The Early Miocene Cape Melville Formation Fossil Assemblage and the Evolution of Modern Antarctic Marine Communities

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Abstract

The fossil community from the early Miocene Cape Melville Formation (King George Island, Antarctica) does not show the archaic retrograde nature of modern Antarctic marine communities, despite evidence, such as the presence of dropstones, diamictites and striated rocks, that it was deposited in a glacial environment. Unlike modern Antarctic settings, and the upper units of the Eocene La Meseta Formation on Seymour Island, Antarctica, which are 10 million years older, the Cape Melville Formation community is not dominated by sessile suspension feeding ophiuroids, crinoids or brachiopods. Instead, it is dominated by infaunal bivalves, with a significant component of decapods, similar to present day South American settings. It is possible that the archaic retrograde structure of the modern community did not fully evolve until relatively recently, maybe due to factors such as further cooling and isolation of the continent leading to glaciations, which resulted in a loss of shallow shelf habitats.

Keywords: Fossil, Antarctica, early Miocene, Community Structure, Decapod, Assemblage

Introduction

Modern Antarctic marine benthic communities are dominated by sessile suspension feeding organisms in many shelf areas (Gili et al. 2006; Clarke et al. 2004; Aronson et al. 2007; Gutt et al. 2013). There are very few crushing predators in Antarctic shallow marine environments. Sharks and rays and most durophagous reptant decapods, which are important community structuring predators elsewhere in the shallow oceans, are absent from Antarctic waters (Hall and Thatje 2011; Griffiths et al. 2013), allowing dominance by groups such as sponges and ophiuroids. The top predators of the living Antarctic benthos are asteroids, nemertean worms and other slow moving invertebrates of a Palaeozoic functional grade (for example pycnogonids and isopods) that are not durophagous (Aronson et al. 2009). Colder water temperatures in the Antarctic make it difficult to extract calcium ions from sea water, and this, in addition to a lack of predators; means that recent Antarctic shelled organisms such as bivalves are very thin shelled (Nicol 1967; Vermeij 1978; 1987; McClintock et al. 2009). Modern communities in regions outside the Antarctic where durophagous decapods are present, such as the South American Magellan Province, have much higher relative abundances of infaunal taxa, especially molluscs (Thatje and Mutschke 1999).

The general lack of sharks, rays and durophagous decapods on the high-Antarctic continental shelves has been given as one of the primary explanations for the retrograde structure and function of shelf benthos when compared with shallow water communities elsewhere (Hall and Thatje 2011). However, there are a number of factors that may have shaped the modern fauna including oceanographic changes, the onset of Cenozoic glaciations, sea-water cooling, changes in habitat driven by variations in ice extent and habitat disturbance caused by ice-berg scouring (Clarke et al. 2004). There is little direct fossil information about the evolution of Antarctic marine fauna (Barnes and Clarke 2011). The only known examples of studies on Antarctic Cenozoic marine invertebrate community structure are from the Eocene of Seymour Island (Aronson and Blake 2001; Aronson et al. 1997; 2009). Some modern Antarctic taxa evolved as early as the late Cretaceous (Beu 2009; Crame 2013). Studies from Seymour Island, Antarctica, suggest that the modern Antarctic community structure had its origins in the late Eocene (Aronson and Blake 2001; Aronson et al. 1997; 2009).

Fossil evidence from Seymour Island shows that shallow, subtidal communities in the early to middle Eocene contained durophagous taxa such as teleostean fish, decapod crustaceans and neoselachian sharks and rays typical of other regions at the present day (Aronson et al. 2009; 2011). Evidence for Antarctic climate at this time suggested seasonality in temperature and precipitation in a warm, humid, temperate environment (Jacques et al. in press). Changes in the Seymour Island communities were linked with a cooling trend towards the end of the Eocene, and this was linked to a fundamental shift in the structure of benthic communities in Antarctica (Aronson and Blake 2001; Aronson et al. 1997; 2007; 2009; 2011). This resulted in changes in faunal composition and a decrease in taxonomic diversity, which included the disappearance of durophagous predators such as most reptant decapods, sharks, and teleost fish (Aronson and Blake 2001; Eastman 2005; Aronson et al. 1997; 2007; 2009; 2011). The reasons for the absence of these groups are complex, but have been linked to historical biogeography, physiology, and phylogenetic constraint (Aronson et al. 2007; 2011). For example, the absence of certain reptant decapod crustaceans (benthic, walking decapods, including brachyuran crabs and astacid lobsters) from Antarctic waters today has been cited as a direct result of their physiological intolerance of cold sea temperatures (Frederich et al. 2001; Wittmann et al. 2010; Aronson et al. 2011). However, Griffiths et al.

(2013) show that one group of decapods, lithodids, are found in many areas of Antarctic waters that are warmer than 0°C, and conditions have been suitable for their colonisation for at least 9,000 years (Griffiths et al. 2013).

The loss of durophagous predators and the resultant lowered predation pressure led to stalked crinoids and epifaunal ophiuroids moving to shallower Antarctic waters from deeper water environments (Aronson et al. 1997; Aronson and Blake 2001). However, Aronson and Blake (2001) stated that causal connections between global cooling and durophagous predation must be complex and indirect as durophagous predation remains strong in the recent Arctic (Dayton 1990). Timing of the post-Eocene Antarctic extinctions of durophagous predators is uncertain (Aronson et al. 2009). One of the few post-Eocene marine fossil sites in the Antarctic is the Cape Melville Formation (CMF) on King George Island, West Antarctica.

The Cape Melville Formation (Moby Dick Group, King George Island Supergroup) comprises an approximately 150 m thick exposure on the narrow Melville Peninsula, which lies at the eastern extremity of King George Island (Troedson and Riding 2002) (Fig. 1). Age constraints include andesite dykes, which cut through the CMF and thus post date the unit; these have been radiometrically dated at 20 Ma using K-Ar (Birkenmajer et al. 1985). Fossils from the unit have early Miocene affinities (Biernat et al. 1985; Bitner and Crame 2002). The formation has also been dated as 22.6 +/- 0.4 Ma (Early Miocene), based on Sr isotope data from bivalves (Dingle and Lavelle 1998).

The formation consists of horizontal to sub-horizontally bedded mudstones and silty mudstones. There is also a diverse assemblage of glacially rafted lithological material in the unit (Birkenmajer et al. 1983), some of which is facetted and striated (Birkenmajer 1982; 1984; Troedson and Riding 2002). The wide regional source area for this material indicates the presence of widespread regional ice, calving ice margins, and the presence of large icebergs (Troedson and Riding 2002). The unit provides rare evidence of extensive glaciation in the Antarctic Peninsula region in the earliest Miocene, with regional marine based grounded ice on the continental shelf (Troedson and Riding 2002).

