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Nuculidae (Bivalvia) in the Cape Melville Formation, King George Island, Antarctica, with an overview of the bivalve fauna

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Abstract: Nuculid bivalves of the Cape Melville Formation (Early Miocene, King George Island) are reviewed. Ten bivalve taxa are listed from the formation in the families Nuculidae (two species), Sareptidae, Malletiidae, Limopsidae (two species), Limidae, Pectinidae, Hiatellidae, and Periplomatidae. The Nuculidae consist of two species of *Leionucula* Quenstedt, 1930. One of these, *L. melvilleana* n. sp., is described and the other consists of the two species named previously by Anelli *et al*. (2006), which are demonstrated to be synonymous and are assigned to the species *Leionucula frigida* (Anelli, Rocha-Campos, Santos, Perinotto & Quaglio 2006). This assemblage, dominated by protobranchs (89% of specimens), is a typical fauna of offshore soft substrates, with a few specimens transported from hard substrates nearby. The diversity of Nuculidae has decreased in the Antarctic region through the Cenozoic.

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Key words: biogeography, Cenozoic, Southern Ocean, taxonomy

Introduction

Antarctic Cenozoic fossil deposits give us important information about a period of environmental change in the Southern Hemisphere. This includes the final break-up of Gondwana, the onset of the Antarctic Circumpolar Current and the first major expansion of Antarctic ice (Zachos *et al*. 1992). Establishment of present-day oceanographic and atmospheric circulation patterns also took place in the Cenozoic (Ivany *et al*. 2008).

The Cape Melville Formation preserves one of the most important glacial faunal assemblages from Antarctica during the Cenozoic. Study of the British Antarctic Survey (BAS) Cape Melville Formation collection has increased our knowledge of the bivalve assemblage, which contributes to the overall community structure of the formation and of Antarctica in the Early Miocene. The exposures of the Cape Melville Formation on King George Island, located to the north-west of the Antarctic Peninsula (Fig. 1), preserve a Miocene marine invertebrate fauna. Few fossiliferous outcrops are found from this age in Antarctica (Beu 2009), therefore this assemblage is extremely important in understanding Cenozoic biodiversity in Antarctica. Along with the underlying Late Oligocene Destruction Bay Formation (Quaglio *et al*. 2010), the Cape Melville Formation provides a unique fossil record in the Antarctic Peninsula region during a latest Oligocene to earliest Miocene interglacial to glacial transition (Birkenmajer *et al*. 1983, Dingle & Lavelle 1998, Troedson & Riding 2002).

Geology and stratigraphy of the Cape Melville Formation

The Cape Melville Formation (Moby Dick Group, King George Island Supergroup) comprises a *c*. 150 m thick exposure on the narrow Melville Peninsula, which lies at the eastern extremity of King George Island, West Antarctica (Troedson & Riding 2002) (Fig. 1). The unit consists of horizontal to sub-horizontally bedded mudstones and silty mudstones, which are characterized by a diverse assemblage of glacially rafted lithological material (Birkenmajer *et al*. 1983). It has been dated as 22.6 ± 0.4 Ma (Early Miocene) based on Sr isotope data from bivalves (Dingle & Lavelle 1998).

Overall, the assemblage has a deepwater, outer-shelf aspect (Förster *et al*. 1987, Feldmann & Crame 1998). The fauna includes gastropods (Karczewski 1987), solitary corals (Roniewicz & Morycowa 1985), a nephropid lobster (Feldmann & Crame 1998), crabs (Förster *et al*. 1987), brachiopods (Bitner & Crame 2002), bryozoans (Hara & Crame 2004), echinoids (Jesionek-Szymańska 1987), scaphopods, polychaetes (Szaniawski & Wrona 1987) and bivalves (Jonkers 2003, Anelli *et al*. 2006, Whittle *et al*. 2011).

The Family Nuculidae

The Family Nuculidae Gray, 1824 belongs to the Protobranchia, a bivalve subclass that is an understudied but important component of extreme environments at the present-day. They are common in polar regions and the deep sea (Allen 1978). The family Nuculidae is also known from the shelf and slope, as well as abyssal depths (Allen 1978), and they are active infaunal deposit feeders (Rhind & Allen 1992). Nuculidae are characterized by small- to medium-sized, ovate to ovate-trigonal shells and taxodont dentition. The beaks are opisthogyrate, the ligament is internal and a resilifer is present. Ornamentation typically consists of fine radial striae, usually with a smooth, shiny periostracum in living forms

