Late Cenozoic evolution of the latitudinal diversity gradient

J. Alistair Crame

British Antarctic Survey, Cambridge, UK

Correspondence
J. Alistair Crame, British Antarctic Survey, Cambridge, UK.
Email: jacr@bas.ac.uk

Abstract

Aim: The Late Cenozoic flourishing of polar marine ecosystems, just when temperatures were reaching their lowest levels, has always seemed anomalous. Such an observation is coupled with an increasing volume of molecular phylogenetic evidence to indicate that some polar taxa radiated at exceptionally high evolutionary rates. The canonical latitudinal diversity gradient (LDG) may not be underpinned by a parallel gradient in evolutionary rates. This study provides a review of this critical question.

Location: A variety of polar – tropical comparisons are made, with some emphasis on the Southern Ocean.

Taxa: Both marine and terrestrial taxa are used, with some emphasis on marine Mollusca.

Methods: High – low latitude comparisons of evolutionary rates over the last 66 Myr are made using two approaches: rates derived from molecular phylogenies, and rates derived from the fossil record. For the former of these data are taken from various marine and terrestrial taxa, and for the latter use is made of the excellent fossil record of marine Mollusca.

Results: For approximately the first half of the Cenozoic era (i.e., 66 Ma onwards) there is strong palaeontological evidence to suggest that the global LDG developed in a conventional way, with higher rates of origination in the tropics than at the poles. However, there then appears to have been a marked change in the latter half of the Cenozoic when origination rates increased in the high-latitude and polar regions. The modern latitudinal diversity gradient may be a fossil feature that formed in the Early Cenozoic.

Main Conclusions: As the extra-tropical regions expanded through the Cenozoic they provided increasingly more ecological opportunities for a wide variety of marine and terrestrial taxa. Substantially lower temperatures in the polar regions were clearly not an obstacle to spectacular evolutionary radiations such as that based on the krill ecosystem.

KEYWORDS
Cenozoic evolutionary rates, ecological opportunity, evolutionary radiations, fossil record, latitudinal diversity gradients, molecular phylogenetics, polar–tropical comparisons, Southern Ocean

1 | INTRODUCTION

One of the most unusual features of the evolutionary history of the Southern Ocean is a significant burst of origination within the last 10–15 Myr, just when temperatures reached their lowest levels and there was a major expansion of both the East and West Antarctic ice sheets (Figure 1). Vertebrate taxa to proliferate at this time include both mysticete and odontocete whales, many seals, crown group penguins and notothenioid fish, while invertebrates include deep sea octopus, octocorals, various gastropods, isopods and amphipods (Crame, 2018, and references therein; Holt et al., 2020; Vianna et al., 2020; González-Wevar et al., 2022). Coupled with this phenomenon is the recent demonstration, in two separate taxonomic groups, fishes and ophiuroids, that rates of origination over approximately the same time interval were significantly higher in the Southern Ocean than in the tropics (O'Hara et al., 2019; Rabosky et al., 2018). And this is despite the fact that both these groups show regular gradients of decreasing taxonomic diversity with increasing latitude. In the past there has perhaps been a tendency to assume that taxonomic diversity in the Southern Ocean has steadily declined through the Cenozoic in parallel with temperature (Figure 1), but we are now beginning to appreciate that this may well be an oversimplification of a much more complicated process (Crame, 2020; Erwin, 2009; Jablonski et al., 2017). With recent developments in both molecular phylogenetics and the fossil record it may be possible to reappraise the evolutionary history of the Southern Ocean and thereby cast further light on the evolution of the global latitudinal diversity gradient (LDG).

2 | IS THERE A LATITUDINAL GRADIENT IN RATES OF ORIGINATION?

Using a time-calibrated phylogenetic tree of some 31,500 species of ray-finned fishes, Rabosky et al. (2018) demonstrated that the fastest speciation rates were consistently linked to the coldest oceans. The Antarctic notothenioids in particular show one of the fastest known speciation rates of any fish group over approximately the last 5 Myr (Near et al., 2012; Rabosky et al., 2018) and high rates can also be demonstrated in other groups such as Liparidae, Zoarcidae and Sebastes (rockfishes) over a 10–20 Myr timescale. Arctic taxa also show high speciation rates and overall it is estimated that cold-temperate and polar lineages are speciating approximately twice as fast as tropical ones (Rabosky et al., 2018). A very similar inverse relationship between speciation rates and latitude has also been demonstrated in benthic ophiuroids (brittlestars; Echinodermata) which show their highest species richness values in tropical southern latitudes (0–35°S) and then a steep decline into Antarctica (O'Hara et al., 2019). But this classical LDG is also accompanied by an inverse origination gradient where the highest values again occur in Antarctica, the coldest biome (O'Hara et al., 2019).

