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Paleobiological significance of the James Ross Basin

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Abstract The extensive Late Mesozoic–Early Cenozoic sedimentary succession exposed within the James Ross Basin, Antarctica has huge potential to enhance paleobiological investigations into both the marine and terrestrial fossil records. In excess of 7 km in total thickness and spanning the Early Cretaceous (Aptian)–Late Eocene in age, it represents an invaluable high-latitude (~65°S) site for comparison with lower latitude, tropical ones in an essentially greenhouse world. The Early Cretaceous (Aptian–Albian) sequence is deep-water but there are indications of shallowing to inner shelf depths in both the Turonian and Coniacian stages. The first prolific shallow-water marine fauna occurs in the Santonian–Campanian Santa Marta Formation and this is followed by repeated occurrences through the later Campanian, Maastrichtian, Danian and Middle Eocene (Lutetian). In this study an attempt has been made to compare these Antarctic faunas directly with the well-known ones of the same age from the US Gulf Coast. Detailed comparisons made for three time slices, Late Maastrichtian, Danian and Middle Eocene, indicate that the Antarctic is characterised by both low taxonomic diversity and high levels of endemism. The James Ross Basin is providing important evidence to indicate that the highest southern latitudes have always been characterised by a distinctive temperate biota, even on a pre-glacial Earth. The roots of at least some elements of the modern Southern Ocean biota can be traced back to a Late Mesozoic–Early Cenozoic austral realm.

Keywords **James Ross Basin, biostratigraphy, molluscan faunas, US Gulf Coast, biodiversity patterns, evolution of temperate biotas**

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1 Introduction

As recently as forty years ago, upon the publication of a new geological map of northern Graham Land (BAS, 1979), the extensive sequence of Cretaceous sedimentary rocks exposed within the James Ross Basin (JRB) (Figure 1) was regarded as essentially Campanian in age (i.e. 70.6–83.5 Ma). Even though the stratigraphy had been significantly improved by the pioneering study of Bibby (1966), and his estimate of the total thickness of strata present within the basin (5.18 km) subsequently proved to be reasonably accurate, ammonite dating restricted the age to essentially Early–Late Campanian (Howarth, 1958, 1966). These Cretaceous beds had been traced as far east as Seymour Island (Figure 1) where early studies correctly established that they were unconformably overlain by Cenozoic strata of very similar lithologies. However, the Cretaceous–Paleogene (K/Pg) boundary sequence was largely unrecognised, and the true nature and extent of the Paleogene sequence unknown (Zinsmeister, 1982).

The proliferation of international research efforts in the JRB over the last four decades has been truly impressive. A series of detailed revisions to the geological map have now been made (Montes et al., 2010; Smellie et al., 2013; Mlčoch et al., 2015), and a combination of palaeontological and radiometric dating techniques has demonstrated that the Cretaceous succession in fact spans Aptian–Maastrichtian, and the Paleogene, Early Paleocene–Late Eocene (Rinaldi, 1992; Hathway, 2000; McArthur et al., 2000; Francis et al.,

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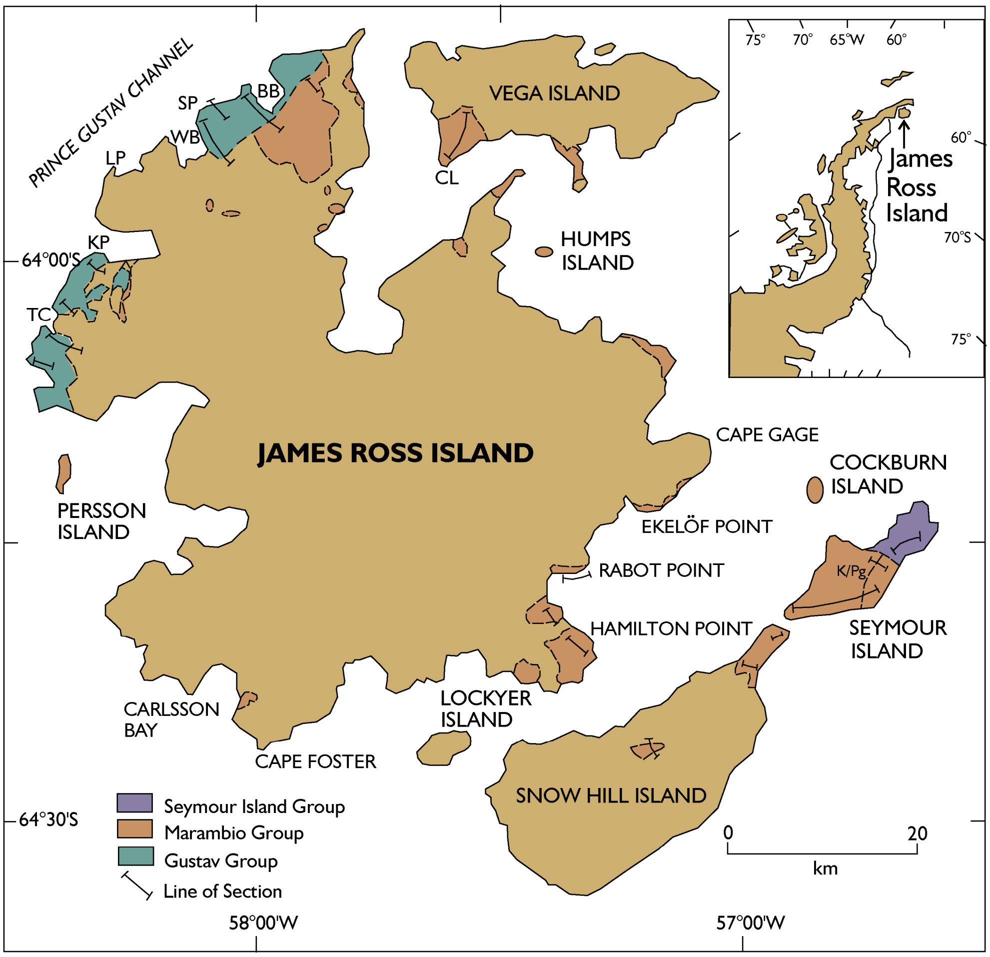

Figure 1 Locality and sketch geological map of the James Ross Basin showing the distribution of the three main lithostratigraphical groups. Based in part on the locality maps given in Crame et al. (2004, 2006). Key to locality abbreviations: BB–Brandy Bay; CL–Cape Lamb; KP–Kotick Point; LP–Lagrelius Point; SP–Stoneley Point; TC–Tumbledown Cliffs; WB–Whisky Bay.