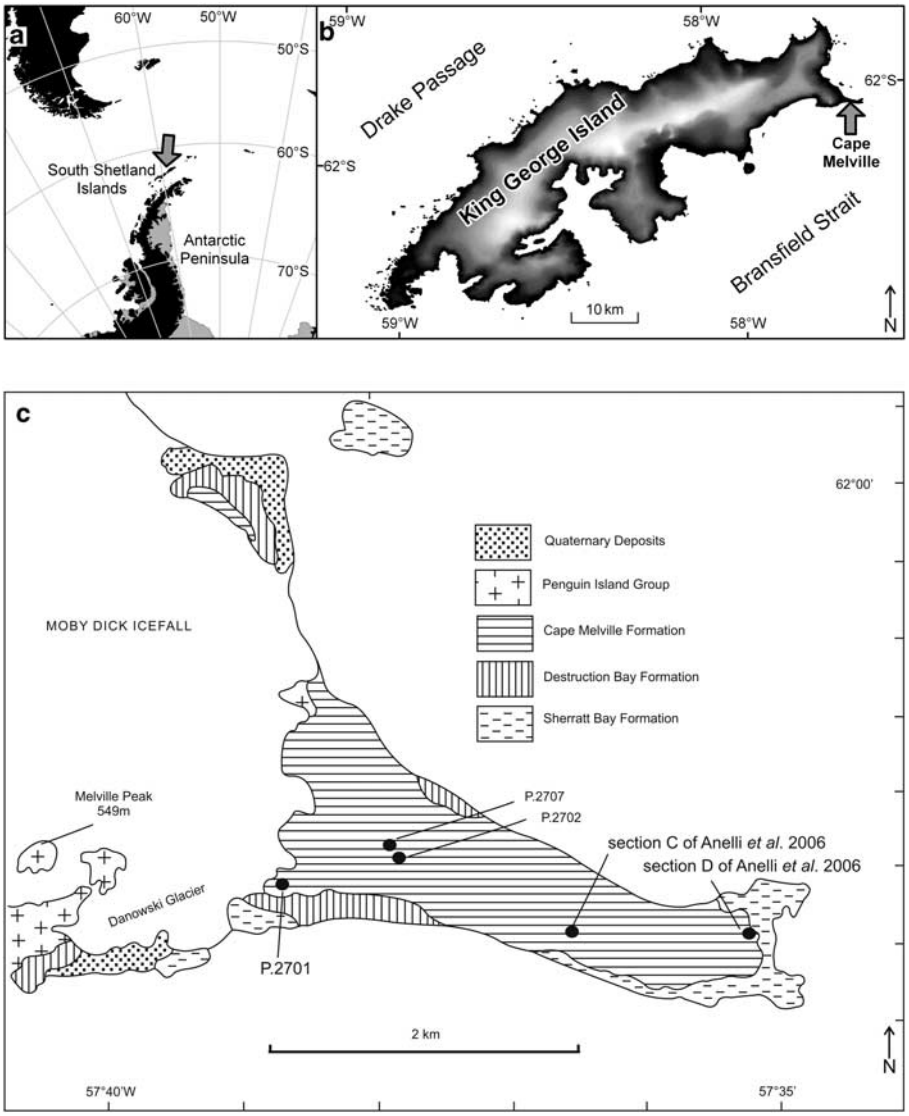

Fig. 1. a. Location of the South Shetland Islands, **b.** location of Cape Melville on King George Island, and **c.** Cape Melville geology and site localities (P. 2701, P. 2702 and P. 2707) for nuculid specimens from BAS and the Instituto de Geociências, Universidade de São Paulo (adapted after Feldmann & Crame 1998).

(Keen 1969). Nuculidae range in age from the Ordovician to the present (Keen 1969). There are many taxonomic issues within this family based on the low numbers of polymorphic shell characters (McAlester 1964, Rhind & Allen 1992, Beu 2006). To date there have been no molecular phylogenetic or barcoding analyses (Beu 2006), so morphological aspects are currently used to identify modern genera and species. A problem with studying the morphology of the Nuculidae is that they retained primitive characters as they are well adapted to their environment (McAlester 1964) and this conservatism in evolution, at the species and the genus level, means that they are difficult to characterize for taxonomic and phylogenetic analysis (McAlester 1964, Rhind & Allen 1992, Beu 2006). Nuculids from King George Island have been described from the Cape Melville Formation by Anelli *et al.* (2006). The material was placed into two species of the genus *Ennucula* Iredale, 1931, but was subsequently re-assigned by Beu (2009) to the genus *Leionucula*.

In this paper the composition of an assemblage of Cape Melville fossil bivalves from the BAS collections is identified and a new species is described.

Methods

Cape Melville Formation bivalve specimens were collected by J. Alistair Crame in the 1994–95 field season. Bivalve specimens are housed in the BAS collections, Cambridge, under the prefixes P. 2701 (22 specimens), P. 2702 (751 specimens) and P. 2707 (123 specimens), the locations for which are shown in Fig. 1.

