

Origin of the tropical–polar biodiversity contrast

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Abstract

Aim: The aim was to investigate the evolutionary origins of the striking biodiversity contrast between high- and low-latitude regions in the present day. Is this a relatively recent phenomenon, causally linked in some way to the greenhouse–icehouse transition and onset of global cooling c. 34 Myr ago, or does it have deeper temporal roots and thus other potential causes?

Location: Early Cenozoic fossil assemblages from two tropical and one polar region, and modern counterparts from various tropical localities and Antarctica.

Time period: The Cretaceous–Palaeogene (K/Pg) mass extinction event, Early Cenozoic (Palaeocene–Eocene) and the present day.

Major taxa studied: Shelf-depth marine Mollusca; the four richest modern benthic clades: Imparidentia, Pteriomorpha, Neogastropoda and Littorinimorpha.

Methods: The K/Pg mass extinction and subsequent recovery was compared between two tropical and one polar region at four distinct stratigraphic intervals. Taxa were identified to species level and assigned to principal families within the four largest benthic molluscan clades. Taxon counts were compared between the three regions at each level and also compared with standardized tropical and polar modern faunas.

Results: The mass extinction was followed by a distinct 25 Myr phase of evolutionary radiation, during which the tropical–polar contrast in the taxonomic composition of all four clades was strongly enhanced; as the global molluscan fauna expanded, it differentiated into distinct low- and high-latitude components.

Main conclusions: A marked differentiation of tropical and polar molluscan faunas occurred in the immediate aftermath of the K/Pg mass extinction; it is likely that, at least for the two bivalve clades investigated, this differentiation was initiated well within the Mesozoic era. The greater antiquity of the tropical–polar split suggests that it was not the product of any single controlling factor during the Cenozoic.

KEYWORDS

Cretaceous–Palaeogene extinction, early Cenozoic radiations, marine Mollusca, tropical–polar biodiversity

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1 | INTRODUCTION

Explaining why high taxonomic diversity is very largely concentrated in the low-latitude and tropical regions has been of long-standing interest in ecology and evolutionary biology. Through processes not yet fully understood, the accumulation of taxonomic richness in these regions seems to have been accelerated with respect to higher latitudes, leading to a disproportionate concentration of species richness in the tropics (Brown, 2014; Gagné et al., 2020; Gaston, 2000; Jablonski et al., 2017; Worm & Tittensor, 2018). Our understanding of the processes influencing high-latitude and polar regions is much less well developed. Extensive theoretical and empirical evidence has been amassed to show that the poles act largely as evolutionary sinks for taxa that originated at lower latitudes (Goldberg et al., 2005; Jablonski et al., 2006). However, there is also evidence from both the terrestrial and marine realms that distinct evolutionary centres have existed in the polar regions, but with intrinsically lower net rates of diversification (i.e., speciation minus extinction) (Briggs, 2003; Convey et al., 2008). As with many cases where two end-member processes exist, the task is to consider the relative frequency of the two end-member models.

Independent evidence from molecular phylogenies and the fossil record suggests that the tropical–polar diversity contrast in a variety of different marine and terrestrial taxa became significantly more pronounced in the wake of the greenhouse–icehouse transition, 34 Ma (Prothero et al., 2003). Before this event, the tropics were geographically much more extensive, and many modern taxa originated within them. However, with the onset of global cooling many of these taxa retreated latitudinally and comparatively few of them subsequently reoccupied the newly expanded temperate and polar regions. Tropical niche conservatism (TNC) has come to be recognized as an important factor contributing to the origin and maintenance of large-scale diversity patterns in the terrestrial realm (Fine & Ree, 2006; Hawkins et al., 2006, 2007; Ricklefs & Schluter, 1993; Wiens & Donoghue, 2004). The signature of the onset of Late Eocene global cooling might also be present in the deep-sea fossil record, with the sudden appearance of a distinctive, low-diversity assemblage of benthic foraminifera in the Southern Ocean (Culver & Buzas, 2000; Thomas & Gooday, 1996; Wilson, 1998). Some authorities have proposed that the steep latitudinal diversity contrast characterizing the present day might have existed for no longer than 34 Myr (Archibald et al., 2010; Mannion et al., 2014).

But balanced against these views is a recent expansion in our knowledge of the biology and palaeobiology of the polar regions, especially that of the Antarctic marine realm. The difference in taxonomic structure between the tropics and Antarctica in the present day in one very large clade (Neogastropoda) is almost identical to differences found in Middle Eocene assemblages, c. 45 Ma. Both the modern and fossil polar faunas are characterized by low diversity but high dominance, whereas the two tropical ones are richer and more even with regard to the taxonomic structure of species within families (Crame et al., 2018). An explanation of the earlier emergence of

this pattern is that polar faunas were already distinctive macroecological/evolutionary entities before the transition to icehouse conditions. Other factors besides temperature might be important in the formation and persistence of these entities (Crame, 2020; Crame et al., 2018).

A further, independent line of evidence supports the idea that distinctive polar marine faunas might have originated even further back in time, in the immediate aftermath of the Cretaceous–Palaeogene (K/Pg) mass extinction event. This comes from an investigation into the geological ages of a global database of living marine bivalves comprising some 5,000+ species (Jablonski et al., 2017; Krug et al., 2009a). A plot of the ages of genera within the entire global fauna, as estimated from the fossil record, defines an exponential probability function, also known as a backward survivorship curve (BSC), governed only by the rate of origination (λ) (Foote, 2001; Krug & Jablonski, 2012). The BSC does not record a smooth, exponential rise over approximately the last 200 Myr; instead, it shows two distinct phases of origination separated by a significant and permanent increase in origination rates that is almost exactly coincident with the K/Pg boundary, as reported by Krug et al. (2009a). We may infer that, immediately after the mass extinction event, a permanent increase in origination rates commenced within the global bivalve fauna that continues through to the present day. No significant latitudinal trend in these rates is detectable before the K/Pg boundary, but there was a very marked one afterwards (Krug et al., 2009a). Over the last 66 Myr, tropical bivalve faunas have accumulated taxa at a much faster net rate than polar ones.

It was the aim of this study to investigate whether the origin of highly distinctive polar biotas can be traced further back in the fossil record to the immediate aftermath of the K/Pg mass extinction event 66 Ma, and perhaps, even further than that. Previous studies have identified a striking imbalance in the structure and composition of tropical and polar biotas in one major clade since at least the Middle Eocene (i.e., c. 45 Ma, 10 Myr before the proposed development of the modern steep latitudinal gradient; Crame, 2020; Crame et al., 2018), but might this feature be of considerably greater antiquity? If it is, and if it is present in a variety of major taxa, then it might well reinforce the role of other biotic and abiotic factors besides the onset of global cooling.

2 | MATERIALS AND METHODS

In this study, we investigated changes in marine benthic faunas in three separate regions from the Late Cretaceous Maastrichtian stage to the late Middle Eocene Bartonian one (i.e., c. 70–40 Ma). Two of the regions are in the formerly much more extensive tropical realm, Western Europe (palaeolatitude c. 40° N) and US Gulf Coast (palaeolatitude c. 30° N), and the third is Seymour Island, Antarctica (palaeolatitude c. 65° S). These regions were chosen to satisfy two basic criteria: to provide as strong a contrast as possible between the tropics and a polar region, and to provide as complete a stratigraphic record as possible during this time interval.

The study concentrated on the two most diverse and abundant benthic groups throughout the Cenozoic: bivalve and gastropod molluscs (Alroy, 2010; Close et al., 2020; Stanley, 2007). Faunas from each time interval at each locality were first split into major clades, then into the principal families within each clade. The aim was to trace the trajectory of each family through the Early Cenozoic and into the present day, as measured by the number of component species. In particular, we sought to trace the rise of those species-rich families of both bivalves and gastropods that form a key component of molluscan taxonomic diversity in the present day (Stanley, 2007; Taylor et al., 1980; Vermeij & Carlson, 2000).

Bivalve clades used in this study are based on those established in recent molecular phylogenetic studies (Bieler et al., 2014; Combosch et al., 2017), and estimates of their relative global importance are based on proportional representation in the six faunas used to establish a modern tropical fauna (Supporting Information, S3) plus the Arctic and Antarctic faunas: Protobranchia (14%), Pteriomorpha (29%), Archiheterodonta (6%), Anomalodesmata (9%) and Imparidentia (43%) (Palaeoheterodonta omitted). It should be noted that within this classification, the familiar clade Heterodonta is now subsumed within the larger Imparidentia (Bieler et al., 2014; Combosch et al., 2017). Definition of gastropod clades is essentially as in the study by Crame (2013): Patellogastropoda (1%), Vetigastropoda (11%), Neritimorpha (1%), Cerithioidea (2%), Littorinimorpha (23%), Ptenoglossa (7%), Neogastropoda (42%), Heterobranchia (4%) and Opisthobranchia (9%) (Patellogastropoda and Neritimorpha omitted). Littorinimorpha is used in the sense of Bouchet and Rocroi (2005), but relationships within this large clade remain poorly resolved by both molecular and morphological analyses, and it might be regarded better as a group rather than a true monophyletic clade (Ponder et al., 2008).

A key part of this study was to track the development of the Early Cenozoic faunas in each region through to those of the present day. Unfortunately, there is no direct means of doing this owing to the extensive palaeogeographical changes that occurred throughout the Cenozoic in each of the three selected regions. These changes were particularly profound in the tropics, where a formerly continuous, circum-equatorial Tethyan Ocean was progressively dissected by a series of tectonic events that led eventually to the formation of two tropical high-diversity foci: Indo-West Pacific (IWP) and Atlantic-Caribbean-East Pacific (ACEP) (Leprieur et al., 2016; Perrin, 2002; Veron, 1995). In Antarctica, Seymour Island was connected by shallow seas to a series of K/Pg basins in southern Patagonia (Aberhan & Kiessling, 2015; Aberhan et al., 2007) and to the south with a probable series of basins as far as the southern McMurdo Sound region (Klages et al., 2020; Stilwell & Feldmann, 2000). These connections were progressively disrupted from the Late Eocene onwards, and the most extensive stratigraphic section currently available for study is the Maastrichtian–Eocene one exposed on Seymour Island, Antarctic Peninsula.

Samples at each of the three regions were grouped into four stratigraphic intervals: Late Maastrichtian, Early Palaeocene, Early Eocene and Middle Eocene (see section 2.1, below). Given that the

Early Eocene fauna from Seymour Island is incomplete, it was excluded. Two standardized modern tropical faunas were established, one for bivalves and the other for gastropods. Each of these is, in turn, based upon a subset of six faunas, four from the IWP and two from the ACEP (with full details of how these faunas were constructed being given in the Supporting Information, S3). In the following analyses, particular reference is made to the two largest bivalve clades, Imparidentia and Pteriomorpha, and the two largest gastropod clades, Neogastropoda and Littorinimorpha.