2006; Olivero, 2012). The basin has also revealed, at a range of different levels, evidence of a prolific biota that comprises both marine and terrestrial vertebrates, a wide variety of marine invertebrates, and a diverse flora (Feldmann and Woodburne, 1988; Marenssi et al., 2002; Reguero et al., 2002; Cantrill and Poole 2012; Roberts et al., 2014). The K/Pg boundary sequence is exceptionally well exposed on Seymour Island and can be traced laterally for some 7 km (Montes et al., 2010), making it an invaluable international resource for tracing both lateral and vertical variation at this key interval in time (Elliot et al., 1994; Zinsmeister, 1998; Bowman et al., 2012, 2014; Tobin, et al., 2012; Witts et al., 2016; Tobin, 2017). Even though there are some hiatuses within this extensive sedimentary sequence its total thickness from Aptian–Late Eocene is in the region of 7000 m (Figure 2). It is fast becoming a key global locality for investigating latest Cretaceous–earliest Paleogene paleoclimates, paleoenvironments, and biotic evolution (e.g. Anderson et al., 2011; Olivero, 2012; Douglas et al., 2014; Barreda et al., 2015).

The importance of the JRB lies in its near-polar location. The paleolatitude is not precisely known but it is approximately 65°S throughout the Late Mesozoic–Early Cenozoic (Lawver et al., 2014) and as such represents the highest latitude onshore locality for this time interval in either hemisphere. Although further work remains to be done on both the stratigraphy and taxonomic paleontology of the JRB, we are beginning to assemble detailed time-series data sets that can be compared with equivalents from lower latitude localities. This is particularly so with benthic marine invertebrates, which play a key role in regional biodiversity studies. In this investigation an assessment of benthic marine diversity levels in the Late Mesozoic–Early Cenozoic of Antarctica will be made by focusing on bivalve and gastropod molluscs. How does the composition of benthic faunas change through this interval, and what are the similarities and differences with lower latitude regions?

2 Geological setting

The JRB is the northernmost segment of the extensive

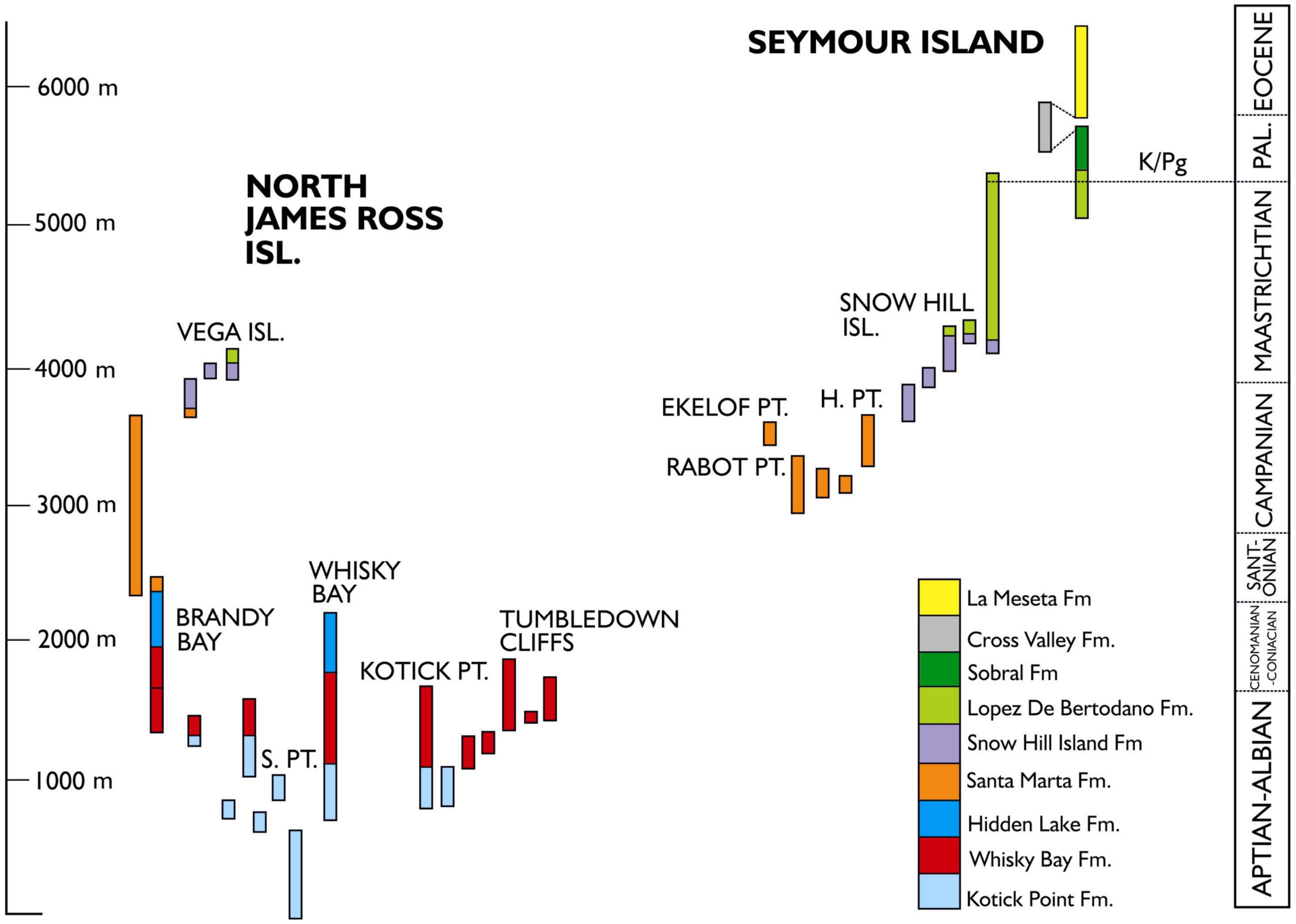

Figure 2 Simplified stratigraphical correlation scheme for the James Ross Basin to show the distribution of the principal Cretaceous–Early Paleogene sedimentary formations. The basal Lagrelius Point Formation is not shown but is estimated to be in the region of 500 m thick (see text). Key to abbreviations: H. PT.–Hamilton Point; S. PT.–Stoneley Point; PAL.–Paleocene.

Larsen Basin, which can be traced along the east coast of the Antarctic Peninsula (AP) from its northernmost tip to at least 69°S (Del Valle et al., 1992; Hathway, 2000) (Figure 1). The basin formed as a direct result of Jurassic lithospheric extension during the early stages of Gondwana break-up and subsequently developed into a back-arc setting relative to the magmatic arc that now forms the spine of the AP. Subsequent tectonic evolution of the basin and progressive marine sedimentary fill has been summarised in diagrammatic form by Hathway (2000, figure 5).

Earliest Cretaceous sedimentary rocks (i.e. Berriasian–Barremian in age) comprise the uppermost levels of a mudstone–tuff unit (Nordenskjöld Formation) and small, isolated outcrops of interbedded mudstones and sandstones of probable Valanginian–Barremian age (Whitham and Doyle, 1989). As these exposures are confined to the AP margin and are poorly fossiliferous, they are not considered further in this study. Within the James Ross Island group, Cretaceous–Paleogene sedimentary rocks have now been formally assigned to three lithostratigraphic groups: Gustav Group (Aptian–Coniacian), Marambio Group (Santonian–Danian), and Seymour Island Group (Selandian – ?Priabonian) (Figures 1 and 2).