Bivalves in the BAS assemblage were studied using an optical microscope, measured using Vernier callipers, drawn with the aid of a camera lucida and photographed using a digital camera. The BAS bivalve specimens were also compared to those held at IGc-USP (Instituto de Geociências, Universidade de São Paulo), especially with

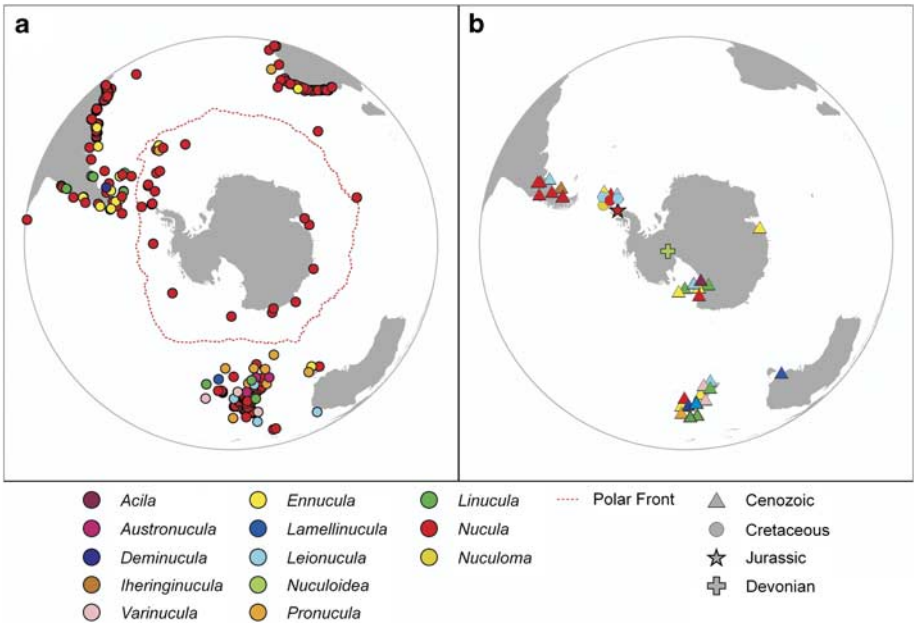

Fig. 2. Distribution of Nuculidae in the southern high latitudes. **a.** Nuculid records at the present-day. **b.** Nuculid records through time. Colours represent genera, shapes represent time periods.

the type material. These are housed in the Coleção Científica (Scientific Collection) of the Departamento de Geologia Sedimentar e Ambiental, Instituto de Geociências, Universidade de São Paulo, under the prefix GP/1T and GP/1E (Anelli *et al*. 2006).

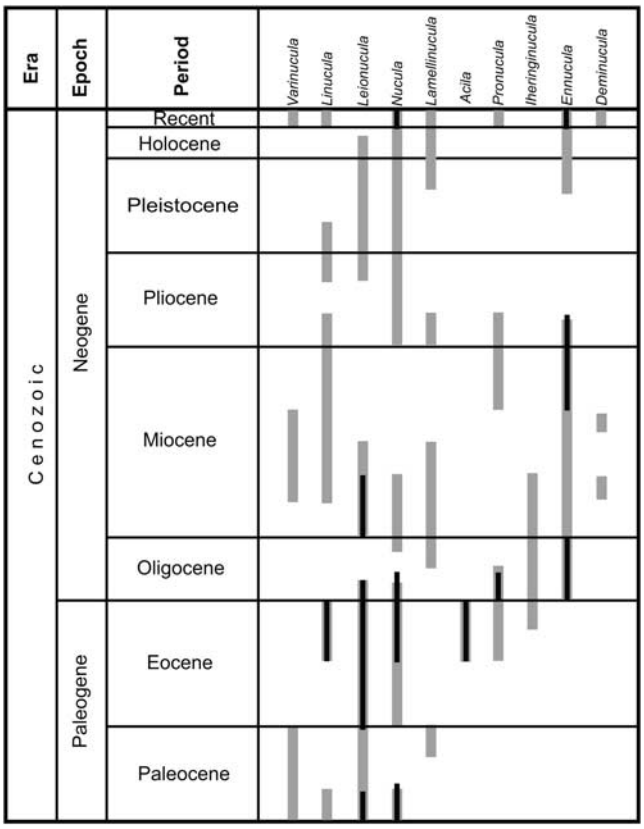

Fig. 3. Time ranges of southern high latitude nuculid genera (grey), with Antarctic genera (black), through the Cenozoic.

Length of the shell was measured by taking the greatest distance along the antero-posterior axis. Height was the greatest measurement at right angles to the length and inflation was measured by taking the maximum measurement of two valves together in complete specimens. A total of 542 nuculid specimens from three locations in the Cape Melville Formation were studied. All available specimens per locality were measured, unless they had undergone significant distortion or flattening. SCAR-MarBIN (www.scarmarbin.be, accessed February 2011) was used to access data on the distribution of recent nuculids in Antarctica and the southern high latitudes (Bouchet 2012). SOMBASE-GSCM (the Cenozoic Marine Fauna Database, developed by H. Griffiths, BAS) and the Paleobiology Database (http://paleodb.org/cgi-bin/bridge.pl, accessed February 2011) were used to access data on the distribution of fossil nuculids. These occurrences were checked against the original published literature (Ihering 1897, Ihering 1907, Wilckens 1910, Doumani *et al*. 1965, Dell & Fleming 1975, Gaździcki & Pugaczewska 1984, Zinsmeister 1984, Stilwell & Zinsmeister 1987, 1992, Pickard *et al*. 1988, Zinsmeister & Macellari 1988, Beu & Maxwell 1990, Del Río & Camacho 1996, Del Río & Chiappara 1998, Taviani *et al*. 2000, Stilwell 2000, 2003, Taviani & Beu 2001, Stilwell *et al*. 2004, Anelli *et al*. 2006, Beu 2009).