2.1 | Palaeontological analysis

When making comparisons across such large geographical distances and a broad stratigraphic interval, it is essential to minimize mismatches in correlation between rock units (Carter & McKinney, 1992). The three Late Maastrichtian regional faunas are all from the uppermost levels of the stage, and the three succeeding Early Palaeocene ones are all from the basal Danian stage; a single component fauna from the US Gulf Coast does range into the succeeding Selandian stage in its uppermost levels (Supporting Information Table S1). The two tropical Early Eocene faunas are stratigraphically comparable, but in the following extensive Middle Eocene interval the Western Europe fauna is Lutetian, the US Gulf Coast is Bartonian (i.e., slightly younger), and the Antarctic fauna is undifferentiated Lutetian–Bartonian in age (Supporting Information Table S1). Nevertheless, it should be stressed that in all three regions there is a clear trend of increasing taxonomic diversity from the Early Palaeocene to Middle Eocene, followed by a decline in the Late Eocene (Crame et al., 2014; Dockery & Lozouet, 2003; Huyghe et al., 2015; Piccoli et al., 1987). The degree of latitudinal or longitudinal asynchronicity in this diversification phase has yet to be established fully.

Although limestones occur throughout the sedimentary sequence at both tropical localities, it should be emphasized that they are typically interbedded with clastic lithologies, such as calcareous and glauconitic sands (Supporting Information Table S1). Coral reefs occur in both regions, but they are usually small patches and mounds that are not comparable to later Cenozoic and modern reefs (Kiessling, 2002; Perrin, 2002). The Early Cenozoic tropics were characterized by a series of extensive, shallow-water carbonate platforms and shoals rather than true reefs (Supporting Information Table S1). Limestones are particularly prominent in the Western Europe region, and in the Early Palaeocene the fauna has been obtained very largely from a sequence of well-indurated carbonate lithologies (Calcaire de Mons and equivalents). Such rocks, which are hard to break up, can hinder the collection of a representative fauna, but it is apparent that the casts and moulds obtained from the limestones are of a high quality (Supporting Information Table S1).

The estimated richness of lithified sedimentary units in general can be less than half that of unlithified ones, owing to much poorer recovery of specimens of small taxa (Cooper et al., 2006; Sessa et al., 2009). In this study, a tripartite scale of lithification, comprising unlithified, partly lithified and lithified categories, has been

adopted in all three regions studied (Hendy, 2009), and consideration has been given to the size range of fossil assemblages (Supporting Information Table S1). An assessment was also made of the degree of shell dissolution, because aragonitic shells are more vulnerable to diagenetic alteration than calcitic ones (Bush & Bambach, 2004). These and other lithological characteristics in all three regions are summarized in the Supporting Information (Table S1).

The primary focus of this study was a taxonomic comparison of tropical and polar faunas over the 30-Myr interval between the Late Maastrichtian and late Middle Eocene; which taxa are common to both regions and which are restricted to either the high or low latitudes? Species lists for each family within each clade were compiled from the literature and reference collection sources cited in the Supporting Information (Table S1). Statistical analysis of the taxonomic structure of the number of species per genus was performed with non-metric multidimensional scaling (NMDS; Bush & Brame, 2010) in the R package *vegan* v.2.5-7 (Oksanen et al., 2020; contact A.J.M. for R code and input files). This procedure was complemented by use of Sørensen's dissimilarity index, which is a measure of β diversity dependent upon the proportion of shared taxa between two or more assemblages (Baselga, 2010; Magurran, 2004). The latter index is of particular interest because it can, in turn, be partitioned into spatial turnover and nestedness components (whereby, for example, a polar fauna could simply be a species-poor subset of a richer tropical one, which gives insight into differences in taxonomic composition). Continuity of the taxonomic identity of dominant families was assessed by comparing the relative ranking by species richness per family, through time in each of the three regions. Families known from the Antarctic, from any interval, for each clade formed the focus of the analytical dataset, with the assumption that families would show similar diversification rates in all three regions. This procedure, by focusing only on families found in both the Antarctic and at least one tropical area, offers a fairer set of rankings than using full faunas. This was assessed by Kendall's coefficient of rank correlation, tau (τ), which ranges between plus one and minus one. High positive values would signify that families with high rank in the preceding interval retain that high rank in the following interval. This is a default expectation if diversification rates are stochastically constant across regions, because having more species in one interval offers more chances of speciation per unit time or the accumulation of immigrant taxa that are likely to have similar ecological requirements. However, speciation and immigration cannot be separated by this test. High negative values would signify a pattern whereby high-ranking taxa in one interval were likely to become low-ranking taxa in the next interval. Kendall's Tau-b coefficient was used, which takes account of ranking ties.

In making numerical comparisons in this way within both tropical and polar regions, it is important initially to standardize sample sizes wherever possible. Normally, this would involve a technique such as rarefaction or shareholder quorum subsampling (SQS) that can consider both richness and abundance. Nevertheless, when dealing with stage-level assemblages some of the samples are extremely large, and accurate counts of numbers of individuals are simply not

available. This means that in practice, considerable weight has to be placed on the raw number of species alone, and although such a practice might be adequate in well-studied regions, such as Western Europe and the US Gulf Coast, is it appropriate in Antarctica?

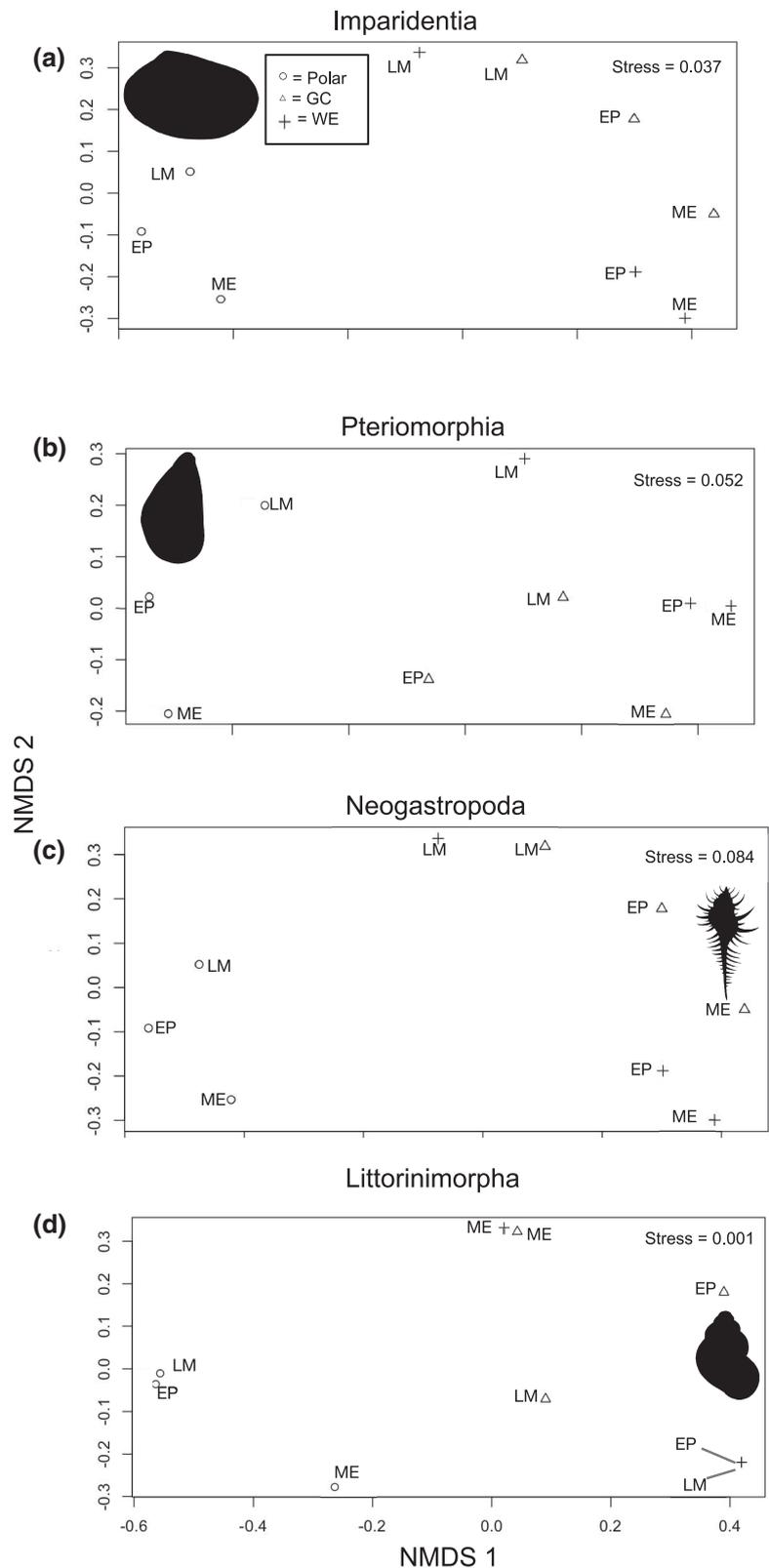
Although Seymour Island represents a single region of comparatively small area, exposure is almost 100% over much of the island, and there is some excellent preservation of fossils at all levels (Supporting Information Table S1). Approximately 5,000 bivalve and gastropod specimens in collections have been examined from the Late Maastrichtian López de Bertodano Formation, $\geq 3,000$ from the Early Palaeocene Sobral Formation and some 15,000–20,000 from the Middle Eocene La Meseta Formation (Crame, 2019). Small to very small taxa (i.e., <10 mm) appear to be under-represented in the Late Maastrichtian and Early Palaeocene assemblages, and this is almost certainly because well-indurated concretions have not been systematically broken down for detailed investigation. However, such taxa are reasonably well represented in the Middle Eocene La Meseta Formation, especially by bivalves within the Nuculidae, Montacutidae, Gaimardiidae and Cyamiidae and gastropods within the Buccinidae, Volutomitridae, Pyramidellidae and superfamily Conoidea (Beu, 2009; Crame et al., 2014, 2018; Stilwell & Zinsmeister, 1992; Stilwell et al., 2004). Finally, it should be emphasized that the area of exposed rock investigated in each interval shows no major variation up-section on Seymour Island (Crame, 2019; Supporting Information Table S1). To a first approximation, the same is essentially true of both the tropical regions investigated.

3 | RESULTS

The effects of the K/Pg mass extinction event were notable in all three regions but most apparent on the US Gulf Coast. Here, all four clades suffered a significant reduction in the number of species between the Late Maastrichtian and Early Palaeocene stages (Supporting Information Table S2), perhaps reflecting the close proximity to the bolide impact site in the Gulf of Mexico and the related tsunami events (Goderis et al., 2021). Thereafter, however, the numbers of both species and families increased from the Early Palaeocene to Middle Eocene in all three regions and all four clades (Supporting Information Table S2). In all instances, the increases were more modest in the polar region than in the tropics, and this was especially marked in both the bivalve clades, which are still relatively species poor in the present day.