2.1 Gustav Group

The stratigraphically oldest *in-situ* sedimentary rocks exposed on the north-west coast of James Ross Island are of probable Aptian age and form the lowermost levels of the Gustav Group. They are assigned to the Lagrelius Point Formation and comprise a sequence of massive-bedded conglomerates with thin, interbedded sandstones (Ineson et al., 1986; Riding et al., 1998). However, the true stratigraphical relations of this largely inaccessible unit are unknown and for this reason it has not been included in the correlation scheme shown in Figure 2. The succeeding Kotick Point Formation is a mudstone-dominated unit that is characterized by interbedded, pale-weathering breccias and conglomerates. A particularly distinctive feature of the latter is large clasts of the Nordenskjöld Formation, which is only found *in-situ* on the eastern margin of the AP (Ineson et al., 1986). A distinctive ammonite–pteriomorph bivalve macrofauna from the mudstones has strong Aptian–Albian affinities and fits in well with the interpretation of a series of deep water, submarine fan and slope-apron depositional environments (Ineson, 1989; Buatois and Medina, 1993). This unit represents the early stages of the accumulation of a deep-marine clastic wedge close to the fault-bounded basin margin.

The Kotick Point Formation grades upwards into the sandstone- or conglomerate-dominated Whisky Bay Formation. This is a complex unit which shows considerable lateral variation when traced south-west from Brandy Bay and Whisky Bay towards Tumbledown Cliffs (Figures 1 and 2). At Brandy Bay the three component members are, in ascending order: Bibby Point Member, comprising distinctive, green-weathering silty sandstones and breccia-conglomerates; Lewis Hill Member, dominated by channelled conglomerates and pebbly sandstones; Brandy Bay Member, exhibiting thinner-bedded sandstone and conglomerates, with occasional mudstones (Ineson et al., 1986). However, it is difficult to trace each of these units laterally and in the Tumbledown Cliffs area three further members are recognised, collectively exhibiting a similar wide range of lithologies: Gin Cove Member, Tumbledown Cliffs Member, and Rum Cove Member (Ineson et al., 1986; Crame et al., 2006).

The Bibby Point Member is mid- to Late Albian in age and passes conformably upwards into the Late Albian Lewis Hill Member (Crame et al., 2006) (Figure 2); palynological dating suggests that the Albian–Cenomanian boundary may be placed in the uppermost levels of this unit (Riding and Crame, 2002) (Figure 2). The Gin Cove Member and lower Tumbledown Cliffs Member in the region to the south-west are lateral equivalents, although it has to be noted that there are some distinct differences between the two component macrofaunas, and especially the pteriomorph bivalves (Crame et al., 2006). The precise position of the Albian–Cenomanian boundary in the Tumbledown Cliffs Member is uncertain but in its upper levels a distinctive macrofossil assemblage, including the ammonites *Newboldiceras*, *Sciponoceras* and *Desmoceras*, and the bivalve *Inoceramus pictus*, has strong mid- to Late Cenomanian affinities (Olivero and Palamarczuk, 1987; Crame et al., 2006). However, this fauna is completely absent in the Brandy Bay reference section and the Lewis Hill–Brandy Bay Member junction is marked by a sharp change in dip and a pronounced unconformity. The latter unit has strong Late Turonian age affinities based on dinoflagellate cyst assemblages, inoceramid bivalves and strontium isotope dating (McArthur et al., 2000) (Figure 2). The Rum Cove Member in the south-western region is at least partially laterally equivalent to the Brandy Bay Member.

The presence of discontinuous unconformities within the Whisky Bay Formation has been taken as evidence of an active fault zone along the margin of the basin that exerted strong local control over sedimentation on a series of conglomeratic submarine fans and slope apron deposits (Whitham and Marshall, 1988). It should also be mentioned that the mid-levels of the Turonian Brandy Bay Member contain the first evidence of shallow-water (i.e. shelf-depth) marine faunas. This comprises fragments of an oyster 'pavement', a distinctive large heterodont bivalve (carditid/astartid group), and a colonial coral (Crame et al., 2006). Palynological data from the same level indicates the diversification of various plant taxa, including a number of angiosperms (Hayes et al., 2006; Poole and Cantrill, 2006). The pronounced Late Cretaceous radiation of both shallow-marine and terrestrial biotas in Antarctica may be traced back to at least Turonian origins (Crame et al., 2006).

The Hidden Lake Formation (HLF), the topmost lithostratigraphic unit of the Gustav Group, forms a distinctive sequence of rusty-brown to pale green-brown-weathering sandstones that can be traced across north-west James Ross Island (Ineson et al., 1986; Whitham et al., 2006). The formation shows an overall fining upwards trend linked to the evolution of a volcaniclastic fan-delta association. A characteristic ammonite–inoceramid bivalve assemblage is *in-situ*, but other benthic elements, including poorly preserved gastropods, oysters, brachiopods, bryozoans and corals, are probably derived (Whitham et al., 2006). A notable additional feature is the presence of charcoalified wood fragments and a moderately diverse leaf flora (Hayes et al., 2006). Some distinctive cross-bedded sandstones in the upper levels are of likely tidal origin and indicate partial basin inversion and the onset of shallow-marine shelf sedimentation (Whitham et al., 2006). Strontium isotope dating constrains the age of the entire formation to Coniacian (McArthur et al., 2000; Riding and Crame, 2002).

2.2 Marambio Group

The Gustav Group passes conformably up into the Marambio Group, which can be traced south-eastwards across the James Ross Island group at a shallow regional dip of approximately 10° (Figure 1). This second of the three main groups comprises essentially finer-grained sediments that were deposited in a variety of shallow marine fan and shelf environments adjacent to an active volcanic arc (Olivero et al., 1986; Pirrie, 1989). It is fossiliferous throughout, although the standard of preservation is somewhat variable.

The basal Santa Marta Formation (SMF) is best exposed in the region immediately to the south-east of Brandy Bay (Figure 1). It was originally divided into three component members, Alpha, Beta and Gamma (Olivero et al., 1986) but subsequent lithostratigraphic revisions suggested that the first two of these could be combined into a Lachman Crags Member and the latter renamed as the Herbert Sound Member (Crame et al., 1991; Pirrie et al., 1997). The Alpha Member (i.e. lower Lachman Crags Member) comprises a sequence of tuffaceous silty sandstones and mudstones that grade up into the coarser-grained Beta Member (upper Lachman Crags

Member), which includes distinctive fossiliferous conglomerates and coquinas. The SMF is characterized by the first abundant and relatively diverse macrofauna in the JRB. Scasso et al. (1991) recorded in excess of 5000 individual specimens from 48 different localities, with the majority being either bivalve or gastropod molluscs.