Southern high latitude Nuculidae

The four genera belonging to the Family Nuculidae that are currently found in southern high latitude waters (Fig. 2a) are *Austronucula* Powell, 1939, *Ennucula*, *Nucula* Lamarck, 1799 and *Pronucula* Hedley, 1902. The nuculids have a high

Table I. The BAS Cape Melville Formation bivalve fossils.

Order	Family	Genus	Species	Reference	BAS specimens
Nuculoida	Nuculidae	*Leionucula*	*frigida*	Anelli *et al.* 2006	495
		Leionucula	*melvilleana*	This paper	41
		Indeterminate	Indeterminate		6
Nuculanoida	Sareptidae	*Yoldia*	*peninsularis*	Anelli *et al.* 2006	148
	Malletiidae	*Neilo* (*Neilo*)	*rongelii*	Anelli *et al.* 2006	69
	Indeterminate	Indeterminate	Indeterminate		39
Arcoida	Limopsidae	*Limopsis*	*psimolis*	Anelli *et al.* 2006	3
		Limopsis	*infericola*	Whittle *et al.* 2011	4
		Limopsis	Indeterminate		4
Pectinoida	Pectinidae	*Adamussium*	*alanbeui*	Jonkers 2003	1
Limoida	Limidae	*Limatula* (*Antarctolima*)	sp.		1
Myoida	Hiatellidae	*Panopea*	sp.		17
		? Panopea	Indeterminate		14
Pholadomyoida	Periplomatidae	*Periploma*	*acuta*	Anelli *et al.* 2006	9
Indeterminate	Indeterminate	Indeterminate	Indeterminate		45
					Total 896

species-richness north of the Antarctic Polar Front and a lower species-richness south of the Polar Front (dominantly of the genus *Nucula*, but occurrences of *Pronucula* and *Ennucula* have also been found near the South Shetland Islands) (Fig. 2a) (Linse *et al.* 2006, Bouchet 2012). Specimens are mostly identified from the Antarctic Peninsula region and occur in water depths of 6–4209 m (Dell 1990). At present Nuculidae are species rich in waters around New Zealand and South America (Bouchet 2012).

The oldest recorded occurrence of a fossil nuculid in the southern high latitudes is of *Nuculoidea* Williams & Breger, 1916, which is Lower Devonian in age; it was collected from the Ohio Range in Antarctica (Doumani *et al.* 1965) (Fig. 2b). Apart from a Jurassic record of *Nucula* from the Antarctic Peninsula, the rest of the fossil Antarctic nuculids are from the Cretaceous period and younger, and most are Cenozoic (Figs 2b & 3). Ten genera of fossil nuculids have been found in the southern high latitudes in the Cenozoic, with six of these genera occurring in rocks from Antarctica (Figs 2b & 3). However, New Zealand fossil nuculid diversity is significantly greater than the published diversity (A. Beu, personal communication 2012). Generic diversity has decreased in the southern high latitudes through time as only three genera occur south of the Polar Front at the present-day (Fig. 2a).

Antarctic fossil species (Figs 2b & 3) have been found from the drill cores DSDP 270 (Dell & Fleming 1975) and CRP-2/2A (Taviani *et al.* 2000), plus in the vicinity of Mount Discovery (Stilwell 2000), which are all in the McMurdo Sound region and also from the Antarctic Peninsula region (Wilckens 1910, Stilwell & Zinsmeister 1987, Zinsmeister & Macellari 1988, Stilwell & Zinsmeister 1992, Stilwell *et al.* 2004, Anelli *et al.* 2006), Marine Plain (Pickard *et al.* 1988) and the Ohio Range (Doumani *et al.* 1965).

Nuculids occurred sporadically through the Cenozoic in the southern high latitudes (Fig. 3) in units deposited in a variety of water depths. No genus has a continuous fossil record through the Cenozoic to the present. The fossil record in Antarctica is very patchy, with most occurrences in the Eocene–Miocene periods (Fig. 3). There are no Antarctic fossil occurrences in the Pleistocene or Holocene, probably related to glaciation in Antarctica. Generic diversity of the family Nuculidae decreased in the Antarctic region through the Cenozoic to the Recent (Fig. 2). The cause of this decrease in diversity is unknown but it may have been related to environmental reasons such as changes in oceanic circulation or extension of ice sheets onto continental shelves, which led to a change in species composition.

The BAS Cape Melville Formation bivalve assemblage

The BAS Cape Melville Formation bivalve assemblage consists of 896 specimens. Of these 770 specimens have been identified to species level, 783 to genus, 851 to family and 45 fossil specimens were too badly preserved to be assigned (Table I). In total eight bivalve families have now been identified from the Cape Melville Formation: Nuculidae, Sareptidae, Malletiidae, Limopsidae, Pectinidae, Limidae, Hiatellidae and Periplomatidae. Generally families in the Cape Melville Formation bivalve assemblage are monospecific, except for the Limopsidae and Nuculidae, which are both represented by two species (Table I).

