues Jahrbuch für Geologie und Paläontologie, Monatshefte*, **12**, 727–735.
- GAZDZICKI, A. & PUGACZEWSKA, H. 1984. Biota of the “*Pecten* conglomerate” (Polonez Cove Formation, Pliocene) of King George Island (South Shetland Islands, Antarctica). *Studia Geologica Polonica*, **79**, 59–120.
- HABE, T. 1977. Notes on *Antarctolima* (n. gen.) *hodgsoni* (Smith, 1907). *Venus*, **36**, 105–107.
- HEDLEY, C. 1916. Mollusca. *Australasian Antarctic Expedition 1911–1914, Scientific Reports C, Zoology and Botany*, **4**, 1–80.
- HOWELL, B.F. 1962. Worms. In MOORE, R.C., ed. *Treatise on Invertebrate Paleontology, Part W, Miscelanea*. New York: Geological Society of America, 144–177.

- IHERING, H. VON. 1907. Les Mollusques fossiles du Tertiaire et du Crétacé Superior de l'Argentine. *Anales del Museo Nacional de Buenos Aires*, **14** (III, IV), 611 pp.
- JESIONEK-SZYMANSKA, W. 1984. Echinoid remains from "Pecten conglomerate" (Polonez Cove Formation, Pliocene) of King George Island (South Shetland Islands, Antarctica). *Studia Geologica Polonica*, **79**, 125–130.
- JESIONEK-SZYMANSKA, W. 1987. Echinoids from the Cape Melville Formation (Lower Miocene) of King George Island, West Antarctica. *Palaeontologia Polonica*, **49**, 163–168.
- JONKERS, H.A. 1998. Stratigraphy of Antarctic late Cenozoic pectinid-bearing deposits. *Antarctic Science*, **10**, 161–170.
- JONKERS, H.A. 2003. Late Cenozoic–Recent Pectinidae (Mollusca: Bivalvia) of the Southern Ocean and neighbouring regions. *Monographs of Marine Mollusca*, **5**, 1–125.
- JONKERS, H.A. & TAVIANI, M. 1998. Lower Miocene macrofossils from CRP-1 drillhole, Cape Roberts (Victoria Land Basin), Antarctica. *Terra Antarctica*, **5**, 493–498.
- KIDWELL, S.M., FÜRSICH, F.T. & AIGNER, T. 1986. Conceptual framework for the analysis and classification of fossil concentrations. *Palaios*, **1**, 228–238.
- KRAUSE JR, R.A. 2004. An assessment of morphological fidelity in the sub-fossil record of a terebratulide brachiopod. *Palaios*, **19**, 460–476.
- LAZARUS, D. & CAULET, J.P. 1993. Cenozoic Southern Ocean reconstructions from sedimentologic, radiolarian, and other microfossil data. *Antarctic Research Series*, **60**, 145–174.
- LEE, D.E. & SMIRNOVA, T.N. 2006. Terebratuloidea. In SELDON, P., ed. *Treatise on Invertebrate Paleontology*, Part H (Revised). Boulder, CO: The Geological Society of America, 2054–2081.
- MACKINNON, D.I. & LEE, D.E. 2006. Terebratuloidea. In SELDON, P., ed. *Treatise on Invertebrate Paleontology*, Part H (Revised). Boulder, CO: The Geological Society of America & The University of Kansas, 2229–2244.
- MEYER, D.L. & OIL, T. 1993. Eocene crinoids from Seymour Island, Antarctica Peninsula: paleobiogeographic and paleoecological implications. *Journal of Paleontology*, **67**, 250–257.
- NARCHI, W., DOMANESCHI, O. & PASSOS, F.D. 2002. Bivalves antárticos e subantárticos coletados durante as expedições científicas brasileiras à Antártica I a IX (1982–1991). *Revista Brasileira de Zoologia*, **19**, 645–675.