The formation is separated into four units, which were described and interpreted by Troedson and Riding (2002). Unit A was interpreted as a proximal glaciomarine facies, deposited by glaciogenic debris flows, ice rafting and suspension settling. Unit B, also a proximal glaciomarine facies, was deposited by turbidites, hemipelagic sedimentation and suspension settling. Unit C, a distal glaciomarine facies, with a minor carbonate ooze component, was deposited through ice rafting, hemipelagic sedimentation, gravity flows and biogenic pelagic sedimentation. Unit D, a distal glaciomarine facies, was deposited by ice rafting and hemipelagic sedimentation. Macrofossils are moderately common in this unit (Troedson and Riding 2002).

Birkenmajer (1982; 1984; 1987) stated that sedimentological data and the benthic fauna point to the CMF as being a quiet, low energy environment comparable with a flat or gently sloping submarine plain of outer shelf or more restricted basin, below wave base. A comparatively deep-water, outer shelf environment for the unit was later suggested based on the composition of the macrobenthic assemblage (Förster et al. 1987; Feldmann and Crame 1998; Hara and Crame 2004). This was supported by evidence from microfaunal and microfloral data (Dudziak 1984; Birkenmajer and Łuczkowska 1987; Troedson and Riding 2002; Hara and Crame 2004). The presence of infaunal bivalves in life position, horizontal crab burrows, and the vertical growth position of corals led Roniewicz and Morycowa (1987) to suggest deposition in low energy water interspersed with chaotic burial.

Previous studies on the CMF focussed on taxonomic descriptions of the different marine invertebrate groups (Roniewicz and Morycowa 1985; Förster 1985; Förster et al.

1987; Jesionek-Szymańska 1987; Karczewski 1987; Szaniawski and Wrona 1987; Feldmann and Crame 1998; Bitner and Crame 2002; Jonkers 2003; Hara and Crame 2004; Anelli et al. 2006; Whittle et al. 2011; 2012; Beu and Taviani 2013), or intra-taxon assemblage characterisation (Whittle et al. 2012). Microfossils identified from the CMF included Polychaeta in the form of jaw elements, Foraminifera, Radiolaria, Ophiuroidea elements and Ostracoda (Birkenmajer and Łuczkowska 1987; Szaniawski and Wrona 1987). Fossils have been found from 14 different sites along the Cape Melville Peninsula (Fig. 1).

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 and Lavelle 1998; Troedson and Riding 2002). Based on evidence from Cape Melville fossils we hypothesise that the evolution of modern Antarctic marine community structure was still incomplete in the early Miocene.

Materials and Methods

British Antarctic Survey (BAS) specimens were collected from the CMF by one of us (JAC) in the 1994/1995 field season using the numbers P. 2701 (75 specimens), P. 2702 (1321 specimens) and P. 2707 (155 specimens). Fossils in the BAS assemblage were studied using an optical microscope, measured using Vernier callipers, identified to lowest possible taxonomic level and counted. All specimens were collected from approximately the uppermost 75 m of Unit D of Troedson and Riding (2002) and can be regarded as one time-averaged assemblage for the purposes of this study (Fig. 1b, c). Infaunal fossils from the

CMF are relatively well preserved, and can be counted as individual animals. The majority of the bivalves have both valves, only the very rare epifaunal species are preserved as single valves. The epifaunal gastropods are not well preserved, but they still occur as complete specimens. However, nearly all are internal moulds and key features such as ornaments, apertures, and protoconchs are frequently missing. Most of the decapod specimens are preserved as articulated specimens, although there are also disarticulated appendages in the collection. Only decapods that could be identified as belonging to a single specimen were included in taxon counts, so their contribution to the overall fauna is a minimum estimate.

Data for the assemblage reconstruction for the CMF came from this study, and are based on the relative proportions of taxa found. Community comparisons were undertaken using assemblage data from several sources. Recent relative abundance data, at order, class, and phylum level, for the West Antarctic Peninsula region came from the unpublished results of the BAS expedition JR230 (data held by Dr DKA Barnes of BAS. http://www.bodc.ac.uk/data/information_and_inventories/cruise_inventory/report/14037/) from a total of 39 stations at approximately 500 m deep (collected using a 2 m wide Agassiz trawl with an inner net mesh size of 10 mm). The Recent Beagle Channel (23 stations, 14 – 348 m), South Patagonian Ice-Field (20 stations, 20 – 711 m), and Straits of Magellan (29 stations, 8 – 571 m) data were from Thatje and Mutschke (1999). Only taxa that are likely to fossilise and were found in the CMF were compared to modern data to account for taphonomic bias in the fossil record, e.g. taxa such as the holothurians and ascidians were excluded. The multivariate statistical software PRIMER 6 (Clarke and Warwick 2001) was used to analyse faunal similarities between communities by implementing the Bray-Curtis measure performed on relative abundance data. The similarity matrix was then used for a cluster analysis.

Results

The BAS invertebrate macrofauna collection comprises 1,551 individuals belonging to seven phyla (Cnidaria, Mollusca, Annelida, Arthropoda, Bryozoa, Brachiopoda, and Echinodermata), collected from the three localities in the uppermost 75m of the CMF (Fig. 1, Table 1). Twenty two families, eighteen genera, and fourteen species were identified. All fossils identified to species level in the collection are endemic to the CMF. Bivalves dominated the assemblage, making up 57.8% of the total fauna, then gastropods at 20.4%, and the only other taxa that contributed significantly to the fauna were corals (13.5%) and decapods (6.1%). A reconstruction of the community, based on the relative abundances of taxa, is shown in Fig. 2.

The bivalve assemblage included eight bivalve families, Nuculidae (60.5% of the bivalves), Sareptidae (16.5% of the bivalves), Malletiidae (7.7% of the bivalves), Hiatellidae (3.5% of the bivalves), Periplomatidae (1.0% of the bivalves), Limopsidae (1.2% of the bivalves), Limidae (0.1% of the bivalves), and Pectinidae (0.1% of the bivalves), and 10 species have been identified (Jonkers 2003; Anelli et al. 2006; Whittle et al. 2012). It is dominated by protobranchs (89% of the bivalves), with the Nuculidae forming the most numerous component (60% of the bivalves) (Whittle et al. 2012). The BAS collection contained two recently described species (Whittle et al. 2011; 2012) and an as yet undescribed limid (Quaglio et al. in prep) in addition to those already described from the CMF (Anelli et al. 2006).