The lower levels of the Alpha Member are populated by an unusual large inoceramid bivalve provisionally assigned to an *Inoceramus expansus* group, and the heteromorph ammonite, *Baculites* cf. *kirki* (McArthur et al., 2000; Olivero, 2012). Both these taxa have strong Santonian affinities and it has been suggested that the Coniacian–Santonian boundary is best placed at the HLF–SMF boundary (Crame et al., 2006) (Figure 2).

Taxonomic diversity increases through the upper Alpha Member into the lower Beta Member where a shallow-water trigoniid bivalve facies is exposed for the first time (Scasso et al., 1991). In the upper Beta Member a *Pterotrigonia*–aporrhaid gastropod biofacies includes a range of other suspension-feeding bivalves, deposit feeding nuculanids and scaphopods, fossil leaves, and large petrified logs (Scasso et al., 1991). The upper levels of the Beta Member also record the first occurrence of a giant inoceramid bivalve, *Antarcticeramus rabotensis*, and this taxon is particularly effective in establishing correlations with the SMF exposed on south-eastern James Ross Island (Strelin et al., 1992; Crame and Luther, 1997; Pirrie et al., 1997; Olivero, 2012) (Figures 1 and 2). The Santonian–Campanian boundary is placed at approximately the 250 m level in the Alpha Member at the first occurrence of the kossmaticeratid ammonite, *Natalites rossensis* (Olivero, 2012) (Figure 2).

The Gamma (or Herbert Sound) Member and its lateral equivalent, the Hamilton Point Member, has a Late Campanian–earliest Maastrichtian age range and belongs within either the uppermost SMF (Pirrie et al., 1991, 1997) or the lowermost Snow Hill Island Formation (SHIF) (Olivero, 2012). It sees a return to predominantly finer-grained lithologies, which include intervals of dark, carbonaceous mudstone. The lower Gamma Member has a comparatively sparse macrofauna of bivalves, gastropods, occasional fish teeth and vertebrae, and rare dinosaur bones. It passes upwards into a more prolific benthic macrofauna in which infaunal bivalves such as *Cucullaea*, *Eriphyla*, *Oistotrigonia* and *Panopea* are prominent, together with the gastropods *Taioma*, a turritellid, and a naticid (Pirrie et al., 1991, 1997; Scasso et al., 1991). The Gamma Member is marked by the incoming of the kossmaticeratid ammonite genus *Neograhamites* and, subsequently, by *Gunnarites* and *Maorites* (Olivero, 2012).

At least at the Cape Lamb locality on Vega Island, the SMF is conformably overlain by the SHIF which crops out extensively over eastern and south-eastern James Ross Island, as well as on Snow Hill and Cockburn islands (Figures 1 and 2). The basal Cape Lamb Member of the SHIF is composed of bioturbated silty mudstones to silty sandstones with abundant early diagenetic concretions. Many of the latter are fossiliferous, with the benthic fauna being moderately rich but, in places, extremely abundant. Infaunal bivalves, such as *Nordenskjöldia*, *Pinna*, *Modiolus*, *Dozyia*, *Lahillia*, *Panopea* and *Goniomya*, predominate, together with pycnodontid oysters, gastropods (*Perissoptera*, "*Cassidaria*"), echinoids, decapod crustaceans (*Hoploparia*), scaphopods, annelids (*Rotularia*), and large pieces of fossil wood infested with *Teredolites* (Pirrie et al., 1991; Marenssi et al., 2001). The distinctive *Gunnarites antarcticus* ammonite assemblage includes taxa such as *Maorites* spp., *Jacobites crofti*, *Kitchinites darwini*, *Grossouvrites gemmatus*, and the large heteromorph, *Diplomoceras lambi* (Olivero, 2012). It has been suggested that the Campanian–Maastrichtian boundary is best placed at the incoming of this fauna (Crame et al., 2004). The Cape Lamb Member of the SHIF has been interpreted as a prograding deltaic wedge at mid- to outer-shelf depths (Roberts et al., 2014).

The Cape Lamb Member is laterally equivalent to the Karlsen Cliffs and Haslum Crag members exposed on Spath Peninsula, north-eastern Snow Hill Island (Figures 1 and 2). The lower Karlsen Cliffs Member represents a more distal, mudstone facies but contains the distinctive *Gunnarites antarcticus* ammonite fauna and associated benthos (Pirrie et al., 1997). The upper Haslum Crag Member is unconformable on the lower unit and is characterized in its lower levels by grey-green-weathering glauconitic sandstones and both low-angle and channel-like erosional features (Pirrie et al., 1997). However, it too, is characterized by the *G. antarcticus* fauna, and in the upper levels by an abundant concretionary bivalve assemblage in which "*Trigonia*" *regina* and *Lahillia luisa* are particularly prominent. It is likely that this upper member represents a shallower water, regressive facies closer to the shoreline (Olivero, 2012).

The Haslum Crag Member is in turn unconformably overlain by the basal unit of the López de Bertodano Formation (LBF), and this contact can be traced north-eastwards from Snow Hill Island onto the south-western tip of Seymour Island (Crame et al., 2004) (Figures 1 and 2). Here, the LBF is very well exposed over an area of approximately 70 km^2, revealing a basal fine-grained, mudstone-dominated unit that is sparsely fossiliferous and very likely deposited in shallow-water, tidally influenced settings (Olivero et al., 2008). This lower unit is succeeded by a thick, monotonous sequence of mudstones with interbedded glauconitic sandstones that become steadily more fossiliferous up-section. A single belemnite-rich horizon from a low level has been strontium isotope dated at 67.5 Ma (McArthur et al., 1998), but it is not until approximately the mid-levels of informal mapping unit Klb 6 that a more prolific fauna is found. Ammonites and bivalves again predominate with bivalve genera such as *Cucullaea*, *Pinna*, *Dozyia*, *Oistotrigonia*, *Pycnodonte*, *Thyasira*, *Panopea*, *Solemya*, and *Thracia* all being abundant at various levels (Macellari, 1988; Zinsmeister and Macellari, 1988; Crame et al., 2004; Witts et al., 2015, 2016). Medium–large gastropods are locally abundant, together with *Rotularia*, echinoderms, solitary corals, decapod crustaceans and occasional crinoids. This fauna is strongly linked to inner- to mid-shelf depths (Witts et al., 2015, 2016). In total, units Klb 6–9 of the LBF are approximately 850 m thick and entirely Maastrichtian in age (Montes et al., 2010).