- NEALL, V.E. 1970. Notes on the ecology and paleoecology of *Neothyris*, an endemic New Zealand brachiopod. *New Zealand Journal of Marine & Freshwater Research*, **4**, 117–125.
- NEALL, V.E. 1972. Systematics of the endemic New Zealand brachiopod *Neothyris*. *Journal of the Royal Society of New Zealand*, **2**(2), 229–247.
- NEWELL, N.D. 1969. Order Arcoida Stoliczka, 1871. In MOORE, R.C., ed. *Treatise on Invertebrate Paleontology*, Part N, Mollusca. Lawrence, KS: Geological Society of America, 248–270.
- NICOL, D. 1966. Descriptions, ecology and geographic distribution of some Antarctic pelecypods. *Bulletin of American Paleontology*, **51**, 1–102.
- NIGRO, M. 1993. Nearshore population characteristics of the circumpolar Antarctic scallop *Adamussium colbecki* (Smith, 1902) at Terra Nova Bay (Ross Sea). *Antarctic Science*, **5**, 377–378.
- OWEN, E.F. 1980. Tertiary and Cretaceous brachiopods from Seymour, Cockburn and James Ross Islands, Antarctica. *Bulletin of the British Museum of Natural History*, **33**, 123–145.
- PAGE, T.J. & LINSE, K. 2002. More evidence of speciation and dispersal across the Antarctic Polar Front through molecular systematics of Southern Ocean *Limatula* (Bivalvia: Limidae). *Polar Biology*, **25**, 818–826.
- PECK, L.S. 1996. Metabolism and feeding in the Antarctic brachiopod *Liothyrella uva*: a low energy lifestyle species with restricted metabolic scope. *Proceedings of the Royal Society of London*, **B263**, 223–228.
- PECK, L.S. & ROBINSON, K. 1994. Pelagic larval development in the brooding Antarctic brachiopod *Liothyrella uva*. *Marine Biology*, **120**, 279–286.
- PECK, L.S., BROCKINGTON, S. & BREY, T. 1997. Growth and metabolism in the Antarctic brachiopod *Liothyrella uva*. *Philosophical Transactions of the Royal Society of London*, **B352**, 851–858.
- PFUHL, H.A. & MCCAVE, I.N. 2005. Evidence for late Oligocene establishment of the Antarctic Circumpolar Current. *Earth and Planetary Science Letters*, **235**, 715–728.
- POREBSKI, S.J. & GRADZINSKI, R. 1987. Depositional history of the Polonez Cove Formation (Oligocene), King George Island, West Antarctica: a record of continental glaciation, shallow-marine sedimentation and contemporaneous volcanism. *Studia Geologica Polonica*, **97**, 7–62.
- POREBSKI, S.J. & GRADZINSKI, R. 1990. Lava-fed Gylbert-type delta in the Polonez Cove Formation (Lower Oligocene), King George Island, West Antarctica. *Special Publications, International Association of Sedimentologists*, **10**, 335–351.
- PUGACZEWSKA, H. 1984. Tertiary Bivalvia and Scaphopoda from glaciomarine deposits at Magda Nunatak, King George Island (South Shetland Islands, Antarctica). *Studia Geologica Polonica*, **79**, 53–58.
- RAMOS, A. & SAN MARTÍN, G. 1999. On the finding of a mass occurrence of *Serpula narconensis* Baird, 1885 (Polychaeta, Serpulidae) in South Georgia (Antarctica). *Polar Biology*, **22**, 379–383.
- SANTOS, P.R.D., ROCHA-CAMPOS, A.C., TOMPETTE, R., UHLEIN, A., GIPP, M. & SIMÕES, J.C. 1990. Review of Tertiary Glaciation in King George Island, West Antarctica: Preliminary results. *Pesquisa Antártica Brasileira*, **2**, 87–99.
- SCHWEITZER, C.E., FELDMANN, R.M., MARENSSI, S. & WAUGH, D.A. 2005. Remarkably preserved annelid worms from the La Meseta Formation (Eocene), Seymour Island, Antarctica. *Paleontology*, **48**, 1–13.