Six gastropod families were identified in the BAS CMF collection (Volutidae, Cerithiidae, Epitonidae, Turritellidae, Naticidae, and Buccinidae, s.l.). Most designations have been made to family level, some of these are tentative identifications, and 42% of the gastropod fauna is classed as indeterminate. The gastropods are dominated by predatory naticids (23% of the gastropods). Originally, Karczewski (1987) identified 18 gastropod families, 26 genera and 30 species based on 63 fossil specimens from 6 localities in the Cape Melville Formation. Specimens were mostly compared with taxa from North America and Europe (Karczewski 1987). More conservative identifications for this material were made by Beu (2009), who placed fossils in five families, with a further two questionable family assignments. In total nine genera were listed, six of which were of uncertain taxonomic status, and several gastropods were indeterminate (Beu 2009). Families that were identified by Beu (2009) that are found in our collection are Turritellidae, Naticidae, and Buccinidae, s.l.. Families that Beu (2009) identified that are not found in our collection are Aporrhaidae, ?Philinidae, and ?Mathildidae and the superfamily Conoidea, including the former family Turridae (Bouchet et al. 2011; Engl 2012), whose Antarctic fossil members are of uncertain taxonomic status at present.

The BAS collection contained 210 specimens of *Flabellum* corals (13.5% of the invertebrate fauna), and was the second most abundant group after the Mollusca. Corals were originally described from Polish CMF material, and were assigned to the species *Flabellum rariseptatum* Roniewicz and Morycowa 1985. Corals from other collections were found either in life position (Birkenmajer et al. 1983; Birkenmajer 1984) (vertically orientated) or overturned (Roniewicz and Morycowa 1987). All post-larval skeletal stages were represented (Roniewicz and Morycowa 1987).

Two decapod taxa were found in the unit, and they accounted for at least 6.1% of the fauna (Table 1). Prolific remains of *Antarctidromia inflata* Förster, 1985, (Family Homolodromiidae) were found in the BAS collection (91 specimens that can be attributed to single animals and a further 51 disarticulated appendages have been found, which have not been counted in the overall fauna). Preservation ranged from incomplete carapaces, with or without some articulated appendages, to individual claws. Crab remains have been found by other workers; Förster et al. (1987) described the remains of nearly 200 almost complete crab carapaces, which they suggest to be body fossils as opposed to moults. The crabs were associated with burrow structures found on the Melville Peninsula, suggesting that they are the remains of an ancient community (Förster et al. 1987; Uchman and Gaździcki 2010). All growth stages from juveniles to adults were found, and males were more abundant than females (Förster et al. 1987). Homolodromiidae is a primitive brachyuran family with a sparse fossil record in the Mesozoic and Cenozoic (Förster 1985; Schweitzer et al. 2004). However, two different fossil genera, *Antarctidromia* and *Antarctiprosopon*, have been found in Antarctica (Förster 1985; Feldmann and Wilson 1988; Schweitzer and Feldmann 2011). These occurred in very different environmental settings, but reasonably close in geographical terms. In the late Eocene, *Antarctiprosopon* lived in a shallow water, nearshore environment (Feldmann and Wilson 1988), but in the early Miocene *Antarctidromia* inhabited a deeper water setting in a muddy environment, and had a burrowing mode of life (Förster et al. 1987). There is little information about the ecology of recent Homolodromiidae. The two modern genera (*Dicranodromia* and *Homolodromia*) are found in water depths ranging from 35 to 1080 m, with the highest number of records at around 700 m in depth (supplementary table 1). The BAS CMF collection also contained 4 specimens of the lobster *Hoploparia gazdzickii* originally described by Feldmann and Crame (1998).

The remaining groups in the CMF BAS collection accounted for just over 2% of the fauna (Table 1). Scaphopods have been mentioned in several publications but formal identifications have not been published. BAS specimens belong to *Dentalium* sp.. The genus is also known in the Antarctic fossil record from the Oligocene Polonez Cove Formation at Magda Nunatak on King George Island (Pugaczewska 1984). Bryozoans from the BAS collection were described by Hara and Crame (2004) in the family Aspidostomatidae and identified to the species *Aspidostoma melvillensis*. Brachiopods were identified from the family Terebratulidae, genus *Liothyrella* and the family Laqueidae, genus *Paraldingia* (Bitner and Crame 2002). Bryozoan fragments were noted by Birkenmajer and Łuczkowska (1987) in their microfossil collections. Echinoderms from Polish collections were identified to 3 genera in the families Cidaridae, Echinidae and Schizasteridae (?*Notocidaris*, ?*Sterechinus* and ?*Schizaster*). Assignments were tentative due to the poor preservation of the material (Jesionek-Szymańska 1987). Echinoids from the BAS collection can be identified to the family Cidaridae and slightly better material can be placed in ?*Notocidaris*. Echinoid spine fragments were also identified from Polish collections (Birkenmajer and Łuczkowska 1987), but were not found in the BAS collection. Serpulid worm tubes are found preserved in the BAS CMF assemblage in low numbers (Table 1).

Feeding strategy

In the CMF assemblage only ten out of the 22 families identified could be classed as purely suspension feeding (45%); and considering total abundance numbers, only 22% of the invertebrate fauna could be classed as purely suspension feeding (indeterminate bivalve and gastropod taxa, for which feeding strategy could not be determined, were not included in the total). Overall, it is clear that the CMF is not dominated by sessile suspension feeding communities of sponges, cnidarians, bryozoans, ascidians, and echinoderms that are seen in many modern Antarctic communities (Dayton et al. 1986; Gili et al. 2006; Gutt et al. 2013).

Numerically, the majority of Cape Melville invertebrates were deposit feeders (Table 1). Bivalves were the dominant taxa and of the 851 specimens identifiable to family level or higher (the 45 indeterminate specimens were excluded), 93.8% were deposit feeders and 6.2% were suspension feeders; this is because the bivalve fauna is dominated by deposit feeding nuculids. These percentages are similar to relative abundances from the modern day Beagle Channel, Patagonia, where bivalve species are overwhelmingly infaunal (98.12%) with only 1.88% being epifaunal, and the nuculids account for the largest percentage of the bivalves (33%) (percentages for the soft bottomed stations, ranging from 25 to 665 m deep, were taken from Linse and Brandt 1998).

Taxonomically, 3 bivalve genera were deposit feeders and 5 were suspension feeders in the CMF. It is difficult to assess feeding strategies of gastropods, and some taxa may exhibit more than one feeding strategy at different stages of development (Allmon 1988). For example, most Turitellidae species are ciliary suspension feeders, but some or all may be deposit feeders or grazers for at least part of the time (Allmon 1988); in Table 1 they have been counted as suspension feeders. However, they were the only suspension feeding gastropod taxon identified (accounting for 13% of the gastropods). 79.3% of the gastropods were carnivorous (predatory or a mixture of predatory/scavenging), and some of these taxa have specialised feeding preferences, such as the Epitoniidae, which feed on sea anemones and corals (Robertson 1963), and the Conoidea, which mainly feed on polychaetes (Kantor and Taylor 1991). The remaining taxa were a mixture of deposit feeding and grazing.