Overall, ten species of bivalve have been identified from the BAS Cape Melville collection (Table I). Of these, one species was originally identified by Jonkers (2003) and seven species by Anelli *et al.* (2006). Five of the species originally identified by Anelli *et al.* (2006) are also in BAS collection, and two species of nuculid are re-assigned and synonymized into the species *Leionucula frigida* (Anelli, Rocha-Campos, Santos, Perinotto & Quaglio, 2006) (see Systematics below), based on new data from the BAS nuculid collection. A second taxon of nuculids can be identified from the BAS Cape

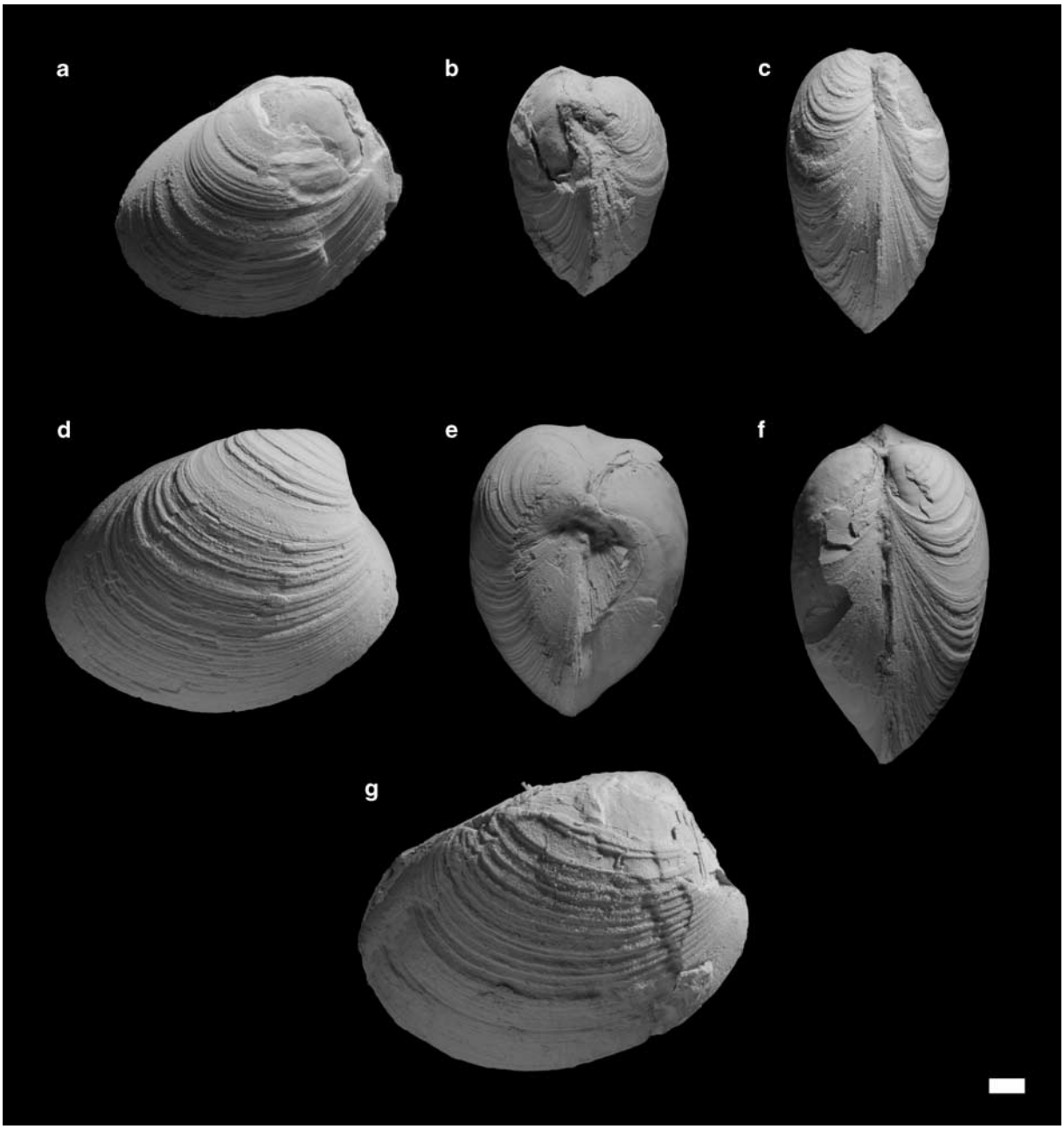

Fig. 4. Shells of *Leionucula frigida* from the BAS collection. **a.–c.** P. 2702.340, **a.** left valve, **b.** posterior, **c.** anterior. **d.–f.** P. 2702.341, **d.** left valve, **e.** posterior, **f.** anterior. **g.** P. 2702.339 left valve. Scale bar = 2 mm.