The NMDS plots for the Late Maastrichtian show a consistent separation of Antarctica (Seymour Island) from the two tropical regions (Western Europe and US Gulf Coast) in all four clades (Figure 1). The distinction is perhaps sharpest in the two largest clades, Imparidentia and Neogastropoda, but nevertheless still apparent in both the Pteriomorpha and Littorinimorpha. The situation in the Early Palaeocene interval is somewhat different. Here, the Imparidentia still show a clear separation of Antarctica from the two tropical regions, but the second bivalve clade, Pteriomorpha, show

FIGURE 1 Non-metric multidimensional scaling (NMDS) ordination, based on Bray–Curtis dissimilarity, for relative proportions of species per genus for each major clade to investigate taxonomic structure among sites through time: (a) Imparidentia; (b) Pteriomorpha; (c) Neogastropoda; and (d) Littorinimorpha. Each panel has a stress value, and all these values are indicative of good agreement between the original distances and the NMDS plots. Sensitivity was examined for presence/absence and \log_{10} -transformed data and found to be limited. Given that there are close links between Sørensen's dissimilarity index used in Figure 2 and NMDS based on presence/absence data, the two values complement each other. The image of *Pomatias elegans* (Müller, 1774) used as a pictograph for Littorinimorpha is used under CC-BY-SA 3.0 as specified by Armelle Ansart (photograph), Maxime Dahirel (digitization). Abbreviations EP = Early Palaeocene; GC = US Gulf Coast; LM = Late Maastrichtian; ME = Middle Eocene; Polar = Seymour Island, Antarctica; WE = Western Europe. Only three time intervals are shown because the Early Eocene dataset from Antarctica is incomplete



only a relatively small separation (not shown in Figure 1). In addition, the two gastropod clades do not converge on a clear three-way solution, and this is almost certainly attributable to the very sparse post-extinction faunas obtained from Antarctica. A clear separation between Antarctica and the two tropical regions is re-established in

the Middle Eocene, where the sharpest definition between the three regions is again shown by the Imparidentia and Neogastropoda (Figure 1).

A high level of taxonomic differentiation between Antarctica and the two tropical regions is also recorded in all four clades and three

time intervals using Sørensen's dissimilarity index (Figure 2). As might be expected, there are somewhat lower values for the inter-tropical comparisons. The nestedness values are consistently low throughout, but there is a tendency for them to be slightly higher in bivalves than in gastropods (Figure 2), and this might be a reflection of their longer evolutionary legacy. The highest nestedness values are for the Late Maastrichtian Imparidentia and Pteriomorpha clades, but there is no overall trend of increasing nestedness through the Early Cenozoic (Figure 2).

It can be concluded that the Early Cenozoic polar benthic molluscan fauna is not obviously a nested subset of the tropical one. However, it is important to emphasize that a low incidence of nestedness cannot necessarily be taken as evidence against an out of the tropics (OTT) evolutionary dynamic. OTT was established at a higher taxonomic level (i.e., genera) and might have been operating extensively on longer time-scales (Tomašových & Jablonski, 2016). In their original formulation of this concept, Jablonski et al. (2006) stressed that many tropical clades might reach the mid-latitude regions only after extended intervals of time and that independent polar clades were likely. Alternatively, some elements of the fauna might have tropical roots but then diversify in the polar regions owing to pre-existing characteristics that enhance speciation after they become established in the high latitudes. Further investigation of Late Mesozoic–Early Cenozoic mid-latitude regions might provide a better test of the OTT hypothesis and refine the NMDS and β -diversity analyses.

An analysis of changes in the relative strengths of the five bivalve and seven gastropod clades through time is presented in section S1 of the Supporting Information. In essence, the distinct shift in dominance between the essentially epifaunal Pteriomorpha and essentially infaunal Imparidentia across the K/Pg boundary reflects a key stage in the progressive infaunalization of the bivalves through the latest Mesozoic–Early Cenozoic (Aberhan, 1994; Stanley, 2007). The relative proportions of these five clades then remains remarkably constant in the two tropical regions through the Early Cenozoic (Supporting Information Figure S1). This switch in dominance between the two main bivalve clades across the K/Pg boundary is less obvious in Antarctica but is well established by the Middle Eocene (Supporting Information Figure S1). However, the two main clades are of equal prominence in the modern fauna, where numbers of suspension-feeding bivalves overall are extremely low (Supporting Information Figure S1) (Beu, 2009; Nicol, 1967, 1970). The Neogastropoda are the dominant gastropod clade throughout the interval of study in all three regions (Supporting Information Figure S1). The only exception to this pattern occurs across the K/Pg boundary in Western Europe and is almost certainly a reflection of the prevalent shallow-water, high-energy carbonate substrates in both these intervals (Supporting Information Figure S1; Table S1). The Neogastropoda is today one of the largest clades in the sea (Crame, 2013; Ponder & Lindberg, 1997).

Changes at the family level through the Early Cenozoic in the four principal clades examined (Imparidentia, Pteriomorpha,

Neogastropoda and Littorinimorpha) are reviewed in the following two sections.

3.1 | Bivalve radiations

3.1.1 | Imparidentia

During the Late Maastrichtian, richness in Imparidentia in Western Europe is comparatively low (18 species in 10 families), but this increases significantly across the K/Pg boundary into the Early Palaeocene (69 species in 17 families) (Figure 3; Supporting Information Table S2). Thereafter, richness increases again in both the Early Eocene (175 species in 25 families) and Middle Eocene (324 species in 29 families); estimated family richness for the Middle Eocene is only one family less than that for the present day (Figure 3; Supporting Information Table S2). The US Gulf Coast has a significantly higher Late Maastrichtian species richness value (75 species) contained within 14 families (Figure 3; Supporting Information Table S2), and this changes across the K/Pg boundary to 43 species in 16 families in the Early Palaeocene and 50 species in 19 families in the Early Eocene. It is not until the Middle Eocene (173 species in 23 families) that a major increase in estimated richness is detected (Figure 3; Supporting Information Table S2).

Examination of the standardized modern tropical bivalve fauna used in this study at the family level shows that only four families (Veneridae, Tellinidae, Cardiidae and Lucinidae) make up 54% of the species within the total Imparidentia fauna (30 families) (Figure 3). It is noteworthy that the same four families maintain their prominence when traced back through time in the Western Europe region, with 45% of the Middle Eocene fauna (29 families) and 46% of the Early Eocene one (25 families) (Figure 3). This figure rises to 51% in the Early Palaeocene (17 families) and as high as 56% in the Late Maastrichtian (10 families). There is a strong element of taxonomic continuity at the family level through time in the Imparidentia bivalve fauna, and this might extend back to the Late Cretaceous (Figure 3). Comparisons across the four time intervals using Kendall's τ were all positive and highly significant, emphasizing continuity in clade structure through time at the family level (Late Maastrichtian–Early Palaeocene, $\tau = .280$; Early Palaeocene–Early Eocene, $\tau = .548$; Early Eocene–Middle Eocene, $\tau = .844$; Middle Eocene–Recent, $\tau = .522$; all $p < .001$; Figure 3).

At the US Gulf Coast locality, Veneridae + Tellinidae + Cardiidae + Lucinidae comprise 48% of the Middle Eocene Imparidentia fauna (23 families), 52% of the Early Eocene (19 families), 53% of the Early Palaeocene (16 families) and 56% of the Late Maastrichtian (14 families) (Figure 3). There is again a strong impression of continuity through time within the fauna, and all the upward transitions were strongly positive (Late Maastrichtian–Early Palaeocene, $\tau = .408$, $p < .05$; Early Palaeocene–Early Eocene, $\tau = .504$; Early Eocene–Middle Eocene, $\tau = .658$; Middle Eocene–Recent, $\tau = .620$; with the latter three transitions all $p < .001$; Figure 3).

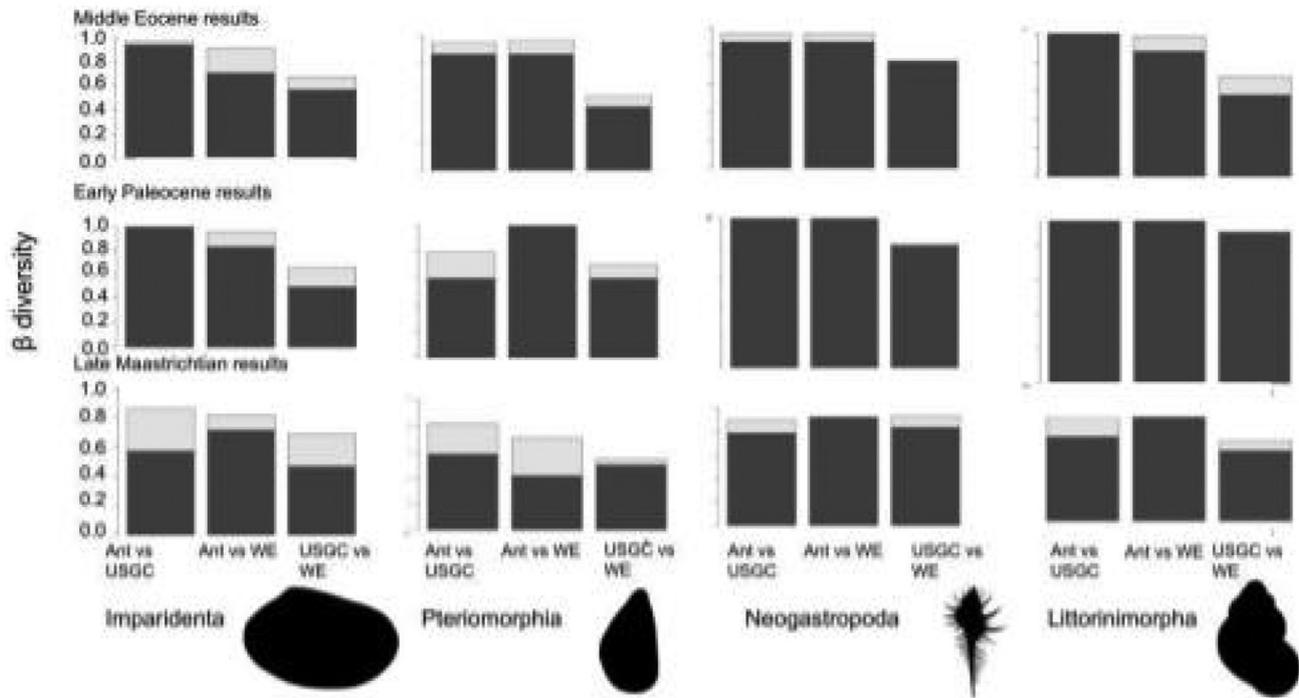


FIGURE 2 Plots of Sørensen's dissimilarity index, calculated using the R package betapart v.1.5.4 (Baselga et al., 2021), based on pairwise comparisons among sites for each clade, compressing all genus records into a presence/absence single matrix for each area to compare taxonomic composition. Completely dissimilar sites with no taxa in common have a value of one, whereas two sites with identical suites of taxa have a value of zero. Sørensen's index gives an estimate of β diversity and can be divided into two additive components: taxonomic turnover, whereby one taxon is replaced by a new taxon (β similarity, shown as dark grey bars); and nestedness, whereby the site with fewer taxa has a subset of the taxa known from the more diverse site (β nestedness, shown as light grey bars). Abbreviations Ant = Seymour Island, Antarctica; USGC = US Gulf Coast; WE = Western Europe. Only three time intervals are shown because the Early Eocene dataset from Antarctica is incomplete. The image of *Pomatias elegans* (Müller, 1774) used as a pictograph for Littorinimorpha is used under CC-BY-SA 3.0 as specified by Armelle Ansart (photograph), Maxime Dahirel (digitization)

It is very noticeable that in all four time intervals in the Antarctic region, the number of component taxa is extremely small (Figure 3; Supporting Information Table S2). There are only seven species in seven families in the Late Maastrichtian, seven species five families in the Early Palaeocene and 26 species in 11 families in the Middle Eocene; even in the present day, there are only 59 species in 11 families (Supporting Information Table S2). In the fossil record, no family has more than eight species, and in the present day only four have nine or more. In very marked contrast to the tropics, there are no species-rich families in any interval (Figure 3).