Dentalium is also thought to be a strongly specialised feeder; it was classed as a predator based on the work of Morton (1959), who observed that they used prehensile tentacles (captacula) to actively search out and locate Foraminifera.

Assemblage structure

The overall composition of the CMF assemblage showed a much more marked similarity to the Recent Beagle Chanel (>85% similarity) and Straits of Magellan (~74% similarity) community structures than it did to the modern West Antarctic Peninsula (<35% similarity), when the relative abundances of preservable taxonomic groups were compared (Fig. 3).

At the taxonomic levels shown in figure 3, the only obvious difference between the CMF assemblage composition and that of the Beagle Channel is the relative abundance of Cnidaria (13% and <0.5% relative abundance respectively). Figure 3 shows that when durophagous decapods are present in modern settings (such as the Beagle Channel, South America), bivalves and gastropods dominate the assemblage (>90% of collected preservable samples), and the proportions of many groups such as scaphopods (<1%), brachiopods (<0.5%), and bryozoans (<0.5%) are lower (Fig. 3). Durophagous decapods are absent from the fauna in the Western Antarctic Peninsula, here groups that are minor elements in the Beagle Channel, such as bryozoans (~14%) and echinoids (25%) are much more prevalent (Fig. 3).

Species level data from mollusc collections from Beagle Channel (Linse and Brandt 1998) show large percentages of infaunal molluscs, which is similar to the CMF assemblage.

33% of the bivalves in the Beagle Channel are nuculids (Linse and Brandt 1998); in the CMF 60.5% of the bivalves are nuculids. Other dominant bivalve families identified from the Beagle Channel include Lasaeidae (an infaunal family accounting for 29% of the bivalves), Malletidae (16% of the bivalves), and Nuculanidae (9% the bivalves). In the CMF the other dominant bivalve families are Sareptidae (16.5% of the bivalves), Malletiidae (7.7% of the bivalves), and Hiatellidae (3.5% of the bivalves).

Discussion

Outcrops of fossiliferous rocks are comparatively rare in Antarctica and, obviously, trends cannot be inferred for the whole of Antarctica based on evidence from a single locality as depositional settings vary between fossil sites. Also, variations in physical setting and differential preservation of taxa make it difficult to make firm conclusions based on comparisons of fossil occurrence data with modern data. However, the CMF preserves interesting evidence of a glacial fossil assemblage that has no direct parallels in Antarctica at the present day, but has a greater similarity to the modern day Beagle Channel community structure. There are many explanations why the CMF invertebrate community structure does not resemble that of modern day Antarctica and many of these explanations may be interlinked. Variations in the preservation potential of aspects of the CMF fauna, the presence or absence of community structuring organisms, the amount of terrigenous sediment input, cooling climate, a loss of shelf habitats, lateral heterogeneity, changes in seasonal variations of annual food supply and environmental setting may have all contributed to the differences between communities.

Taphonomy creates a biased record of the living community, as larger organisms with hard parts are preferentially preserved (Staff et al. 1986). Looking at the CMF fauna, there are generally well-preserved infaunal elements, but the epifaunal component is less represented and less well-preserved. Gili et al. (2006) noted 10 major groups of epifaunal sessile suspension feeders in the modern Antarctic fauna (Porifera, Gorgonaria, Pennatularia, Alcyonaria, Stolonifera, Hydrozoa, Actiniaria, Bryozoa, Brachiopoda, and Ascidiacea), most of these have a very low fossilisation potential, so it is possible that these elements were present but not preserved. Conversely, the epifaunal suspension feeding component may not have been as numerous or taphonomic processes, like destruction by iceberg scouring, destroyed evidence of them. There are other factors that may have affected the community structure, for example if active iceberg scouring had occurred then the fauna may have developed predominantly infaunally in response to this. This is seen in some modern Antarctic assemblages, which are seemingly well adapted to rapid recovery following disturbance events by having a simple infaunal structure (Smale et al. 2008). Given these limitations the reconstruction of the Cape Melville Formation fossil assemblage (Fig. 2) was made to the best of our knowledge using only the data we have available.

Aronson et al. (2009) suggested that the evolution of the modern Antarctic community structure initiated towards the end of the Eocene, with the start of a major decline in global temperatures, based on evidence from the late Eocene of Seymour Island (Aronson et al. 1997). This cooling was thought to have led to a reduction in activity and eventual loss of durophagous predators such as decapods, sharks, and many teleosts, resulting in communities with an archaic state, low in predators and high in epibenthic sessile suspension feeding groups such as ophiuroids and crinoids. This structure is seen in modern Antarctic environments (Aronson et al. 2009). Evidence from the CMF assemblage does not fit with the modern Antarctic community structure, or that of the late Eocene of Seymour Island. The dominance of communities composed of suspension feeders and associated fauna in Antarctica today has been confirmed by Gutt et al. (2013). However, this study also shows that there is heterogeneity in Antarctic macrobenthic communities. A reason that the CMF community structure could have differed from that of the late Eocene of Seymour Island is that the community structure could have varied around the continent in the past, as it does today (Gutt et al. 2013). Alternatively deeper water settings (Cape Melville Formation) could have developed a retrograde structure at a different time to shallower water settings (La Meseta Formation).

Purely suspension feeding groups only account for 22% of the CMF assemblage; they are not a dominant element of the community. In particular, dense assemblages of suspension feeding crinoids and ophiuroids, such as those seen in late Eocene Seymour Island assemblages, (Aronson and Blake 2001) were not found in our CMF collection. Also, brachiopods are not found in abundance in the Cape Melville assemblage, but predatory decapod groups are found. The absence of ophiuroids and crinoids may well be taphonomic, however, decapods also have a relatively low preservation potential due to their strong susceptibility to decay early in the post-mortem history (Stempien 2005; Krause et al. 2011), and articulated specimens are found in abundance in the formation. Rare ophiuroid fragments were identified in low numbers (six elements) from Polish Cape Melville collections (Birkenmajer and Łuczkowska 1987), but ophiuroid elements were not found in our CMF collection. Either the presence of a high number of predatory decapods restricted suspension feeding groups like the ophiuroids, or they were not preserved. Ophiuroid ossicle dissolution is relatively rapid and experimental taphonomy has suggested that the stratigraphic record does not accurately reflect the presence and abundance of ophiuroids (Walker et al. 2013). Gilli et al. (2006) stated that durophagous predators do not normally prey on sessile organisms such as sponges, cnidarians and bryozoans, and therefore the lack of large predators is probably not a major factor explaining the make-up of the sessile Antarctic fauna today (Gili et al. 2006). They suggested that a scarcity of herbivores, a lack of terrigenous sediment input, and a paucity of bioturbators, in addition to the low number of predators, may have influenced the modern Antarctic benthos (Gili et al. 2006). It has also been suggested that seasonal variations of annual food supply may strongly influence the production and productivity of Antarctic invertebrates (Arntz et al. 1994; Gorny 1999; Thatje et al. 2003). A marked seasonality of primary production in the Southern Hemisphere, and the resultant restriction on food supplies, is thought to select against certain groups of animals. This is known as Thorson's rule (Mileikowsky 1971). Groups, which in cold waters have prolonged, planktotrophic larval development, for example some reptant decapods, will be selected against at high latitudes (Thorson 1936; Thorson 1950; Thatje et al. 2003).