The Cretaceous–Paleogene (K/Pg) boundary is marked by a prominent glauconitic interval approximately 5–6 m thick. At the base of this interval is a 1 m concretionary glauconitic sandstone which is slightly, but clearly, discordant (Zinsmeister, 1998; Crame et al., 2004). This level is coincident with the last ammonite occurrence and a small iridium spike (Elliot et al., 1994), and is therefore taken to represent the K/Pg boundary in Antarctica (Zinsmeister et al., 1989; Tobin et al., 2012; Witts et al., 2016). Directly above this "Lower Glauconite" is a 2–3 m interval of siltstones and fine sandstones that includes a "fish kill horizon" close to its base (Zinsmeister, 1998). The K/Pg boundary unit is capped by a second, "Upper Glauconite", immediately above which there is a subtle change in lithologies to recessive, grey-brown-weathering muddy siltstones bearing numerous small, early diagenetic concretions. This 55–60 m thick sequence bears a very distinctive low diversity–high abundance molluscan fauna dominated by the suspension-feeding bivalves *Lahillia* and *Cucullaea*, deposit-feeding nuculids, and a probably deposit-feeding aporrhaid gastropod, *Struthiochenopus hurleyi* (Stilwell et al., 2004). This has been informally referred to as the "recovery interval" and mapped as unit Kplb 10 (Sadler, 1988; Montes et al., 2010).

The topmost lithostratigraphic unit within the Marambio Group, the Sobral Formation (SF) (Figure 2), rests with a slight angular discordance on unit Kplb 10 of the LBF. Fossiliferous mudstones predominate in the lowermost levels but they pass upwards into progressively more sandstone-dominated levels with a distinctive pale green, glauconitic weathering tinge. There is an overall coarsening-upwards, regressive trend through the SF, reflecting an eastward progradation of an extensive marine delta system (Marenssi et al., 2012; Bowman et al., 2016). In the lower levels of the SF there is a return to an abundant, molluscan-dominated benthic fauna with a taxonomic diversity level approximately similar to that of unit Klb 9 within the LBF. Infaunal bivalves are again abundant, with genera such as *Leionucula*, *Neilo*, *Cucullaea*, *Pinna*, *Lucinoma*? *Lahillia*, *Marwickia*? and *Panopea* all being prominent. But the diversity of gastropods has notably increased by this level; in addition to genera such as *Conotomaria*, *Struthiochenopus*, *Perissodonta*, and *Amauropsis*?, there are a number of new neogastropod taxa especially within the family Buccinidae (Stilwell and Zinsmeister, 1992; Stilwell et al., 2004; Beu, 2009; Crame et al., 2014). The base of the SF is dated at ~63.8 Ma and the highest levels at ~61 Ma (i.e. Danian–Selandian boundary) (Montes et al., 2010).

2.3 Seymour Island Group

The topmost lithostratigraphic group currently comprises just two formations: the Cross Valley Formation (CVF) and the La Meseta Formation (LMF) (Figures 1 and 2). The CVF represents a deep erosional channel that cuts across not only the outcrop of the SF but also that of the underlying LBF. The channel has a paleotopography of at least 200 m and its fill comprises a thick succession of massively bedded, poorly sorted sandstones, pebbly sandstones and conglomerates; these are thought to be very largely of fluvial origin (Elliot and Trautman, 1982; Doktor et al., 1988; Sadler, 1988). However, the topmost unit of finer-grained sandstones and interbedded mudstones, which are equivalent to "Allomember C" of Marenssi et al. (2012), contains a marine fauna of gastropods, bivalves (and especially oysters), echinoids, crinoids, sharks teeth and penguin bones (Tambussi et al., 2005). The base of the CVF is dated at ~59.3 Ma (i.e. Late Selandian) and the base of Allomember C at ~58.6 Ma. This places the latter unit in the earliest Thanetian, and the closeness of these two age estimates reflects how quickly the whole unit was probably deposited (Wrenn and Hart, 1988; Montes et al., 2010).

The LMF, the principal depositional unit of the Seymour Island Group, occupies the greater part of north-eastern Seymour Island (Figures 1 and 2). It too, has a channel-form base and along its southern margins clearly on-laps onto progressively older strata when traced from east to west (Sadler, 1988; Marenssi et al., 1998, 2002; Montes et al., 2010). The LMF consists of a complex sequence of very shallow-water mudstones, silty mudstones, fine- to medium-grained sandstones and shelly conglomerates that have been split into a sequence of Telm ("Tertiary Eocene La Meseta") informal mapping units. Telm 1 is an irregularly developed marginal facies with a distinctive molluscan assemblage that includes very large oysters and the large limid, *Acesta*, together with small, nodular bryozoans, brachiopods, echinoids and solitary corals. It could well represent a channel-margin, high energy environment and is very probably Ypresian in age (Montes et al., 2010). There is evidence that Telm 2 rests unconformably on Telm 1 and that a considerable portion of the Ypresian stage is missing (Montes et al., 2010; Douglas et al., 2014). Telm 2 is mudstone rich but in its upper levels very thin coquinas and shell hash horizons are present, and these become increasingly prominent at higher levels in the LMF. The relationship between Telms 2 and 3 is unclear as the latter is restricted to just the north-eastern area of outcrop and exhibits distinctive buff-weathering cross-bedded sandstones, siltstones, and conglomeratic shelly sands (Sadler, 1988; Marenssi et al., 1998, 2002; Porębski, 2000).

Telm 4 is a persistent 4 m-thick *Cucullaea raea* shell bed that grades directly up into Telm 5. The latter unit is readily distinguished by alternations of laminated silty sands with bivalve-rich coquinas; *Cucullaea* and the venerid *Retrotapes* are particularly common in these shell-rich horizons (Stilwell and Zinsmeister, 1992). Collectively, Telms 2–5 are believed to be Middle Eocene (Lutetian) in age (Crame et al., 2014, 2018) and represent the most abundant fossiliferous interval within the entire JRB. Common gastropod taxa present include aporrhaids such as *Struthioptera* and *Arrhoges (Antarcthoges)*, the struthiolariid *Perissodonta* (abundant) and *Falsilunatia*, together with various small cerithioids, ptenoglossans and heterobranchs. But by far the largest group, both in terms of numbers of species and numbers of individuals, is the Neogastropoda; 57 neogastropod species have so far been identified. Buccinidae is again the largest component, but there are also a number of representatives of the Volutidae and, for the first time, there is a significant component of Conoidea (Stilwell and Zinsmeister, 1992; Beu, 2009; Crame et al., 2014, 2018).

A total of 49 bivalves species has so far been recorded from Telms 2–5; infaunal and semi-infaunal types again predominate, including: *Leionucula*, *Yoldia* (*Aequiyoldia*), *Neilo*, *Cucullaea*, *Modiolus*, *Pinna*, *Saxolucina* and *Lahillia*. Particularly noticeable is a radiation of euheterodonts (Imparidentia of some authors) that includes one species of Tellinidae, four of Mactridae, and six of Veneridae. Prominent anomalodesmatans include *Mya*, *Panopea* and *Thracia* (Stilwell and Zinsmeister, 1992; Beu, 2009; Crame et al., 2014, 2018). Telm 6 sees a marked facies change to rusty-weathering sands and monospecific venerid bivalve shell beds (Stilwell and Zinsmeister, 1992; Ivany et al., 2008). It passes up into Telm 7, the highest lithostratigraphic unit in the LMF, which exhibits a variety of resistant sandstone lithologies. The fauna from Telms 6 & 7 is much less diverse and very probably Late Eocene in age (Ivany et al., 2008).