Melville Formation assemblage, specimens are described as *Leionucula melvilleana* n. sp. (see Systematics below).

Following study of the BAS collection a further two species are recorded from the unit, *Limopsis infericola* Whittle, Linse & Griffiths, 2011, and *Limatula* (*Antarctolima*) sp. *Leionucula frigida* is the most abundant species, with 495 specimens, *Yoldia peninsularis* is the second most abundant with 148 specimens. The Limidae and Pectinidae are represented by only one specimen each (Table I). Overall protobranch bivalves dominate the Cape Melville Formation bivalve assemblage as they comprise 89% of the BAS collection. As a family, the Nuculidae constitute 60% of the collection.

Systematics

Class Bivalvia Linnaeus, 1785
Order Nuculida Dall, 1889
Family Nuculidae Gray, 1824
Subfamily Nuculominae Maxwell, 1988
Genus *Leionucula* Quenstedt, 1930

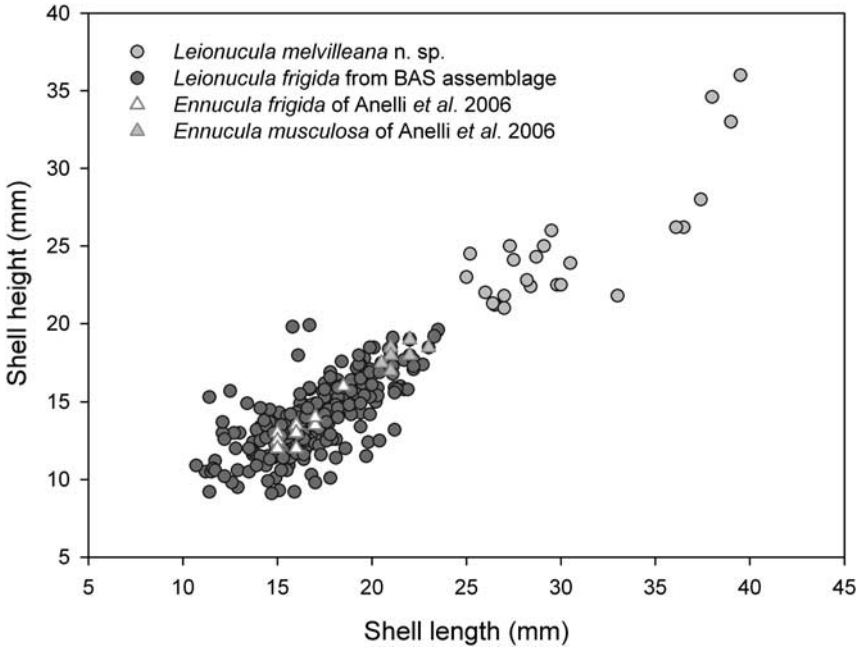

Fig. 5. Shell morphometrics of Cape Melville Formation Nuculidae.

Anelli *et al*. (2006) described two species of nuculid under the names *Ennucula frigida* and *E. musculosa*, based on 84 well preserved specimens. However, several authors have suggested *Ennucula* and *Leionucula* are synonymous (e.g. Keen 1969, Stilwell 2000, Beu 2009). Based on this, Beu (2009) stated that the Cape Melville species of Nuculidae, *E. musculosa* and *E. frigida*, should be re-assigned to the genus *Leionucula*.

Type species: (by original designation) *Nucula albensis* d'Orbigny

Leionucula frigida (Anelli, Rocha-Campos, Santos, Perinotto & Quaglio, 2006)
(Fig. 4)

2006 *Ennucula frigida* Anelli, Rocha-Campos, Santos, Perinotto & Quaglio, pp. 117–119; Fig. 5.

2006 *Ennucula musculosa* Anelli, Rocha-Campos, Santos, Perinotto & Quaglio, pp. 119–120; Fig. 6.

Diagnosis of species: Umbones slightly elevated above hinge line with opisthogyrate beaks, external ornament of fine growth lines overlain by well-marked irregularly spaced commarginal growth corrugations; with a maximum of 20 teeth in the anterior and ten on the posterior regions of the shell; chondrophore short and oblique.

Material examined: 495 specimens from the BAS Cape Melville Formation collection and 15 specimens originally described as *E. frigida* and *E. musculosa* in Anelli *et al*. 2006 from the Instituto de Geociências, Universidade de São Paulo.

Localities: BAS localities P. 2701, P. 2702 and P. 2707, plus section C and D of Anelli *et al*. 2006 (Fig. 1).