The abundance of *Antarctidromia* in the CMF is interesting as the present day Antarctic decapod fauna is impoverished (Thatje and Arntz 2004; Griffiths et al. 2013). Lithodid crabs are found in modern Antarctic seas but brachyuran crabs and lobsters are very rare or even absent from high-Antarctic shelves (Thatje and Arntz 2004; Griffiths et al. 2013). Decapods are also uncommon in the fossil record of Antarctica; the CMF is the second most abundant locality after Seymour Island, where a late Cretaceous to Eocene fauna is found (Feldmann and Wilson 1988; Feldmann et al. 2003; Griffiths et al. 2013). Currently, the exact timing of the extinctions of durophagous predators (such as brachyuran crabs and lobsters) in the Antarctic region is uncertain, but their decline and disappearance has been linked to cooling, which began at the end of the Eocene (Aronson and Blake 2001; Eastman 2005; Aronson et al. 1997; 2007; 2009; 2011). However, the presence of decapod crustaceans in the early Miocene CMF, which is a glacially influenced unit, indicates that the degree of temperature decline in the Eocene was not enough to completely eliminate decapods from Antarctic ecosystems.

There may have been reversals in the trend towards a retrograde community structure in periods that were warmer than at the time of deposition of the La Meseta Formation in the Eocene (Aronson et al. 2007). This would have led to incursions of reptant decapods along the Scotia arc and via the porous Antarctic Circumpolar Current (Aronson et al. 2007). However, the evidence for glaciation during the deposition of the CMF (diamictites, glacial scouring and dropstones) indicates that it was deposited in cooler conditions the La Meseta Formation, which does not preserve any evidence for a glacial depositional environment. There is a later record of a Pliocene lobster from Marine Plain (East Antarctica) (Feldmann and Quilty 1997, Griffiths et al. 2013). It is possible that warmer sea temperatures at this time might have allowed an incursion of decapods (Aronson et al. 2007). However, Marine Plain is on the geographically isolated coast of East Antarctica (Feldmann and Quilty 1997); most recent biogeographic analyses show the strongest affinities between the Antarctic region and Southern South America, along the Scotia arc (Aronson et al. 2007) with little or no biogeographic connections between East Antarctica and its neighbouring regions (Griffiths et al., 2009). Therefore, it is also possible that community structuring durophagous predators such as lobsters, and possibly some crabs, persisted in Antarctica until the Pliocene, but conditions for their preservation were not suitable. Another view on the restriction of brachyuran crabs and lobsters from Antarctic shelves was given by Gorny (1999), who suggested their absence was due to the elimination of the shallow-water fauna during glaciations of the southern hemisphere, after noting the South American brachyuran crab species were restricted to shallower depths, above 200m, on sandy or muddy environments (Gorny 1999). The few modern day shallow water habitats around Antarctica are characterised by strong disturbance from ice, thus restricting shallow water groups (Arntz et al. 1994; Gorny 1999).

The early Miocene CMF shows a greater similarity in community structure to the modern day Beagle Channel than to modern Antarctic communities. This similarity may be due to a similar environmental setting, in an area that experienced seasonal melting and outflow from glaciers causing terrigenous sediment input (Linse and Brandt 1998). The modern Antarctic lacks terrigenous sediment input (Gili et al. 2006), which may explain why the fauna of the early Miocene Antarctic Cape Melville faunal community structure does not resemble that of Antarctica today.

Conclusion

Although it is only one site, evidence from the CMF suggests that the shift to the modern community structure was not a rapid change coincident with cooling in the Eocene, and that the modern Antarctic benthic community structure had still not fully formed in the early Miocene. It is possible that the evolution of the modern community structure occurred more recently, due to factors such as further cooling and isolation of the continent leading to widespread glaciation, which resulted in a loss of shallow shelf habitats.