- SMELLIE, J.L., PANKHURST, R.J., THOMSON, M.R.A. & DAVIES, R.E.S. 1984. The geology of the South Shetland Islands. VI. Stratigraphy, geochemistry and evolution. *British Antarctic Survey Scientific Reports*, No. 87, 1–85.
- SPEYER, S.E. & BRETT, C.E. 1991. Taphofacies controls. Background and episodic processes in fossil assemblage preservation. In ALLISON, P.A. & BRIGGS, D.E.G., eds. *Taphonomy: releasing the data locked in the fossil record*. New York: Plenum Press, 501–545.
- STANLEY, S.M. 1970. Relation of shell form to life habits of the Bivalvia (Mollusca). *Geological Society of America Memoir*, **125**, 1–296.
- STILWELL, J.D. 1997. Tectonic and paleobiogeographic significance of the Chatham Islands, South Pacific, Late Cretaceous fauna. *Palaeogeography, Palaeoclimatology, Palaeoecology*, **36**, 97–119.
- STILWELL, J.D., HARWOOD, D.M. & WHITEHEAD, J.M. 2002. Mid-Tertiary macroinvertebrate-rich clasts from the Battye Glacier Formation, Prince Charles Mountains, East Antarctica. *Antarctic Science*, **14**, 69–73.
- TAVIANI, M. & BEU, A.G. 2001. Paleogene macrofossils from CRP-3 drillhole, Victoria Land Basin, Antarctica. *Terra Antarctica*, **8**, 1–12.
- TAVIANI, M., BEU, A.G. & LOMBARDO, C. 1998. Pleistocene macrofossils from CRP-1 drillhole, Victoria Land Basin, Antarctica. *Terra Antarctica*, **5**, 485–491.
- TROEDSON, A.L. & RIDING, J.B. 2002. Upper Oligocene to lowermost Miocene strata of King George Island, South Shetland Islands, Antarctica: stratigraphy, facies analysis and implications for the glacial history of the Antarctic Peninsula. *Journal of Sedimentary Research*, **B72**, 510–523.
- TROEDSON, A.L. & SMELLIE, J.L. 2002. The Polonez Cove Formation of King George Island, Antarctica: stratigraphy, facies and implications for mid-Cenozoic cryosphere development. *Sedimentology*, **49**, 277–301.
- WILLIAMS, A., BRUNTON, C.H.C., CARLSON, S.J., BAKER, P.G., CARTER, J.L., CURRY, G.B., DAGYS, A.S., GOURVENNEC, R., HONG-FEI, H., YU-GAN, J., JOHNSON, J.G., LEE, D.E., MACKINNON, D.I., RACHEBOEUF, P.R., SMIRNOVA, T.N. & DONG-LI, S. 2006. Brachiopoda. In SELDON, P., ed. *Treatise on Invertebrate Paleontology*, Part H. *Rhynchonelliformea* (Revised). Lawrence, KS: The Geological Society of America, 1689–2320.
- ZACHOS, J., PAGANI, M., SLOAN, L., THOMAS, E. & BILLUPS, K. 1994. Trends, rhythms, and aberrations in global climate 65 Ma to present. *Science*, **292**, 686–693.

- ZINSMEISTER, E.J. 1979. Biogeographic significance of the Late Mesozoic and Early Tertiary molluscan faunas of Seymour Island (Antarctic Peninsula) to the final breakup of Gondwanaland. In GRAY, J. & BOUCOT, A., eds. *Historical biogeography, Plate Tectonics and the changing environment. Proceedings of the 37th Annual Biology Colloquium and Selected Papers*. Corvallis, OR: Oregon State University Press, 349–355.
- ZINSMEISTER, W.J. 1982. Late Cretaceous–Early Tertiary molluscan biogeography of the southern circum-Pacific. *Journal of Paleontology*, **56**, 84–102.