The four dominant tropical families both in the present day and in the fossil record (Veneridae, Tellinidae, Cardiidae and Lucinidae) collectively form only a very minor component of the Antarctic record (Figure 3). The Late Maastrichtian and Early Palaeocene faunas in Antarctica are statistically very similar ($\tau = .714, p < .005$), but it has to be stressed again that the number of species in each family is extremely low (Figure 3). There is still a positive ($\tau = .504$) but not statistically significant link between the Early Palaeocene and Middle Eocene faunas, but this pattern is completely lost when the Middle Eocene fauna is compared with the Recent one ($\tau = -.88, p < .001$; i.e., a strongly discordant pattern). The four largest Imparidentia families in Antarctica in the present day are Montacutidae, Gaimardiidae,

Cyamiidae and Lasaeidae (Figure 3). These comprise predominantly small to tiny taxa (<1 cm in length) with a wide variety of lifestyles that includes both commensalism and parasitism on other benthic organisms (Dell, 1972, 1990; Nicol, 1967, 1970). The first three of these families can be traced back to the Middle Eocene, but not in any great numbers (Figure 3).

3.1.2 | Pteriomorphia

In Western Europe, there is a reduction from 58 species in 16 families in the Maastrichtian Pteriomorphia fauna to 43 species in 14 families in the Early Palaeocene, but this increases to 73 species in 17 families in the Early Eocene and 138 species in 20 families in the Middle Eocene (Figure 4; Supporting Information Table S2). The last figure is the same number of families as in the present day. On the US Gulf Coast, the fauna comprises 87 species in 20 families, but this is significantly reduced to 28 species in 13 families in the Early Palaeocene and 27 species in 14 families in the Early Eocene (Figure 4; Supporting Information Table S2). Even in the Middle Eocene, the richness increases to only 106 species in 15 families, and the Pteriomorphia has barely recovered to its pre-mass extinction richness (Figure 4; Supporting Information Table S2).

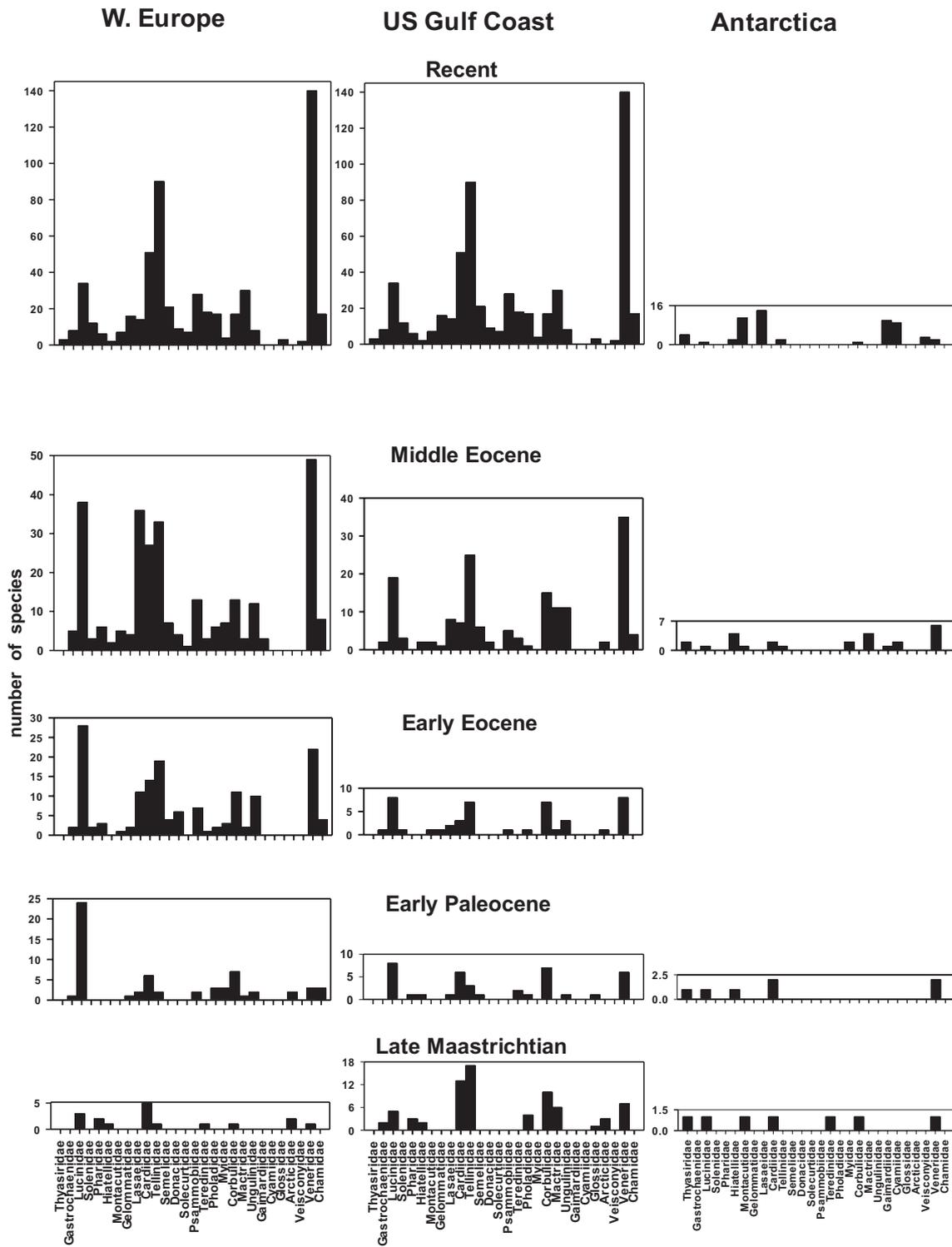


FIGURE 3 A comparison of the principal families within the bivalve Imparidentia clade between Western Europe, US Gulf Coast and Seymour Island, Antarctic Peninsula. The histograms show the number of species within the principal Imparidentia families at four time intervals in the two tropics regions and three in the polar region, and these are compared with standardized faunas from the Recent tropics and Antarctica, respectively (top row). The incomplete Early Eocene fauna from Seymour Island is omitted. The taxonomic order of families along x-axes is based on the study by Combosch et al. (2017); minor families are omitted. Further details on how the various faunas were compiled are contained in the main text and Supporting Information (Table S1). Species names left in open nomenclature (i.e. simply referred to as "sp." or qualified by "cf." or "?") are counted only if they are the sole representative of the genus

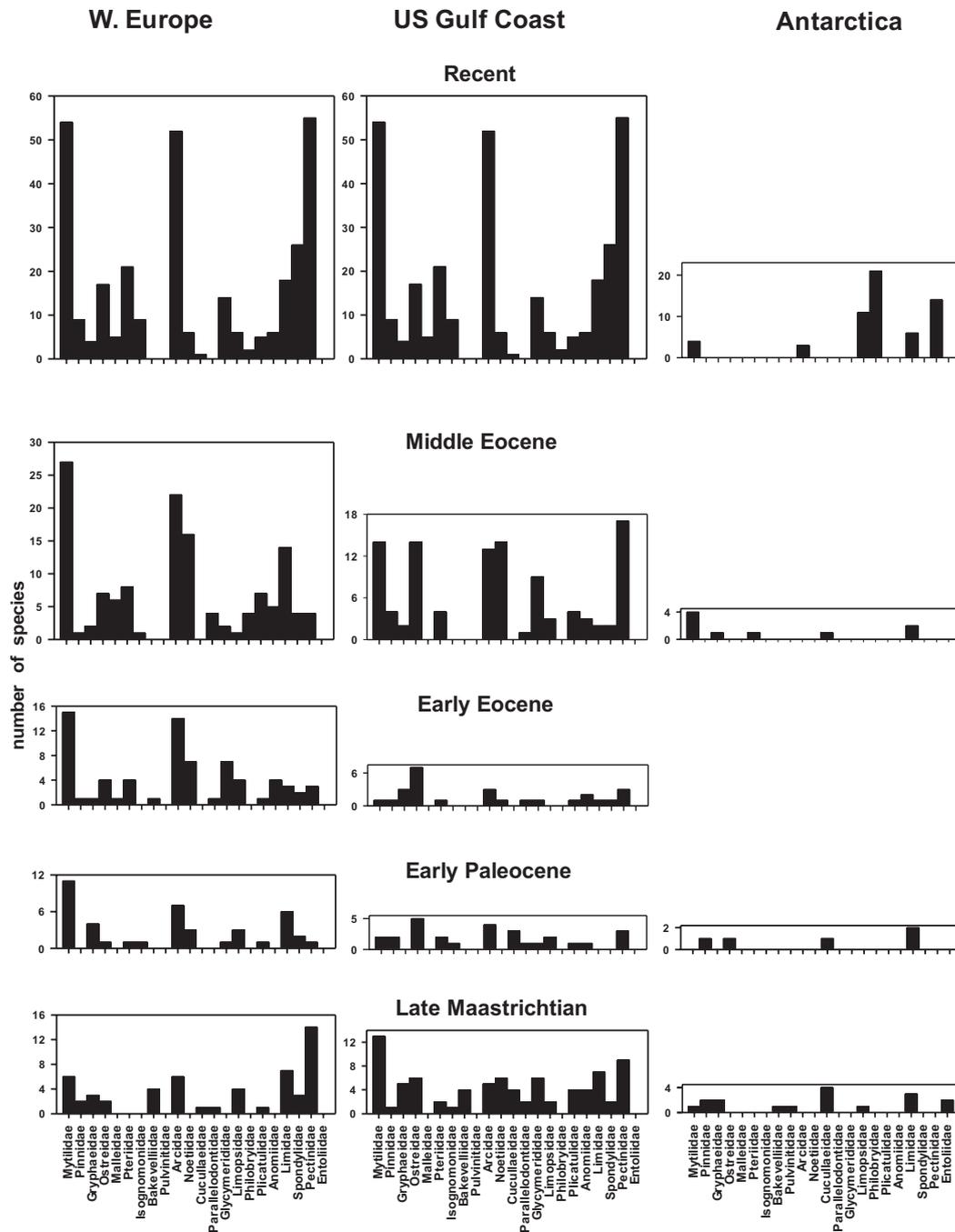


FIGURE 4 A comparison of the principal families within the bivalve Pteriomorpha clade between Western Europe, US Gulf Coast and Seymour Island, Antarctic Peninsula. The histograms show the number of species within the principal Pteriomorpha families at four time intervals in the two tropics regions and three in the polar region, and these are compared with standardized faunas from the Recent tropics and Antarctica, respectively (top row). The incomplete Early Eocene fauna from Seymour Island is omitted. The taxonomic order of families along x-axes is based on the study by Combosch et al. (2017); minor families are omitted. Further details on how the various faunas were compiled are contained in the text and Supporting Information (Table S1). Species names left in open nomenclature (i.e. simply referred to as "sp." or qualified by "cf." or "?") are counted only if they are the sole representative of the genus