Discussion: The BAS collection includes 495 specimens with morphological similarity to the previously described species *E. musculosa* and *E. frigida* (Figs 4 & 5). One of the criteria for the separation of these two species was specimen size, as the IGc-USP specimens fit into two discrete size categories (see *E. frigida* and *E. musculosa* datasets on Fig. 5) (Anelli *et al*. 2006). However, further evidence from the large BAS collection of nuculids has increased our knowledge of the shell morphology and size ranges for Cape Melville nuculids. The BAS specimens of *L. frigida* show a much wider range in shell size than specimens originally described as *E. frigida* and *E. musculosa* (Anelli *et al*. 2006) and there is no distinct division in the BAS data (Fig. 5). Other criteria used to separate the two species were slight differences in margin shape and angles (Anelli *et al*. 2006). However, as with shell size, BAS specimens also show a range in margin morphology that incorporates the *E. frigida* and *E. musculosa* end members of Anelli *et al*. (2006). Therefore, it is not possible to separate the BAS specimens into two species using the descriptions in Anelli *et al*. 2006. Simple morphometric comparisons demonstrate that *E. musculosa* intergrades with *E. frigida*, and we regard the species names *musculosa* and *frigida* as synonymous. As first revisers, we choose the name *Leionucula frigida* for this species.

Leionucula melvilleana n. sp.
Whittle & Quaglio, 2012
(Fig. 6)

Derivation of name: Named for the Melville Peninsula, where the specimens were discovered.

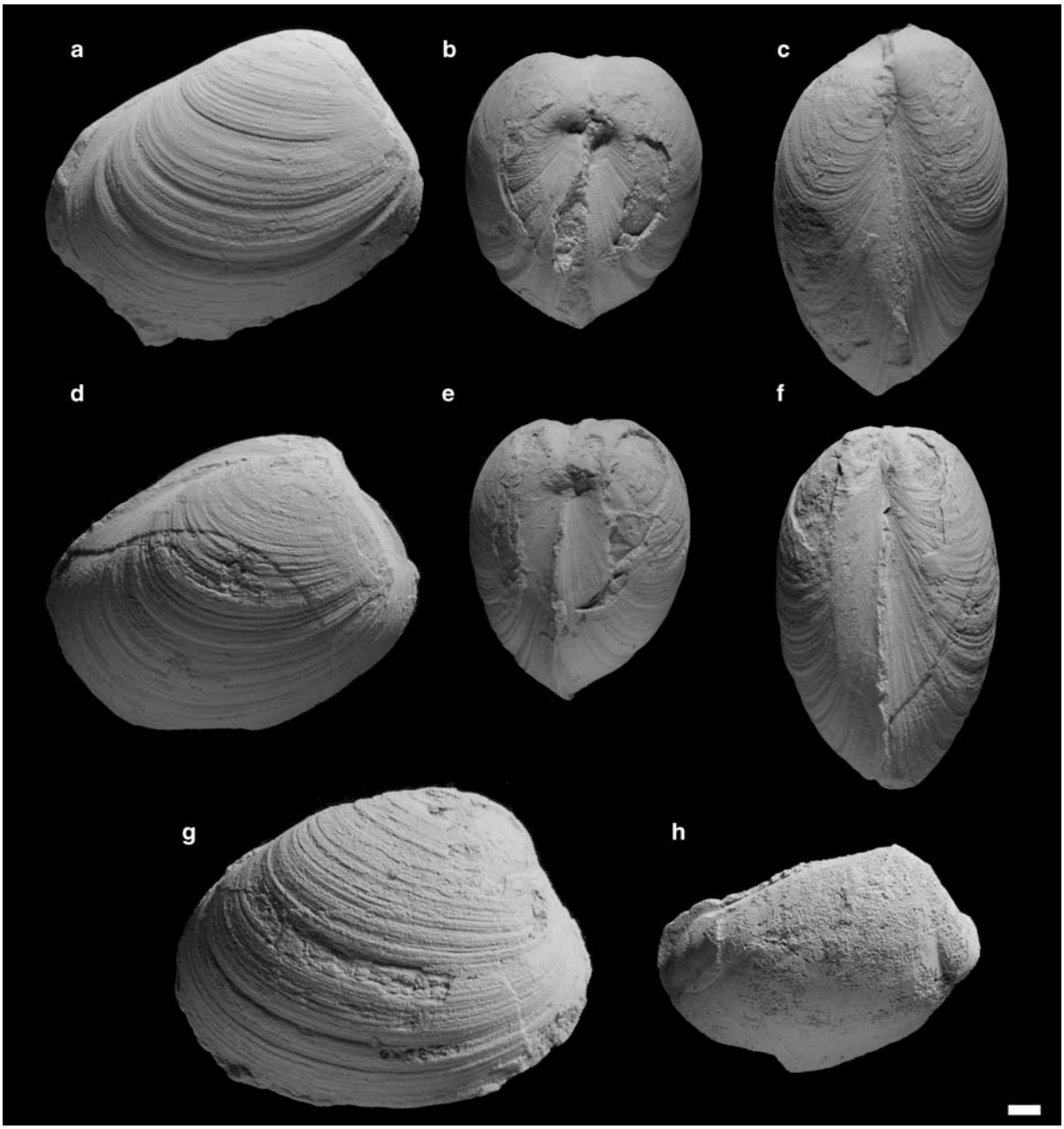

Fig. 6. *Leionucula melvilleana* n. sp. **a.–c.** Holotype, P. 2702.1321, **a.** left valve, **b.** posterior, **c.** anterior. **d.–f.** Paratype P. 2702.1322, **d.** left valve, **e.** posterior, **f.** anterior. **g.** P. 2702.1323 left valve. **h.** Internal mould P. 2702.1328. Scale bar = 2 mm.