3 Comparison of the JRB faunas with those of the US Gulf Coast

3.1 Introduction

The most extensive and complete shallow-water molluscan faunas of the JRB occur within the Campanian–Eocene interval, and Santa Marta, Snow Hill Island, López de Bertodano, Sobral and La Meseta formations (Figure 2). As such, they can be compared directly with the well-known faunas of similar age from the US Gulf Coast (GC). Although situated at approximately 30°N throughout the latest Mesozoic–early Cenozoic, the GC was well within a broad tropical zone; coral reefs are largely absent, but prolific faunas populated a variety of mixed carbonate–clastic ramps and shoals in predominantly inner- to mid-shelf water depths (Toulmin, 1977; Ivany et al., 2004; Kosnik, 2015).

As the Campanian faunas of the Beta and Gamma members of the Santa Marta Formation are still incompletely known, attention will be focused here on detailed comparisons between the JRB and GC at three stratigraphic levels: Late Maastrichtian, Danian and Middle Eocene. The well-known and prolific Late Maastrichtian faunas of the GC Owl Creek, Prairie Bluff, Providence and Severn formations (references contained in the captions to Figures 3–5) can be compared directly with that from the López de Bertodano Formation (Macellari, 1988; Montes et al., 2010). The succeeding SF, which contains an essentially Early–Middle Danian molluscan fauna (Stilwell et al., 2004; Bowman et al., 2016), can in turn be matched with a combined fauna from the GC Kincaid (Early Danian), Clayton (Early Danian), Porters Creek (mid- to late Danian) and Wills Point (Danian–basal Selandian) formations. The Early Eocene fauna of the JRB is believed to be incomplete (Crame et al., 2014; Douglas et al., 2014), so the final comparison is made between the Middle Eocene Telms 2–5 of the LMF and a combined fauna from the GC Cook Mountain, Gosport Sand, Stone City and Moodys Branch formations. The latter unit also contains a basal Late Eocene component (Mancini and Tew, 1990; Dockery and Lozouet, 2003). Further stratigraphic information on these various formations is contained in the captions to Figures 3–5.

Faunal lists for each of the three time intervals at both localities were compiled from a variety of sources (listed in the captions to Figures 3–5). To facilitate comparisons at a relatively coarse taxonomic scale the bivalve faunas were split into six component clades and the gastropods into seven (with further details again being given in the figure captions). In this way taxonomic lists were standardised, and any obvious synonymies and invalid names removed.

3.2 Sample size bias

Care has to be exercised at the outset in making any sort of numerical comparisons between the JRB and GC; perhaps the latter locality will always be more diverse simply because it covers a significantly larger area. Whilst this could indeed be the case, it is worth bearing in mind that the three Antarctic faunas are each prolific, and have been intensively studied. For example, the Zinsmeister Collection, housed in the Paleontological Research Institution, Ithaca, N.Y., contains more than 22000 Maastrichtian–Eocene marine invertebrate specimens, and other large collections are housed in institutions such as the United States National Museum, Washington, D.C., Museo de La Plata, La Plata, Argentina, the Naturhistoriska Riksmuseet, Stockholm, and the British Antarctic Survey, Cambridge, UK.

Although the richest Antarctic fauna, from the Middle Eocene LMF, only crops out over an area of approximately 25 km^2, it is 335 m thick and the levels of exposure are close to 100% over much of this interval (Crame et al., 2018). Stilwell and Zinsmeister (1992) based their taxonomic monograph of the LMF molluscan fauna on approximately 11000 specimens, and there are some 4000+ more in the collections of the British Antarctic Survey. Several thousand specimens have also been collected from Telms 6–9 of the López de Bertodano Formation (Macellari, 1988; Zinsmeister 2001; Witts et al., 2016), and nearly three thousand specimens from the Danian SF are recorded in the monograph by Stilwell et al. (2004) and the collections of the BAS, alone.

Unfortunately, specimen counts are not sufficiently detailed across all localities and time periods to enable sample standardisation techniques such as rarefaction to be applied. Nevertheless, it is maintained that collections from the three time intervals at both the JRB and GC are sufficiently comprehensive to establish at least broad faunal trends.

3.3 Patterns to emerge from a comparison of JRB and GC molluscan faunas

As might be expected, in all three of the intervals investigated taxonomic diversity values are higher in the GC than JRB (Figure 3); this difference is particularly striking in the Middle Eocene, which is the global molluscan diversity maximum for the Paleogene (Dockery and Lozouet, 2003; Crame et al., 2014; Huyghe et al., 2015). When analysed at clade level, the contrast in the structure of both the bivalve and gastropod faunas (Figures 4 and 5) is not significantly different in either the Maastrichtian or Paleocene, but is so in the Middle Eocene (Kolmogorov-Smirnov two-sample test, $P< 0.05$). A very distinct latitudinal contrast in molluscan faunas has developed in the Southern Hemisphere by the Middle Eocene. However, it should be noted that the diversity difference is slightly lower in the Danian (Figure 3), where three of the four categories show reductions from Maastrichtian values, and this is almost certainly a direct consequence of slow recovery from the K/Pg mass extinction. This event has been shown to be just as severe in Antarctica as elsewhere in the world (Zinsmeister et al., 1989; Tobin et al., 2012; Witts et al., 2016), and it is likely that full recovery of the global marine ecosystem took place over a period of several million years (D'Hondt, 2005). The Early Cenozoic is indeed characterized by major evolutionary radiations in both the marine and terrestrial realms, but it is clear that this was by no means instantaneous after the extinction event (Jablonski, 1998, 2005; Erwin, 2001; Krug and Jablonski, 2013). Therefore, it is possible that the latitudinal diversity contrast between the tropics and the poles was significantly reduced during at least the early part of the Danian stage.

The diversity analysis also reveals a change in the relative proportions of bivalves and gastropods through the three time intervals. Whereas the numbers are approximately equal at both localities in the Late Maastrichtian, the balance changes in the Early Cenozoic to progressive dominance of gastropods over bivalves (Figure 3). Both groups do show a significant increase in numbers between the Late Maastrichtian and Middle Eocene, but the rate of increase in gastropod species is far greater than that for bivalves (Figure 3). This is a pattern that is repeated at a number of other global localities (Hansen, 1988; Aberhan, 1994; Sepkoski, 2002).