The modern tropical Pteriomorpha fauna (316 species in 20 families) is dominated by three families (Mytilidae, Arcidae and Pectinidae), which make up 51% of the total Pteriomorpha fauna (Figure 4). When these families are traced back into the Early Cenozoic in Western Europe, they total 45% of the Middle Eocene Pteriomorpha fauna, 44% of both the Early Eocene and Early Palaeocene faunas, and 45% of the Late Maastrichtian one (Figure 4). On the US Gulf Coast, they

comprise 42% of the Middle Eocene Pteriomorpha fauna, but this falls to 26% and 32%, respectively, in the low-diversity faunas of the Early Eocene and Early Palaeocene (Figure 4). Interestingly, this value rises to 47% in the Late Maastrichtian, again suggesting pre-K/Pg extinction roots for a prominent modern bivalve clade (Figure 4).

All the vertical transitions between the various time intervals in the Western Europe region (Figure 4) were positive and statistically

significant (Late Maastrichtian–Early Palaeocene, $\tau = .406$, $p < .05$; Early Palaeocene–Early Eocene, $\tau = .511$, $p < .001$; Early Eocene–Middle Eocene, $\tau = .526$, $p < .001$; Middle Eocene–Recent, $\tau = .403$, $p < .001$). This also looks to be a very stable bivalve fauna through time at the family level (Figure 4). On the US Gulf Coast, all the upward transitions show positive Kendall's τ values, with the Early Eocene–Middle Eocene ($\tau = .598$, $p < .001$) and Middle Eocene–Recent ($\tau = .548$, $p < .001$) being statistically significant (Figure 4).

The Antarctic Maastrichtian Pteriomorpha fauna is considerably more diverse than the Imparidentia one, with 17 species in nine families (Supporting Information Table S2). Nevertheless, it is very strongly reduced across the K/Pg boundary, with only five species in four families in the Early Palaeocene and nine species in five families in the Middle Eocene (Figure 4). The two most characteristic taxa within the modern Antarctic Pteriomorpha are the sister families Limopsidae and Philobryidae (Combosch et al., 2017; Dell, 1990) (Figure 4). Taken together, these comprise a wide variety of tiny to medium-sized, epi- to endo-byssate species from shallow to bathyal water depths (Dell, 1990); indeed, *Limopsis* and *Philobrya* are the two most species-rich Antarctic bivalve genera in the present day (Dell, 1990). Upward transitions between the Late Maastrichtian–Early Palaeocene and Early Palaeocene–Middle Eocene (Figure 4) show positive Kendall's τ values ($\tau = .413$ and $\tau = .232$, respectively), but these are not statistically significant ($p > .05$). The Middle Eocene–Recent transition is significant and negative ($\tau = -.017$, $p < .001$), reflecting the prominence of Philobryidae (21 species), Pectinidae (14) and Limopsidae (11). As with the Imparidentia, there are only very limited taxonomic similarities between the tropics and pole in all four time intervals (Figure 4).

3.2 | Gastropod radiations

3.2.1 | Neogastropoda

The Late Maastrichtian neogastropod fauna from Western Europe comprises the comparatively low figures of 22 species in six families, but this increases significantly to 61 species in 16 families in the Early Palaeocene (Figure 5; Supporting Information Table S2). In the Early Eocene, there is a further increase to 142 species in 22 families, but the really big pulse of diversification occurs between the Early and Middle Eocene, where there is a more than a threefold increase in the number of species to 434 within 24 families (Figure 5; Supporting Information Table S2). Within the superfamilies Buccinoidea and Muricoidea (left-hand half of the x-axis in Figure 5), three families (Buccinidae, Fasciolaridae and Volutidae) can be traced backwards in time from the Middle Eocene (where they make up 26% of the total neogastropod fauna) through the Early Eocene (28%) to the Early Palaeocene (38%) (Figure 5). However, it is interesting to note that, in the present day, this figure declines to only 9% (Figure 5). In a similar way, within the superfamily Conoidea (right-hand end of the x-axis in Figure 5) the progressive development of families such as the Turridae and Clavatulidae can be traced up to the Middle

Eocene, but neither of them is particularly prominent in the present day. It is apparent that the modern tropical neogastropod fauna is characterized by a large number of very species-rich families, including Terebridae (50+ species), Columbelloidea, Costellariidae and Mitridae (all 70+), Conidae (100+) and Muricidae (160+) (Figure 5). Collectively, they represent a prolific later Cenozoic radiation.

The first three Western Europe transitions all yielded positive and statistically significant Kendall's τ values (Late Maastrichtian–Early Palaeocene, $\tau = .399$, $p < .05$; Early Palaeocene–Early Eocene, $\tau = .486$, $p < .05$; Early Eocene–Middle Eocene, $\tau = .501$, $p < .001$). The Middle Eocene–Recent transition is positive ($\tau = .197$) but not statistically significant ($p > .05$), reflecting the continued radiation of this major clade throughout the later Cenozoic.

The Late Maastrichtian neogastropod fauna is much more diverse on the US Gulf Coast, with 84 species in 11 families (Figure 5; Supporting Information Table S2). This is reduced to 69 species (but within 16 families) in the Early Palaeocene, and there is only a modest increase to 97 species in 19 families in the Early Eocene. The steepest rate of increase is again between the Early and Middle Eocene, when the diversity values (450 species in 25 families) are close to those of Western Europe (Figure 5; Supporting Information Table S2). The rise of the Buccinidae, Fasciolaridae and Volutidae can again be traced through time into the Middle Eocene, when they make up 26% of the Middle Eocene neogastropod fauna, a value that is significantly reduced to 12% in the present day. Conoidea also show a strong development through the Early Cenozoic, from 22% of the neogastropod fauna in the Early Palaeocene to 32% in the Early Eocene and 38% in the Middle Eocene (Figure 5). But the Middle Eocene dominance of the Turridae within the Conoidea is lost in the modern fauna, where several other families are more prominent (Figure 5).

The similarity of US Gulf Coast Late Maastrichtian, Early Palaeocene and Early Eocene faunas is reinforced by strongly positive Kendall's τ values (Late Maastrichtian–Early Palaeocene, $\tau = .491$, $p < .005$; Early Palaeocene–Early Eocene, $\tau = .599$, $p < .001$), but the Early Eocene–Middle Eocene transition is only positive ($\tau = .639$) and not statistically significant ($p > .05$). The Middle Eocene–Recent transition is very strongly negative ($\tau = -.013$, $p < .001$), again reflecting a significant later Cenozoic radiation of the clade (Figure 5).

The dominance of both the Middle Eocene and modern Antarctic neogastropod faunas by the Buccinidae forms a striking contrast with contemporary tropical faunas and has been considered in detail in previous studies (Beu, 2009; Crame, 2013; Crame et al., 2018). In the longer fossil record displayed in this study, the dominance at the family level by the Buccinidae can be traced back to the Early Palaeocene, but not Late Maastrichtian (Figure 5). The only other modern Antarctic neogastropod family with >20 species, Muricidae, has a very poor Early Cenozoic fossil record (Figure 5). The Late Maastrichtian–Early Palaeocene transition is positive and statistically significant ($\tau = .490$, $p < .05$) and the Early Palaeocene–Middle Eocene is positive ($\tau = .003$) but not significant. Likewise, the Middle Eocene–Recent transition is positive ($\tau = .118$) but not significant (Figure 5).