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Figure Captions

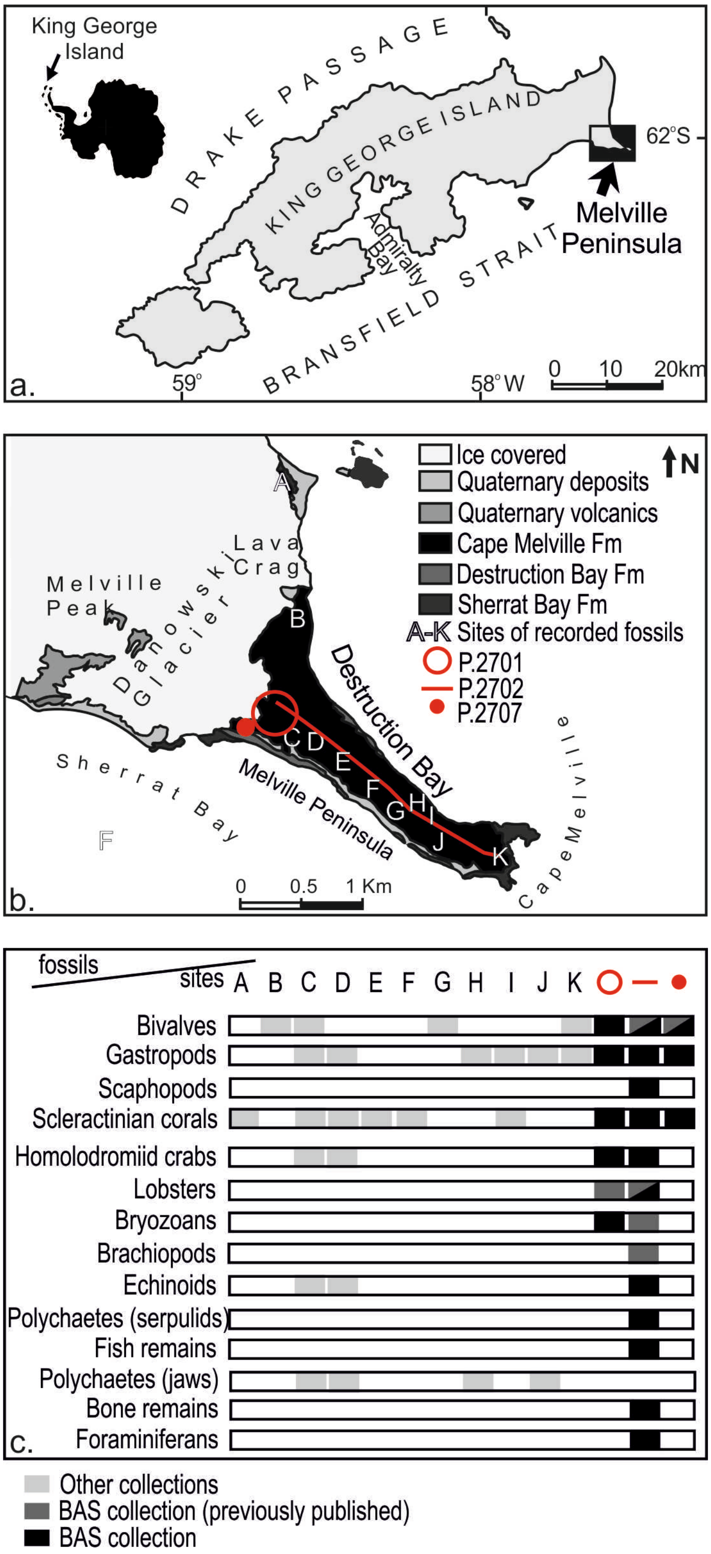

Fig. 1 a. Location map of the Melville Peninsula at King George Island, West Antarctica b. Geological map of Melville Peninsula showing the sites of recorded fossils; sites A-K are the locations of fossils from in previous publications. P.2701 is the area of collection for BAS fossils with this prefix, P.2702 is a line of section along which BAS fossils were collected and P.2707 is the final BAS fossil locality. c. Fauna recorded from the Cape Melville Formation, at locations shown in b. Occurrences of all fossils described from Unit D of the CMF. Data from: Förster et al. (1985; 1987), Jesionek-Szymańska (1987), Karczewski (1987), Roniewicz and Morycowa (1987), Szaniawski and Wrona (1987), Feldmann and Crame 1998, Bitner and Crame (2002), Jonkers (2003), Hara and Crame (2004), Anelli et al. (2006), Whittle et al. (2011), Whittle et al. (2012), Beu and Taviani (2013).

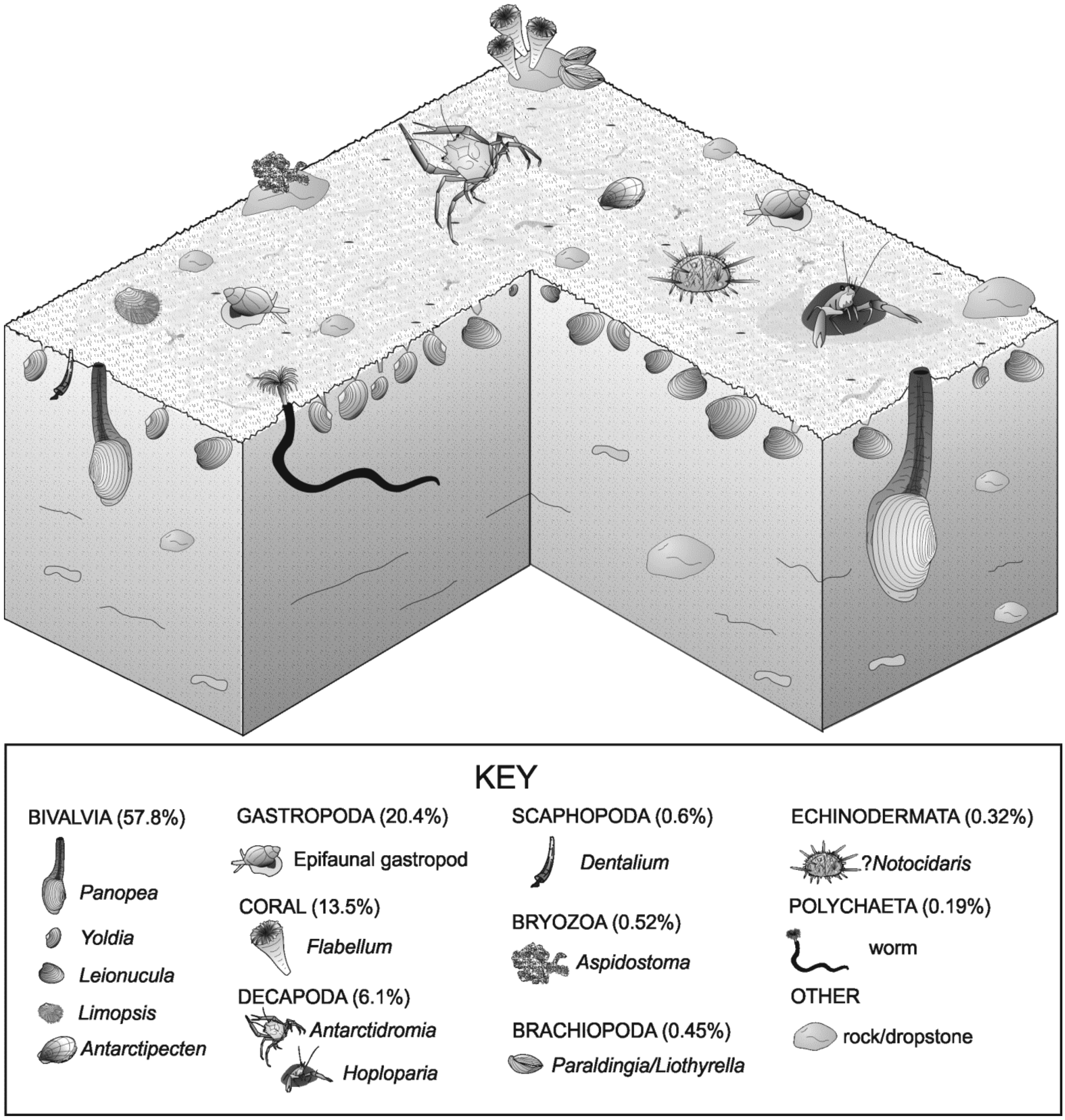

Fig. 2 Reconstruction of the Cape Melville Formation fossil assemblage based on fossil data from this paper, all specimens were collected from approximately the uppermost 75 m of Unit D of Troedson and Riding (2002) and can be regarded as one time-averaged assemblage for the purposes of this study.