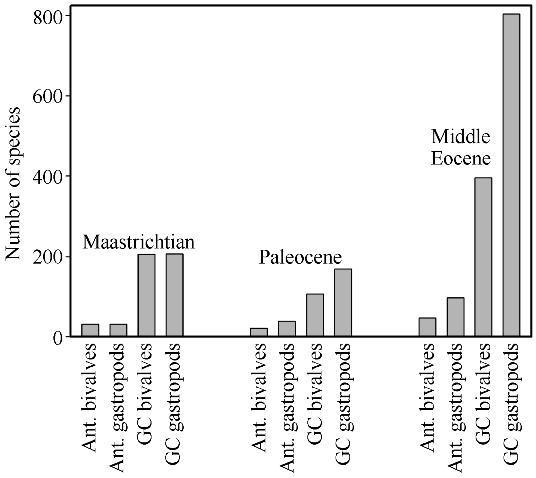

Figure 3 Comparison of the numbers of bivalve and gastropod species between Antarctica and the GC at three different time intervals: Maastrichtian, Paleocene and Middle Eocene. Further details on how the comparisons were carried out are given in the text. Data sources for Antarctic Maastrichtian faunas from units Klb 6−9 of the López de Bertodano Formation are given in full in Crame et al. (2014, Appendix S1), and for the Antarctic Paleocene (unit Kplb 10 and SF) in Crame (2013, Appendix S1). Data sources for the latest Cretaceous–Early Paleogene of the GC are given in Crame et al. (2018, Appendix).

Pteriomorph bivalves, comprising epifaunal and shallow-burrowing groups such as the arcids, mytilids, pectinids and oysters, are the numerically dominant bivalve clades in the Maastrichtian at both localities (Figure 4). However, this dominance is lost in the Paleocene with the rise of the euheterodonts, which comprise many siphonate, deeper-burrowing families. Euheterodonta is clearly the dominant clade by the Middle Eocene, although the Pteriomorphia do form a prominent second group at the GC (Figure 4). It is interesting to note the comparatively low numbers of euheterodonts in Antarctica at all three stages (Figure 4); their relative rarity at the present day in the Southern Ocean (Nicol, 1967; Dell, 1972) may have deep evolutionary roots.

The gastropod faunas at both localities are dominated in each of the three time intervals by just one clade, Neogastropoda (Figure 5), which is very largely, but not exclusively, responsible for the rapid rise in gastropod numbers through the Early Cenozoic. There is again a slight reduction in the diversity contrast between GC and Antarctica in the Paleocene but this is followed by a very rapid strengthening of this difference in the Middle Eocene; there is almost an order of magnitude diversity difference between the two localities in this interval (Figure 5). The striking latitudinal diversity gradient in neogastropods at the present day dates back to at least the Middle Eocene, if not earlier (Crame, 2013; Crame et al., 2014).

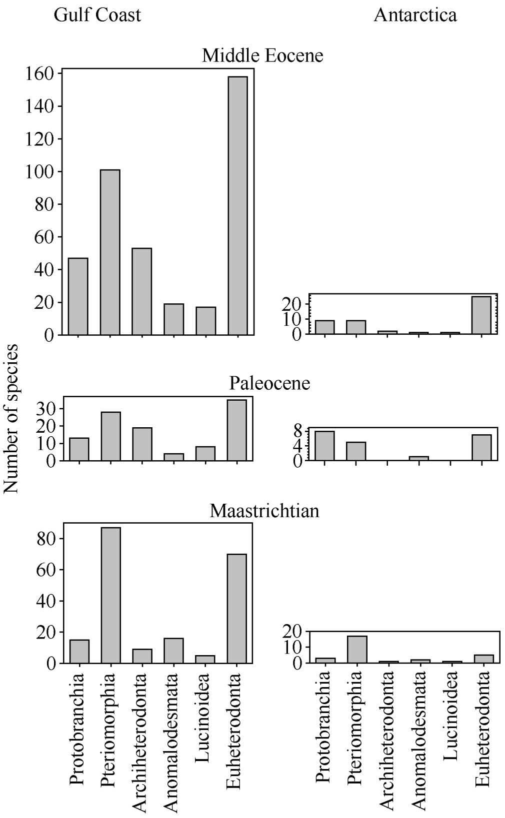

Figure 4 Comparison of the number of species in six major bivalve clades between Antarctica and the GC at three different time intervals: Maastrichtian, Paleocene and Middle Eocene. Clade definition follows recent phylogenetic investigations (Bieler et al., 2014; Combosch et al., 2017), with two exceptions. The term Euhetrodonta is retained here instead of Imparidentia, and Lucinoidea is kept as a separate clade until its position has been fully resolved (following Taylor et al., 2007). Data sources for Antarctic Maastrichtian faunas from units Klb 6–9 of the López de Bertodano Formation are given in full in Crame et al. (2014, Appendix S1), and for the Antarctic Paleocene (unit Kplb 10 and SF) in Crame (2013, Appendix S1). Data sources for the latest Cretaceous–Early Paleogene of the GC are given in Crame et al. (2018, Appendix).

It is also apparent that, although the neogastropod clade maintains its prominence across the K/Pg boundary (Figure 5), there is almost a complete change of constituent taxa. Of the 84 species/50 genera present in the GC Maastrichtian, only three genera and no species cross the boundary; similarly, in Antarctica of 16 monospecific Maastrichtian genera, only one of them makes the transition (Crame et al., 2014, 2018). And the striking feature of the Early Cenozoic neogastropod fauna is its relatively high proportion of modern taxa. On the GC 7% of Maastrichtian neogastropod genera can be assigned to living taxa but this figure rises to 44% in both the Paleocene and Middle Eocene faunas. In Antarctica there are no modern neogastropod genera in the Maastrichtian but the figure rises to 21% in the Paleocene and 40% in the Middle Eocene (Beu, 2009; Crame et al., 2014, 2018).

In a previous analysis (Crame et al., 2014) it was established that 38 modern Southern Ocean molluscan genera could be detected throughout the latest Mesozoic–Early Cenozoic stratigraphic record exposed on Seymour Island (i.e. 26 gastropods and 12 bivalves). Whereas none of the 26 gastropods could be traced backwards in time across the K/Pg boundary, five of the 12 bivalves could (*Leionucula, Limopsis, Limatula, Conchocoele* & *Thracia*). To these can be added at least two other modern Southern bivalve taxa, *Astarte* and *Lucinoma*, that have Cretaceous or older fossil records elsewhere (Crame et al., 2014). The modern Antarctic bivalve fauna has substantially older evolutionary roots than the gastropod one.