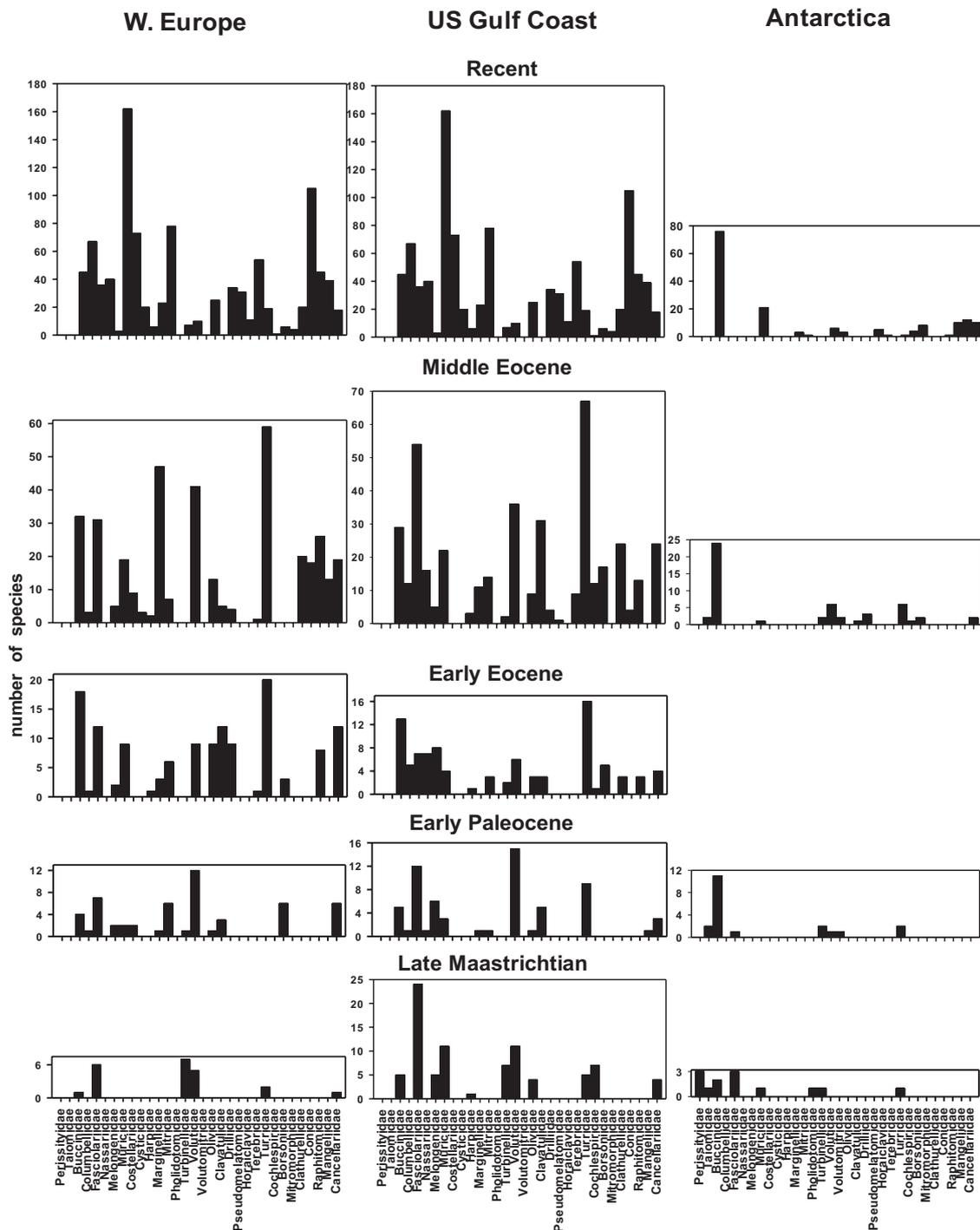


FIGURE 5 A comparison of the principal families within the Neogastropoda clade between Western Europe, US Gulf Coast and Seymour Island, Antarctic Peninsula. The histograms show the number of species within the principal Neogastropoda families at four time intervals in the two tropics regions and three in the polar region, and these are compared with standardized faunas from the Recent tropics and Antarctica, respectively (top row). The incomplete Early Eocene fauna from Seymour Island is omitted. The taxonomic order of families along x-axes is based on the studies by Bouchet and Rocroi (2005) and Bouchet et al. (2011). Further details on how the various faunas were compiled are contained in the text and Supporting Information (Table S1). Species names left in open nomenclature (i.e. simply referred to as "sp." or qualified by "cf." or "?") are counted only if they are the sole representative of the genus

3.2.2 | Littorinimorpha

In Western Europe, there is again a steep rise in richness through the Early Cenozoic into the Middle Eocene (280 species in 33 families),

and this number of families is only one short of that in the present day (Figure 6; Supporting Information Table S2). In comparison, the US Gulf Coast Late Maastrichtian Littorinimorpha is represented by 42 species in 10 families, but this is reduced to 29 species in 11

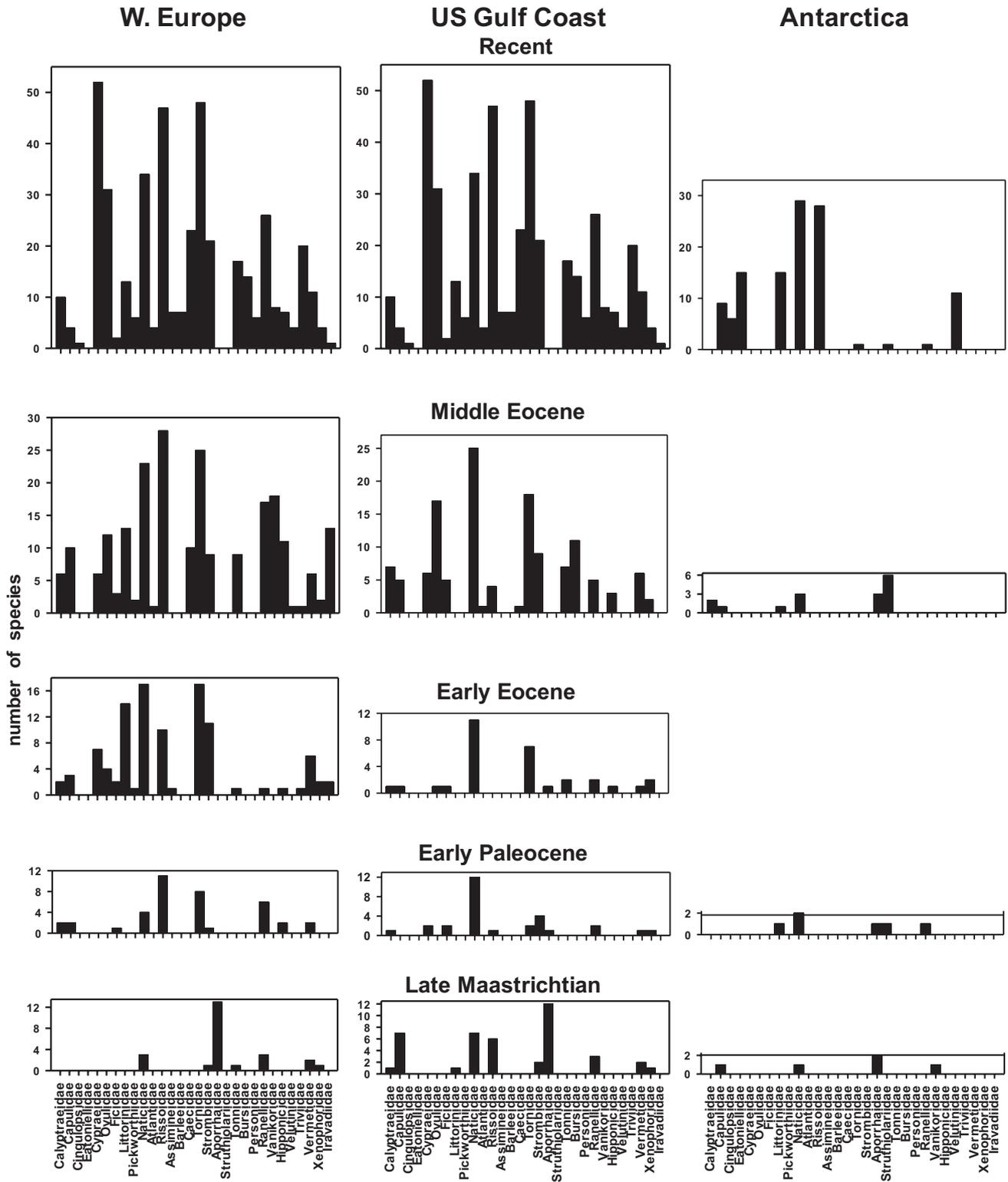


FIGURE 6 A comparison of the principal families within the gastropod clade Littorinimorpha between Western Europe, US Gulf Coast and Seymour Island, Antarctic Peninsula. The histograms show the number of species within the principal Littorinimorpha families at four time intervals in the two tropics regions and three in the polar one, and these are compared with standardized faunas from the Recent tropics and Antarctica, respectively (top row). The incomplete Early Eocene fauna from Seymour Island is omitted. The taxonomic order of families along x-axes is based on the study by Bouchet and Rocroi (2005). Further details on how the various faunas were compiled are contained in the main text and Supporting Information (Table S1). Species names left in open nomenclature (i.e. simply referred to as "sp." or qualified by "cf." or "?") are counted only if they are the sole representative of the genus

families in the Early Palaeocene, when the Cerithioidea temporarily become the second most important gastropod clade (Supporting Information Figure S1). There is still a relatively low richness value at this locality in the Early Eocene (32 species in 13 families), but in the Middle Eocene there is nearly a fourfold increase in the number of species (122 species in 17 families) (Figure 6; Supporting Information Table S2).

Four of the five largest Littorinimorpha families in the present day (Ovulidae, Naticidae, Rissoidae and Tornidae) can be traced back through the Early Cenozoic at both tropical localities (Figure 6). In Western Europe, these families make up 37% of the modern Littorinimorpha fauna (34 families), 31% of the Middle Eocene Littorinimorpha fauna (33 families), 45% of the Early Eocene (22 families) and 49% of the Early Palaeocene (11 families) (Figure 6); corresponding figures for the three Early Cenozoic intervals at the slightly less diverse US Gulf Coast locality are 53% (of the Middle Eocene Littorinimorpha fauna; 17 families), 59% (Early Eocene; 13 families) and 52% (Early Palaeocene; 11 families) (Figure 6; Supporting Information Table S2). The reason why these four families together do not compose a higher proportion of the modern fauna is the presence of the largest family, Cypraeidae, which has >50 component species (Figure 6). Cypraeids do occur at both localities through the Early Cenozoic, but only in comparatively small numbers. Their rise to prominence is most likely to be a later Cenozoic phenomenon, similar to that of the very species-rich families in the modern tropical Neogastropoda fauna. It is also apparent that, like the Neogastropoda, there is less obvious faunal continuity of the clade across the K/Pg boundary. Aporrhaidae, the largest Maastrichtian littorinimorph family (Figure 6; Supporting Information Table S2), was severely reduced across the K/Pg boundary at nearly all localities, and only two genera survive in the present day (Roy, 1994).

The Late Maastrichtian–Early Palaeocene transition in Western Europe is positive ($\tau = .248$) but not statistically significant. However, the Early Palaeocene–Early Eocene transition is both positive ($\tau = .488$) and significant ($p < .005$), as are the Early Eocene–Middle Eocene ($\tau = .523$, $p < .001$) and Middle Eocene–Recent ($\tau = .415$, $p < .005$) ones. On the US Gulf Coast, all four transitions are positive and significant (Late Maastrichtian–Early Palaeocene, $\tau = .497$, $p < .005$; Early Palaeocene–Early Eocene, $\tau = .478$, $p < .005$; Early Eocene–Middle Eocene, $\tau = .521$, $p < .001$; Middle Eocene–Recent, $\tau = .462$, $p < .001$; Figure 6).

Although Littorinimorpha is the second richest clade in the Antarctic gastropod fauna (Supporting Information Figure S1), it is characterized by strikingly low taxonomic diversity. Only five species from four families are recorded from the Maastrichtian, six species from five families in the Danian, and 16 species from six families in the Middle Eocene. Even in the present day, there are only 116 species from 10 families, and only two of the latter have >25 species (Figure 6; Supporting Information Table S2). The largest modern family, the predatory Naticidae, is abundant in the fossil record, particularly in the Middle Eocene, but is not taxonomically diverse in comparison with other regions.

An interesting group of Antarctic Littorinimorpha taxa in the present day are small to tiny (i.e., <5 mm) rissoid form types (*sensu* Ponder, 1983) assigned to the families Cingulopsidae, Eatonellidae, Littorinidae and Rissoidae (Figure 6). These are associated with a range of shallow- to deep-water algal communities throughout the Southern Ocean (Dell, 1990; Ponder, 1983). They have virtually no fossil record in Antarctica but could perhaps have been overlooked because of their very small size.

It should be noted that the stromboidean family Aporrhaidae does cross the K/Pg boundary in Antarctica and occurs in both the Early Palaeocene and Middle Eocene intervals (Figure 6) (Beu, 2009; Stilwell & Zinsmeister, 1992; Stilwell et al., 2004). Here, it is joined by a second stromboidean taxon, Struthiolariidae, which becomes extremely abundant in the Middle Eocene (Stilwell & Zinsmeister, 1992). The Late Maastrichtian–Early Palaeocene transition is positive ($\tau = .884$) but not statistically significant, and the Early Palaeocene–Middle Eocene transition is positive ($\tau = .569$) and significant ($p < .05$). The Middle Eocene–Recent transition is negative ($\tau = -.080$) but not significant (Figure 6).