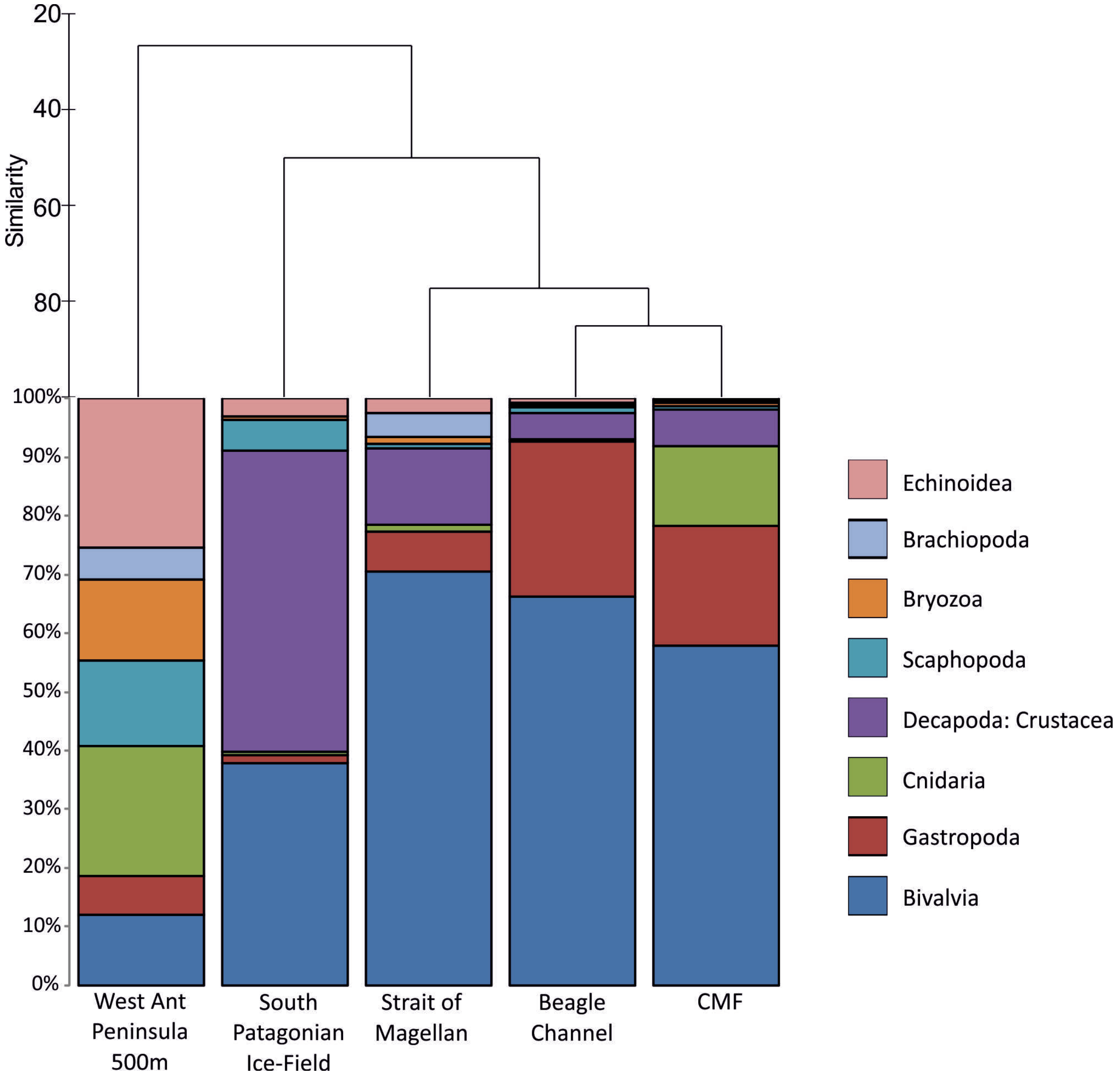

Fig. 3 Percentage similarity between the relative abundances of preservable higher level taxa between the fossil assemblage of the Cape Melville Formation and the Recent assemblages of the West Antarctic Peninsula and Southern South America. Percentage similarity was calculated using the Bray-Curtis coefficient.

Table 1. Invertebrate fossils collected from the Cape Melville Formation in the 1994/5 field season by the British Antarctic Survey. Fossils came from Unit D of Troedson and Riding (2002) and were collected at three different sites, P.2701, P.2702 and P.2707 (localities shown on Fig. 1b). Habitat abbreviations: SI = Shallow infaunal, I = Infaunal, E = Epifaunal, DI = Deep Infaunal. Feeding Strategy abbreviations: DF = Deposit feeder, SF = Suspension feeder, G = Grazer, P = Predatory, SC = Scavenger, O = Omnivorous. Life habits and feeding strategies from Morton 1959; Robertson 1963; Allmon 1998; Jacob et al. 2003; Kase and Ishikawa 2003; Gili et al. 2006, Crame 2013, and the Paleobiology Database (http://paleodb.org/). The worm tubes (Polychaeta) found in the CMF were rare (only 3 specimens), but they appear to be infaunal, a deposit feeding/suspension feeding mode of life is hypothesised. Numbers in brackets indicate fossils that were not able to be counted as whole specimens, e.g. disarticulated appendages. These were not included in any of the total counts of specimens as it cannot be certain that they are from the separate specimens.

Supplementary Table 1. Records of Recent Homolodromiidae occurrences, with minimum and maximum water depths.

Phylum	Class	Order	Superfamily	Family	Genus	Species	H	FS	2701	2702	2707	Total
Mollusca	**Bivalvia**	Nuculoida	Nuculoidea	Nuculidae	?	?	SI	DF		6		**6**
					Leionucula	*frigida*	SI	DF	16	367	112	**495**
					Leionucula	*melvilleana*	SI	DF		41		**41**
		Nuculanoida	Nuculanoidea	Indeterminate	?	?	I	DF	1	33	5	**39**
				Sareptidae	*Yoldia*	*peninsularis*	I	DF		148		**148**
				Malletiidae	*Neilo (Neilo)*	*rongelii*	I	DF	2	65	2	**69**
		Arcoida	Limopsoidea	Limopsidae	*Limopsis*	?	E	SF		4		**4**
					Limopsis	*psimolis*	E	SF		2	1	**3**
					Limopsis	*infericola*	E	SF		3	1	**4**
		Pectinoida	Pectinoidea	Pectinidae	*Antarcticpecten*	*alanbeui*	E	SF		1		**1**
		Limoida	Limoidea	Limidae	*Limatula*	(*Antarctolima*) sp.	E	SF		1		**1**
		Myoida	Hiatelloidea	Hiatellidae	*?Panopea*	?	DI	SF	1	13		**14**
					Panopea	sp.	DI	SF	1	15	1	**17**
		Pholadomyoida	Thracioidea	Periplomatidae	*Periploma*	*acuta*	I	SF	1	7	1	**9**
		Indeterminate	?	?	?	?	?	?		43	2	**45**
	Gastropoda	Neogastropoda	Muricoidea	?Volutidae	?	?	E	P/SC	1	8	1	**10**
				Volutidae	?	?	E	P/SC	6	8	2	**16**
			Buccinoidea	Buccinidae, s.l.	?*Prosipho*	?	E	P/SC		8	1	**9**
				Buccinidae, s.l.	?*Penion*	?	E	P/SC	1	5		**6**
				?Buccinidae, s.l.	?	?	E	P/SC		1		**1**
			Conoidea	?	?	?	E	P	1	27	2	**30**
		Littorinimorpha	Naticoidea	Naticidae	?	?	SI	P	7	56	5	**68**
				?Naticidae	?	?	SI	P		5		**5**
		Caenogastropoda	Cerithioidea	Cerithiidae	?	?	E	DF/G	2	7	3	**12**
				?Cerithiidae	?	?	E	DF/G		2		**2**
				Turritellidae	?	?	E	SF		22	1	**23**