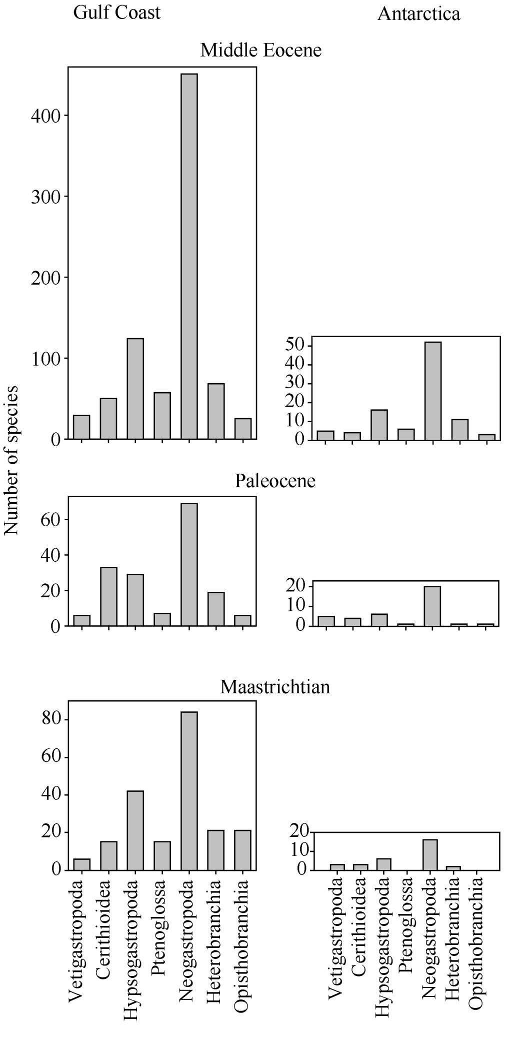

Figure 5 Comparison of the number of species in seven major gastropod clades between Antarctica and the GC at three different time intervals: Maastrichtian, Paleocene and Middle Eocene. Clade definition is given in Crame (2013, Appendix S1). Data sources for Antarctic Maastrichtian faunas from units Klb 6–9 of the López de Bertodano Formation are given in full in Crame et al. (2014, Appendix S1), and for the Antarctic Paleocene (unit Kplb 10 and SF) in Crame (2013, Appendix S1). Data sources for the latest Cretaceous–Early Paleogene of the GC are given in Crame et al. (2018, Appendix).

4 Synthesis

In this study the focus has been much more on relative rather than absolute taxonomic diversity values. In the Late Maastrichtian stage there are nearly seven times more species of both bivalves and gastropods in the tropical GC than polar JRB, and this figure rises to over an eight-fold difference in the Middle Eocene (Figures 3−5). However, there is a reduction in this diversity contrast in the Paleocene to just over a five-fold difference in bivalves, and just over a four-fold one in gastropods. These are essentially Early Paleocene (i.e. Danian) samples which almost certainly still bear the imprint of the K/Pg mass extinction event. It is possible that the latitudinal diversity gradient was significantly reduced in scale at this time (Jablonski, 2005).

The high–low latitude diversity contrast could be extended back to at least the Campanian stage, where preliminary investigations indicate that the Santa Marta Formation molluscan fauna is also considerably less diverse than contemporary GC units such as the Coffee Formation (Sohl, 1964; Scasso et al., 1991; Kosnik, 2005). Cenomanian–Santonian molluscan faunas from the JRB are very incomplete, and Aptian–Albian ones are essentially linked to deep-water outer shelf and slope environments. But if the analysis is extended even further back in time into the Late Jurassic, and covers the AP region as a whole, then there is evidence to suggest that Antarctic Tithonian molluscan faunas are also much less diverse than their tropical counterparts (Crame, 1996, 2002).

Despite the reduction in numbers in the Early Paleocene, a very strong overall diversity increase is recorded between the Late Maastrichtian and Middle Eocene at both localities (Figure 3). Indeed, the latter period appears to be a global diversity maximum in both the marine and terrestrial realms for the Paleogene period (Crame et al., 2018, and references therein). Within the gastropods, this marked phase of diversification could be attributed largely to the expansion of just one major clade, the Neogastropoda (Figure 5). But the story is more complicated than this as it is apparent that there is an almost complete turnover of neogastropod taxa at the K/Pg boundary. A new set of genera populated both the Paleocene tropics and poles and it is these that radiated rapidly through the Paleocene–Eocene, with many of them persisting through to the present day. The modern neogastropod fauna in both the tropics and poles has a clear Early Cenozoic component (Beu, 2009; Crame et al., 2014, 2018).

The Early Cenozoic radiation of the bivalves could similarly be attributed to the pronounced rise of the Euheterodonta, a clade containing a number of species-rich, deeper-burrowing, siphonate families. Bivalves as a whole show greater continuity across the K/Pg boundary and large, modern families, such as the Cardiidae, Veneridae and Tellinidae, clearly have Cretaceous or earlier evolutionary roots. The reason for their accelerated evolutionary radiation in the Early Cenozoic is not immediately apparent, but it could be that they entered into some form of ‘evolutionary arms race’ with the neogastropods and other benthic predators (Vermeij, 1987; Dietl and Kelley, 2002; Harper et al., 2019). It is becoming apparent that the Euheterodonta has never proliferated as much in the polar regions as in the tropics (Figure 4), and this may be because benthic predation is simply less intense in colder waters? A series of complex feedback loops may mean that rates of ecological interaction and coevolution are simply more intense in the tropics than at the poles, and this in some way has a positive effect on net rates of speciation (Brown, 2014).

The Antarctic fossil molluscan fauna is characterized not only by low taxonomic diversity but also by comparatively high levels of endemism. Although comprehensive biogeographic analyses at genus and species level have yet to be completed, it is apparent that distinct Late Cretaceous southern, high-latitude provinces with reduced levels of diversity have been proposed for both bivalves and gastropods (Kauffman, 1977; Zinsmeister, 1982; Sohl, 1987; Kiel, 2002), and this clearly continued into at least the Early Cenozoic (Stilwell, 2003; Beu, 2009). Analysis of the Early Cenozoic neogastropod faunas of Antarctica at the genus level shows very little connection with either the tropical GC or Paris Basin localities (Crame et al., 2018). If this finding is upheld in other major groups then we may be looking at a temperate fauna that has evolved more or less in place over very long periods of time.

Thus, the origins of low diversity faunas in the polar regions may involve something more than a response to the onset of global cooling. Study of Antarctic Late Mesozoic–Early Cenozoic benthic molluscan faunas suggests that some groups, such as several major euheterodont bivalve families, simply ‘never got there’. Others, such as several modern, speciose Southern Ocean neogastropod genera, have a considerable ancestry and must have adapted to a glacial Earth over several tens of millions of years.

The analysis above is necessarily still incomplete but it is presented as a model for the types of paleobiological synthesis that could be accomplished using the JRB fossil record. Similar analyses could be attempted with other benthic groups such as the decapod crustaceans (Feldmann, 2003; Schweitzer and Feldmann, 2015) and echinoderms (Saucède et al., 2014). There is also huge potential to use these long time-series data to investigate the relationship between climate and biodiversity change.

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