3.3 | Synthesis of Results

In common with many other taxa, in both the marine and terrestrial realms, bivalve and gastropod molluscs underwent a significant evolutionary radiation in the immediate aftermath of the K/Pg mass extinction event (Alroy, 2010; Close et al., 2020; Krug et al., 2009a; Stanley, 2007). However, from the comparisons made in this study it is apparent that they did so at very different rates between the tropical and polar regions, with the former diversifying far faster than the latter (Figures 3–6; Supporting Information Table S2). The Middle Eocene acme of this radiation is very clearly seen in the tropics, but it is important to point out that it is almost certainly present in Antarctica too. The total molluscan fauna of the Middle Eocene La Meseta Formation is now known to comprise well in excess of 100 gastropod and 50 bivalve species (Alvarez & Del Rio, 2020; Beu, 2009; Crame et al., 2014; Stilwell & Zinsmeister, 1992), and it co-occurs with a particularly rich shallow-water fish fauna comprising both selachians and teleosts (Eastman, 2005; Reguero et al., 2012). Although the Late Eocene–Oligocene fossil record of Antarctica is very incomplete, there is every indication that the basic Early Cenozoic diversity trend seen in the tropics is repeated in Antarctica, only on a much smaller scale.

The most striking difference between these regions, both throughout the Early Cenozoic and in the present day, is the lack of species-rich families in Antarctica (Figures 3–6). Only the Buccinidae within the Neogastropoda consistently display a level of species richness comparable to the contemporaneous tropical families in all four time intervals (Figures 3–6). Modern tropical high richness in both bivalves and gastropods is linked to the occurrence of a comparatively small number of species-rich families, but why this should be so is currently uncertain. The rise of these

modern species-rich families through the Early Cenozoic is particularly clear in the bivalves and can be traced back over the K/Pg boundary into the latest Cretaceous (Figures 3 and 4). There is less obvious taxonomic continuity across the K/Pg boundary within the gastropod fauna, and there has been a considerable degree of switching in the dominant families between the Early Cenozoic and present day (Figures 5 and 6). This might well be an indication of rapidly evolving clades that have expanded at a significantly faster rate through the Cenozoic than any bivalve one (Alroy, 2010). Significant elements of the modern global gastropod fauna can be traced back to at least the earliest Cenozoic, and the bivalves perhaps even further back in time.

And it is apparent that the very strong taxonomic differences between modern tropical and polar bivalve and gastropod faunas can be traced back over similar lengths of time (Figures 3–6); there are very few genera and virtually no species in common between the tropical and polar regions throughout the Early Cenozoic (Figures 1 and 2). However, two potentially confounding factors are present with regard to the spatial analyses:

1. Geodispersity, as defined by Miller et al. (2009), who explored the issue of increasing dissimilarity among biotas as an effect of geographical distance. Although a valid concern, a follow-on study by Wu and Miller (2014) added the nuanced concept of over-water distance to reflect the geographical barriers. Although there is an option in the betapart package to include geographical distance decay functions, the question would be how to derive these numerical distances. A first approximation would be presumption of lower dissimilarity between the US Gulf Coast and Seymour Island, based on a clear north–south migration route via Patagonian basins outlined in Section 2 above (Materials and Methods).
2. Differences in the spatial extent of the three regions. Both the Bray–Curtis dissimilarity used in the NMDS for taxonomic structure (Figure 1) and the Sørensen dissimilarity calculations (Figure 2) are spatially implicit, but neither can take account of the taxon-area effect. Although this is controllable in studies of extant richness (e.g., Rosenzweig, 2003), the linkage between habitat area in the geological past and richness remains difficult to control for, and sampling concerns tend to revolve around sampling intensity, taxon body size, facies and lithological variations (Supporting Information Table S1). These issues are addressed with regard to the specifics of the bivalve and gastropod datasets in this paper and also with regard to the Neogastropoda in the paper by Crame et al. (2018).

Although the Antarctic Early Cenozoic faunas are taxonomically discrete, it is important to emphasize that they are characterized by a series of distinctive austral evolutionary radiations.

Within the Imparidentia, the largest bivalve clade, there is phylogenetic evidence of a distinct austral subclade within the Veneridae family that is rooted in Middle Eocene taxa from Seymour Island (Alvarez, 2019; Alvarez & del Rio, 2020). This is

the horizon at which the distinctive genus *Retrotapes* first appears in the fossil record, and it can then be traced in the Late Eocene of both Seymour Island and Punta Arenas, southern Chile. There is further palaeontological evidence to show that it then spread northwards along both the Pacific and Atlantic coasts of southern South America through the Oligocene–Miocene and into their respective modern faunas (Alvarez, 2019). Throughout its stratigraphic and geographical range, *Retrotapes* typically exhibits high abundances of individuals, but in total only 14 fossil and modern species are known (Alvarez, 2019; Alvarez & del Rio, 2020). The large family Cardiidae is represented in the Antarctic fossil record by the distinctive subfamily Lahilliinae (Figure 3); *Lahillia larseni* occurs in very large numbers either side of the K/Pg boundary, and further species are recorded in both the Early Palaeocene of Antarctica and the Middle Eocene of Antarctica and southern Argentina (Figure 3) (Beu, 2009). This might be another distinctive austral subclade within the Imparidentia but without any modern representatives (Beu, 2009).

The most species-rich Antarctic bivalve family in the present day is the Philobryidae (Pteriomorphia), with some 21 species recorded south of the Polar Front (Dell, 1990; Jackson et al., 2015). A molecular phylogenetic analysis of these taxa indicates an initial radiation of the most species-rich genus, *Adacnarca*, in the interval between the K/Pg boundary and Middle Eocene, followed by a radiation of other genera in the mid- to late Miocene (Jackson et al., 2015). Limopsidae, which is a sister taxon of Philobryidae, is represented by 12 species of *Limopsis* in the Southern Ocean and Magellan region (Whittle et al., 2011). The fossil record suggests that these taxa might be very largely the product of a Neogene radiation, but Eocene representatives are known from both Australia and New Zealand, and a possible Middle Eocene species has been recovered from glacial erratic deposits in McMurdo Sound, Antarctica (Stilwell, 2000). The genus also pre-dates the K/Pg boundary with the Late Maastrichtian *Limopsis antarctica* from Seymour Island, and possibly, some of the earliest known records of the genus are from the Early Cretaceous of New Zealand (Whittle et al., 2011).

Within the Neogastropoda, some 31% of the Early Palaeocene Antarctic fauna can be assigned to modern genera, and this figure rises to 37% in the much richer Middle Eocene fauna (Figure 5). What is particularly noticeable here is that within the Buccinidae, two of the modern species-rich genera, *Prosipho* and *Chlanidota*, are represented by six and four species, respectively, at this time (Beu, 2009; Crame et al., 2018). The widespread adaptive radiation of these and other Buccinidae taxa (Dell, 1972, 1990) might be rooted in the Early Cenozoic.

Within the second gastropod clade investigated, Littorinimorpha, the austral family Struthiolariidae (Figure 6) is well represented in the Antarctic fossil record by the genus *Perissodonta*. It makes its first appearance in the Early Palaeocene and reaches maximum taxonomic diversity in the Middle Eocene, when some six species are extremely abundant (Beu, 2009; Stilwell & Zinsmeister, 1992). There are no further occurrences in the fragmentary post-Eocene fossil

record of Antarctica, but two further species have been recorded from undifferentiated Oligocene–Miocene strata in central Chile and southern Patagonia, respectively (Nielsen, 2005). In the present day, two species of *Perissodonta* have been recorded from the subantarctic, although it is unclear whether these might be variants of one taxon (Beu, 2009; Zinsmeister & Camacho, 1980). Two species of *Falsilunatia* and one of *Sinuber* (both Naticidae) have been recorded from the Middle Eocene of Antarctica (Beu, 2009), and both these taxa are relatively common in the modern Southern Ocean (Dell, 1990; <http://www.scarmarbin.be>).

It is concluded that Early Cenozoic evolutionary radiations did occur in the benthic marine faunas of Antarctica but at a much slower rate than their tropical counterparts. A combination of palaeontological and phylogenetic evidence indicates that a number of distinct austral clades radiated at this time, but only one gastropod family, the Buccinidae, qualifies as species rich (Figure 5). This overall disparity in rates of evolutionary radiation between tropical and polar clades through the Early Cenozoic is in agreement with the results obtained from the study of backward survivorship curves based on modern bivalve faunas (Krug et al., 2009a). A distinctive Antarctic marine molluscan fauna can be traced back at least to the K/Pg boundary, and there is the very real impression that this has been of consistently low taxonomic richness (Figures 3–6; Supporting Information Table S2).

4 | DISCUSSION

Perhaps the simplest explanation of the 25 Myr Early Cenozoic global radiation of taxa is that it represents a hyper-exponential burst of diversification in the wake of the K/Pg mass extinction (Carvalho et al., 2021; Jablonski, 2008; Krug & Jablonski, 2012; Miller & Sepkoski, 1988). McKenna and Farrell (2006) suggested that the extinction “primed the phylogenetic fuse” for a massive adaptive radiation of tropical plants and herbivorous insects in the Late Palaeocene–Early Eocene, and the same is very probably true for the marine realm too (Crame, 2020, and references therein). Was there simply a scramble to fill vacated ecospace at all latitudes in the wake of the extinction? Nevertheless, recovery from the global mass extinction event on its own does not account for the very strong tropical–polar contrast in taxonomic composition and implied net rates of diversification established in the present study (Figures 3–6). Given that there was no obvious latitudinal variation in K/Pg extinction intensity (Jablonski, 2008), it is highly likely that other drivers must have been involved in its generation.

It is tempting to link the 25 Myr phase of Early Cenozoic diversification directly to the prevailing climate because it was coincident with a major phase of greenhouse warmth (Zachos et al., 2008). On closer inspection, however, it is apparent that there is not necessarily an exact correlation between global climate and biodiversity patterns, and this applies particularly to the Late Mesozoic–Early Cenozoic interval. It is now clear that the Early Cenozoic greenhouse was eclipsed by a relatively far larger Late Cretaceous one, which can

be traced from a pronounced peak at 92 Ma [the Late Cretaceous Thermal Maximum (KTM)] to c. 84 Ma (Huber et al., 2018; Tierney et al., 2020). It is from this point onwards that global temperatures began their progressive decline through to the present day; initially rather gradually, but then at an accelerating rate through the later Cenozoic (Huber et al., 2018; Tierney et al., 2020). None of the four clades investigated in this study shows any obvious peak at the KTM (Hallam, 1994; Morris & Taylor, 2000; Stanley, 2007).