Diagnosis: Large inflated nuculid, with a straight posterior margin.

Holotype: P. 2702.1321 complete articulated shell.

Paratypes: P. 2702.1322, P. 2702.1323, P. 2702.1324, internal mould P. 2702.1328, and partial specimen P. 2702.1329, which was cut in two to see the taxodont dentition. Type specimens are housed in the BAS Type and Figured collection.

Other material: P. 2702.1325–1327; P. 2702.1330–1334 and P. 2702.1097–1113, P. 2702.1115–1117, P. 2702. 1119–1122; P. 2702.1148, P. 2702.1149, which are housed at BAS, and specimen GP/1E 5252, from the Instituto de Geociências, Universidade de São Paulo.

Locality: King George Island, South Shetland Islands, Antarctica. Cape Melville Formation, Moby Dick Group 62°02'S, 57°38'W, locality P. 2702 and section C of Anelli *et al.* 2006 (Fig. 1).

Age: 22.6 ± 0.4 Ma (Early Miocene) based on Sr isotope data from bivalves (Dingle & Lavelle 1998).

Description: Shell longer than high, antero-posteriorly elongate. Length 25–39.5 mm (mean 30.5 mm, SD = 4.7;

holotype length 37.4 mm), height 21–36 mm (mean 25.0 mm, SD = 4.1; holotype height 28 mm), inflation 13.5–23.1 mm (mean 17.4 mm, SD = 2.8; holotype inflation 23.1 mm) (Fig. 5). Umbones somewhat elevated above the hinge line, with slightly curved opisthogyrate beak. Posterior margin almost straight, anterior margin curved, ventral margin broadly rounded. Posterior adductor rounded; anterior adductor sub-quadrate, larger than posterior, with a very clear margin (Fig. 6h). Non-sinuate pallial line. External sculpture of irregularly spaced coarse commarginal growth lines, inner ventral margin smooth. Taxodont dentition visible on some specimens, posterior part of hinge short, with at least seven teeth (GP/1E 5252), anterior part hinge, with at least 15 (P. 2702.1325) to 19 teeth (GP/1E 5252).

Remarks: Specimens are similar to a single *Leionucula* specimen from Eocene erratics of McMurdo Sound identified by Stilwell (2000), who suggested that it may belong to a new species but did not formally describe it. The McMurdo specimen falls within the length, height and inflation range of the Cape Melville specimens. However, *L. melvilleana* n. sp. differs in having a straighter posterior margin. *Nucula* (*Leionucula*) *grandis* Malumian, Camacho & Gorroño, 1978 is also similar in size to *L. melvilleana* n. sp., but differs in having a subrectangular as opposed to subtriangular outline and more pointed umbones (Malumian *et al*. 1978).

The new species differs from specimens belonging to the nuculid genera *Nucula* Lamarck, 1799, *Lamellinucula* Schenck, 1944, *Linucula* Marwick, 1931, *Deminucula* Iredale, 1931, *Pronucula* Hedley, 1902, *Pectinucula* Quenstedt, 1930, *Gibbonucula* Eames, 1951 and *Rumptunucula* Bergmans, 1978 as it has a smooth as opposed to crenulate inner ventral margin (Rhind & Allen 1992). *Acila* (Adams & Adams, 1858) differs from the new species as it has divaricate sculpture (Rhind & Allen 1992).

Leionucula melvilleana n. sp. differs from the *L. frigida* previously described from the Cape Melville Formation by its greater height and length (Fig. 5). *Leionucula melvilleana* specimens are generally more inflated than *L. frigida*, but there is some overlap. Measurements of *L. melvilleana* and *L. frigida* were analysed using unpaired *t*-tests. The two species show highly significant differences for height, length and inflation (length $P = 9.04 \times 10^{-14}$, height $P = 8.80 \times 10^{-13}$, inflation $P = 1.18 \times 10^{-47}$). The *L. melvilleana* specimens have less pronounced commarginal ridges than *L. frigida*. They also have a straighter beak, antero-dorsal margin, and posterior margin. Also, the muscle scars are a different shape and the anterior adductor is much less rounded on *L. melvilleana* n. sp.

Conclusions

The Cape Melville Formation, one of the earliest Cenozoic glacial faunas from Antarctica, preserves a bivalve assemblage that was dominated by protobranchs. The Family Nuculidae, represented by two species, is the most numerous in the unit, with most specimens belonging to *L. frigida*. The fauna of the Cape Melville Formation has been extended by the addition of *L. melvilleana* n. sp. These results increase our knowledge of the Cape Melville Formation fossil assemblage, as well as contributing to knowledge of the overall Antarctic fossil community. Analysis of the Cenozoic fossil record indicates that the generic diversity of the Family Nuculidae has decreased in the Antarctic region through the Cenozoic to the Recent.

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