				?Turritellidae	?	?	E	SF		1		**1**
			Epitonioidea	Epitoniidae	?	?	E	P	1			**1**
		Indeterminate	?	?	?	?	?	?	7	123	3	**133**
	Scaphopoda	Dentaliida		Dentaliidae	*Dentalium*	?	I	P		10		**10**
Cnidaria	**Anthozoa**	Scleractinia		Flabellidae	*Flabellum*	*rariseptatum*	E	SF	21	177	12	**210**
Arthropoda	**Malacostraca**	Decapoda	Homolodromioidea	Homolodromiidae	*Antarctidromia*	*inflata*	E	P	4(4)	87(47)		**91**
			Nephropoidea	Nephropidae	*Hoploparia*	*gazdzickii*	E	P	1	3		**4**
Bryozoa	**Gymnolaemata**	Cheilostomatida	Microporoidea	Aspidostomatidae	*Aspidostoma*	*melvillensis*	E	SF	1	7		**8**
Brachiopoda	**Rhynconellata**	Terebratulida	Terebratelloidea	Laqueidae	*Paraldingia*	?	E	SF		2		**2**
			Terebratuloidea	Terebratulidae	*Liothyrella*	?	E	SF		1		**1**
					?Liothyrella	?	E	SF		1		**1**
	Indeterminate	?		?	?	?	E	SF		3		**3**
Echinodermata	**Echinoidea**	Cidaroida	Cidaridea	Ctenocidaridae	?*Notocidaris*	?	E	O/SF/G		5		**5**
Annelida	**Polychaeta**	?		?	?	?	I?	SF/DF?		3		**3**
								TOTAL	**75**	**1321**	**155**	**1551**

Supplementary Table 1

The Early Miocene Cape Melville Formation Fossil Assemblage and the Evolution of Modern Antarctic Marine Communities. Rowan J. Whittle[1], Fernanda Quaglio[2], Huw Griffiths[1], Katrin Linse[1] and J. Alistair Crame[1]

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Supplementary Table 1. Records of Recent Homolodromiidae Occurrences, with minimum and maximum water depths.

Name	**Min depth (m)**	**Max depth (m)**	**Reference**
Dicranodromia felderi	35	35	GBIF
	346	346	GBIF
	320	340	GBIF
	585	585	GBIF
	585	585	GBIF
	630	630	GBIF
	640	640	GBIF
Dicranodromia doederleini	85	270	Martin (1990)
	120	220	GBIF
	180	200	GBIF
	200	200	GBIF
	200	250	GBIF
	200	250	GBIF
	400	400	GBIF
Dicranodromia spinosa	156	174	Martin (1994)
	165	165	Martin (1994)
	192	201	Martin (1994)
	201	201	Martin (1994)
	278	419	Martin (1994)
Dicranodromia danielae	200	300	Ng and Naruse (2007)
Dicranodromia nagaii	200	200	GBIF
Dicranodromia simplicia	229	229	GBIF
	320	320	GBIF
	320	320	GBIF

Dicranodromia ovata	260	260	GBIF
	329	329	Martin (1990)
	366	375	GBIF
	549	549	GBIF
Dicranodromia chenae	273	356	Ng and Naruse (2007)
Dicranodromia nagaii	300	300	GBIF
Dicranodromia baffini	300	300	GBIF
	461	561	Martin (1990)
	833	833	Martin (1990)
Dicranodromia karubar	356	468	M. Tavares (1998)
	356	356	GBIF
	393	393	GBIF
	393	393	GBIF
	410	410	GBIF
	434	434	M. Tavares (1998)
	443	443	GBIF
	451	451	GBIF
Dicranodromia martini	437	439	Ng and Naruse (2007)
	609	673	Ng and Naruse (2007)
	750	750	GBIF
	762	786	Ng and Naruse (2007)
	929	929	GBIF
Dicranodromia mahieuxii	454	1330	Martin (1990)
Dicranodromia foersteri	495	495	GBIF
	650	650	GBIF
Dicranodromia crosnieri	650	650	GBIF
Dicranodromia spinulata	675	675	GBIF
Dicranodromia sp.	590	590	M. Tavares (1998)
	650	650	M. Tavares (1998)
Dicranodromia	495	495	GBIF
Homolodromia kai	277	355	Ng and Naruse (2007)
	641	641	GBIF
	650	650	Ng and Naruse (2007)
	680	680	GBIF
	688	688	GBIF
	688	688	GBIF
	708	708	GBIF
	709	278	Ng and Naruse (2007)
	799	799	GBIF
Homolodromia paradoxa	457	732	GBIF
	543	783	GBIF
	549	549	GBIF
	624	631	GBIF
	651	651	GBIF
	658	695	GBIF
	750	841	GBIF
	805	841	GBIF
Homolodromia robertsi	500	1000	Pedro Báez and Martin (1989)
	800	800	GBIF
Homolodromia monstrosa	549	604	GBIF

	585	585	GBIF
	631	631	GBIF
	631	631	GBIF
	640	640	GBIF
	644	644	GBIF
	658	695	GBIF
	732	732	GBIF
Homolodromia bouvieri	850	960	Martin (1992)
	863	863	Martin (1992)
Homolodromia	480	480	GBIF
Homolodromia	860	860	GBIF
Homolodromia	886	927	GBIF
Homolodromia	890	955	GBIF
Homolodromia	890	1012	GBIF
Homolodromia	895	895	GBIF
Homolodromia	900	970	GBIF
Homolodromia	900	950	GBIF
Homolodromia	990	1076	GBIF
Homolodromia	1008	1080	GBIF

Supplementary References

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