The latest Cretaceous Campanian and Maastrichtian stages (84–66 Ma) are now assigned to a cool greenhouse phase (Huber et al., 2018), with the next major pulse of global warming beginning in the mid-Palaeocene (c. 61 Ma) (Miller et al., 2020). A Late Palaeocene–Early Eocene hot greenhouse recorded maximum temperatures in the interval 59–54 Ma, punctuated by the Palaeocene–Eocene Thermal Maximum (PETM) and a series of transient Early Eocene hypothermals; the Early Eocene Climatic Optimum (EECO) spanned 55–48 Ma (Miller et al., 2020; Westerhold et al., 2020). But it is interesting to note that the Early Cenozoic taxonomic diversity maximum occurs later in the Middle Eocene cool greenhouse (48–37 Ma) rather than in the EECO hot greenhouse (Figures 3–6; Supporting Information Table S2). Global temperature values do begin to level off and then decline in the later Middle Eocene, but a distinctive Middle Eocene Climatic Optimum (MECO; 40.5–40 Ma) has been recorded in the high southern latitudes on Kerguelen Plateau and Maud Rise (c. 65° S) (Bohaty & Zachos, 2003; Miller et al., 2020).

The overwhelming palaeoclimate signal for the Early–Middle Eocene of the Seymour Island region is temperate, with indications that there might have been both cold- and warm-temperate interludes (Crame et al., 2014, and references therein). Some micro-palaeontological evidence supports the inference of subtropical incursions into the Southern Ocean Atlantic sector between the latest Palaeocene and Middle Eocene (Huber, 1991; Zachos et al., 1993). Nevertheless, it has to be borne in mind that most of Antarctica is subglacial, and the true nature of its Early Cenozoic climates is still uncertain. Integrated ocean drilling programme results from both Wilkes Land, East Antarctica and the East Tasman Plateau indicate persistent, near-tropical warmth in these sectors through at least the Early Eocene (Bijl et al., 2009; Pross et al., 2012). Given that both these regions have similar palaeolatitudes to Seymour Island (i.e., c. 65° S), precise placement of any latitudinal temperature gradient remains problematic. However, there is general agreement that any such gradient in the Early Eocene must have been considerably shallower than that in the present day or at the Eocene–Oligocene boundary 34 Ma (Evans et al., 2018; Greenwood & Wing, 1995; Naafs et al., 2018; Stott et al., 1990).

It should be emphasized that tropical–polar diversity contrasts represent something more than taxonomic richness. This is so because the ambient energy entering any one region is allocated not only to the number of species present but also to their relative abundance and size; the allocation to each of these three categories will not be independent (Blackburn & Gaston, 1996; Brown & Lomolino, 1998). The observed global structure of biodiversity

cannot be explained by variations in species richness alone (Harnik et al., 2010).

Early indications that the tropical–polar contrast in species richness was accompanied by one in species evenness came from the terrestrial realm (MacArthur, 1960; Whittaker, 1975), and now patterns of higher dominance/lower evenness in the polar regions have been recognized in the shallow and deep marine realms too (Culver & Buzas, 2000; Harnik et al., 2010; Rex & Etter, 2010; Rex et al., 1993). Another example of this phenomenon has been recorded in the gastropod family Buccinidae, which dominates the Neogastropoda both in the present day and through the Early Cenozoic (Figure 5) (Crame, 2013, 2020; Crame et al., 2018). Modern Buccinidae are classic trophic generalists, a functional trait shared by many other Antarctic benthic marine groups (Crame, 2020, and references therein).

The combination of low taxonomic diversity and high dominance in the polar marine realm has been linked to the extreme seasonality of primary production at the base of the food chain, and pulsed nutrient loading might limit diversity in marine systems by restricting resource exploitation to only part of the annual production cycle (Chown & Gaston, 1999). Nevertheless, this does not explain fully how standing biomass is then subdivided into separate species, and it is likely that something else must be involved too (Rex & Etter, 2010). One simple line of argument is that, as many species inhabiting trophically variable environments are generalists, they require a greater share of the available diversity-dependent resources (i.e., those that can easily be used up) in order to survive than tropical counterparts; consequently, low polar diversity is not so much a sign of vacant eco-space or available niches but rather an indication of a low inherent carrying capacity (Krug et al., 2009b; Valentine et al., 2008). And as a direct result of this, polar origination, background extinction and immigration rates are all relatively low. Many polar communities are not particularly invasible, and their component taxa can be viewed as incumbents that are possibly dislodged only by a mass extinction event (Krug et al., 2009b; Valentine et al., 2008). Such a line of argument seems plausible, but it has to be balanced against factors such as the potential imminent invasion threat to polar benthic communities in the present day caused by anthropogenic warming (Aronson et al., 2007; Vermeij & Roopnarine, 2008).

However, the link between the seasonality of primary productivity and taxonomic richness is enhanced further by the nature of both the Early Cenozoic and modern bivalve faunas, with their marked lack of many common suspension-feeding groups. Certain representatives of those groups that are present in the Antarctic Late Maastrichtian–Middle Eocene fossil record have been used in a series of investigations into growth patterns preserved in their shell structure, and these have yielded strong indications of very slow growth rates (Buick & Ivany, 2004; Ivany et al., 2008; Moss et al., 2017). Using von Bertalanffy's k value as a proxy for growth rates, it has been shown that specimens of both *Lahillia* (Cardiidae) and *Retrotapes* (Veneridae) typically exhibit extremely narrow growth rings and life spans in excess of 100 years (Buick & Ivany, 2004; Moss et al., 2017). A parallel study based on modern bivalves also indicates slow growth and long life spans in the

high-latitude and polar regions, and this contrasts with faster growth rates (i.e., higher k values) and shorter life spans (typically <20 years) in the tropics (Moss et al., 2016). A strong tropical–polar contrast in bivalve growth rates exists in the present day, and this can be traced back into the Early Cenozoic fossil record.

Given that these very slow growth rates are characteristic of both the present day and a sustained period of Late Mesozoic–Early Cenozoic global warmth, Moss et al. (2017) argued that the primary reason for narrow growth increments was the seasonality of primary production rather than low temperature per se. Many major bivalve groups are obligate suspension feeders and depend upon a regular supply of phytoplankton and other suspended particles; any interruption to this supply might seriously impede their development over both ecological and evolutionary time-scales. And the latter is particularly so in the case of both the Imparidentia and Pteriomorphia clades, which might never have been able to colonize either polar region in anything other than token numbers (Beu, 2009; Nicol, 1966, 1967, 1970; Valentine & Jablonski, 2015). In marked contrast, the relatively small, essentially deposit-feeding Protobranchia clade is prominent at both poles and does not show an obvious tropical–polar diversity contrast in the present day (Crame, 2000; Roy et al., 2000).

Although the precise mechanism linking a pulsed food supply with speciation rate is unknown, this line of reasoning shifts the emphasis in latitudinal diversity comparisons from tropical enhancement to one of polar damping (Blackburn & Gaston, 1996; Roy et al., 1998). The seasonality of primary production in the polar regions is a relatively time-invariant process that would have operated irrespective of prevailing global climates.

But this is not necessarily to say that temperature is unimportant in the formation of large-scale latitudinal diversity contrasts. Many contemporary patterns are clearly accompanied by latitudinal temperature gradients, and it might seem only logical to link the two together (Gagné et al., 2020; Saeedi et al., 2019; Worm & Tittensor, 2018). Nevertheless, a persistent problem with simple temperature/palaeotemperature explanations of large-scale biodiversity patterns lies in determining the precise mechanism that links the two together (Clarke & Gaston, 2006; Erwin, 2009; Mittelbach et al., 2007). Wide support has been given to some form of metabolic theory of biodiversity, whereby the elevated temperatures of the tropics accelerate biochemical kinetics, which in turn promote faster rates of molecular evolution (Boag et al., 2021; Brown, 2014). Such a link would seem to be entirely plausible, but the precise links between metabolic rates and DNA evolution, and in turn speciation, remain unclear (Clarke, 2017; Clarke & Gaston, 2006). Some strong latitudinal temperature gradients in the present day are linked to more or less uniform diversity patterns, whereas there is a latitudinal diversity contrast in the deep sea (where there is virtually no temperature gradient), and many modern endotherms show strong latitudinal diversity contrasts (Clarke, 2017, and references therein). It might be that the metabolic theory of ecology is enhanced in some way in the tropics by more intense biotic interactions (Brown, 2014), but it has yet to be shown that they have facilitated a higher net rate of speciation (Mittelbach et al., 2007).

Latitudinal range shifts are undoubtedly driven by climate change, and they could well have significantly enhanced high–low latitude diversity contrasts through time (Condamine et al., 2012; Huang et al., 2014; Jablonski et al., 2006). This is especially so with the onset of global cooling at the Eocene–Oligocene transition (EOT) and the development of TNC (Fine & Ree, 2006; Hawkins et al., 2006, 2007; Ricklefs & Schluter, 1993; Wiens & Donoghue, 2004). This was the most important climatic transition of the entire Cenozoic (Westerhold et al., 2020) and almost certainly resulted in the retreat of a series of basal terrestrial clades from northern high latitudes towards the equator (Condamine et al., 2012; Hawkins et al., 2006, 2007). Whether this phenomenon occurred on the same scale in the marine realm has yet to be established.

In reality, the types of high–low latitude biotic contrasts established in the present study over a substantial period of time are unlikely to be the product of a single environmental factor. Very probably, the long-term interaction of primary productivity, seasonality and temperature change lie at the heart of their generation and maintenance (Huffeldt, 2020; Boag et al., 2021; Saulsbury et al., 2019; Valentine & Jablonski, 2015).

4.1 | Conclusions

1. The fossil record indicates that the K/Pg mass extinction event was followed by a 25 Myr period of global diversification in the benthic marine realm and the differentiation of distinct tropical and polar faunas.
2. Examination of four major molluscan clades indicates very few shared taxa below the family level between tropical and polar regions; species-rich families are conspicuously absent from the Early Cenozoic polar faunas.
3. It is likely that this tropical–polar asymmetry extends further back in time into the late Mesozoic era, and this is especially so for marine bivalves.
4. Extension of a definitive tropical–polar split in benthic marine faunas further back in deep time indicates that the underlying causes were undoubtedly complex. There might be no simple link to any single cause, such as global temperature change, and we should focus instead on looking at multiple, interrelated causes.
5. The marked absence of many suspension-feeding bivalve groups in the Early Cenozoic of Antarctica and the demonstrably slow growth rates of some of those taxa that are present add weight to the argument that the seasonality of primary productivity had a strong influence on the evolution of polar marine faunas.
6. Slow-growing, generalist faunas of comparatively low taxonomic richness might always have characterized the polar marine realm.

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DATA AVAILABILITY STATEMENT

All taxonomic and stratigraphic data sources used in this study are contained in either the main text or the Supplementary Information. Data files containing the information on which Figures 1–6 are based are deposited in the UK Polar Data Centre: <https://doi.org/10.5285/2CFA78B1-B7A1-411D-89E5-90490482BE79>.

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SUPPORTING INFORMATION

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