Further indications that there may in fact be no obvious latitudinal gradient in diversification rates have come from a number of molecular phylogenetic studies in the terrestrial realm. These include the observation that the age of sister species pairs of New World birds and mammals between tropical and temperate regions over the last 10 Myr actually declined with increasing latitude, the exact opposite of what might be expected if the tropics were acting as a locus of species production (Weir & Schluter, 2007). A subsequent global analysis of New World bird taxa in a Bayesian framework indicated no significant trend in mean diversification rate with latitude (Jetz et al., 2012), and this has been backed up by further analyses using essentially the same dataset by both Schluter and Pennell (2017) and Harvey et al. (2020). Very similar trends have also been detected in both mammals (Kennedy et al., 2014) and flowering plants (Igea & Tanentzap, 2020).

However, it should be emphasised that this lack of an obvious latitudinal gradient in diversification rates may be, in geological terms, a comparatively recent phenomenon. Speciation rates are estimated from essentially the tips of phylogenetic trees and may cover a time interval of no more than 10–20 Myr (i.e., stretching back to the Early Miocene) (Schluter & Pennell, 2017). Some deeper time phylogenetic studies have indicated higher tropical than temperate speciation rates (Rolland et al., 2014) and, using a variety of techniques to estimate the ratio of tropical to temperate speciation rates at various regional localities, Schluter (2016) was able to demonstrate a trend of very similar rates <20 Myr, but higher rates in the tropics >50 Myr. There is a clear implication that the latitudinal gradient in speciation and diversification rates decreased through the Cenozoic era, becoming much flatter towards the present day. The rationale here is that as the temperate and polar regions steadily expanded through the later Cenozoic they generated more ecological opportunities that in turn boosted speciation rates (Schluter, 2016; Weir & Price, 2011). There may in fact be two distinct, contrasting phases to the evolution of the modern LDG through the Cenozoic era.

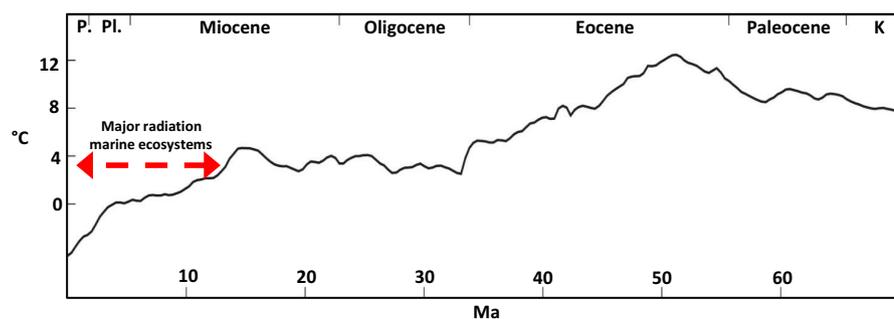
FIGURE 1 The Late Cenozoic evolutionary radiations in the Southern Ocean coincident with the onset of Middle Miocene global cooling. Palaeotemperature curve adapted from Crame (2018, figure 1). Key: K—Cretaceous; P.—Pleistocene; Pl.—Pliocene.

3 | EVOLUTIONARY RATES FROM THE EARLY CENOZOIC FOSSIL RECORD

The mass extinction event at the Cretaceous–Paleogene (K-Pg) boundary was followed by a global pulse of diversification that persisted for *c.* 25 Myr (Crame, 2020; Harvey et al., 2020; Raja & Kiessling, 2021). Although regional LDGs are not yet available for the Early Cenozoic, all the indications are that this pulse was much more intense in the tropics than at the poles; relatively steep LDGs almost certainly existed at this time (Crame, 2020). A recent study of four major benthic marine clades has emphasised that a very strong polar–tropical taxonomic diversity contrast at the present day can indeed be traced back into the Early Cenozoic (Crame & McGowan, 2022; Data S1). It has also been suggested that very high levels of tropical molluscan diversity through the Early Cenozoic are consistently based on a comparatively small number of species-rich families (Data S1).

4 | NO EVIDENCE OF A SIGNIFICANT CHANGE IN EVOLUTIONARY RATES AT THE GREENHOUSE–ICEHOUSE TRANSITION

Because of the incomplete nature of the fossil record it is impossible to accurately assess levels of biodiversity through the later Cenozoic in Antarctica. Globally, there is an extinction event at approximately the Eocene–Oligocene boundary (i.e., 34 Ma; Figure 1) that has traditionally been linked directly to a pronounced cooling event (Aronson, 2009; Westerhold et al., 2020). However, there is evidence to suggest that this extinction was stepped rather than instantaneous, and particularly focused in the tropics (Haasl & Hansen, 1996; Prothero, 1994). Although the Eocene–Oligocene boundary is not recorded onshore in Antarctica, a number of distinctive elements from the prolific Middle Eocene fauna, such as sharks, decapod crustaceans and many benthic molluscs, are clearly missing from the modern fauna and their loss could be interpreted as some form of mass extinction due to global cooling (Thatje et al., 2005). Nevertheless, there is just enough fossil record preserved in Antarctica to suggest that this is very probably not the case.

Eastman (2005) recorded some 29 separate taxa from the Antarctic Middle Eocene fish fauna and indicated that no more than two of these show close taxonomic affinities with any modern Southern Ocean forms. However, 21 of these 29 taxa are neoselachians (i.e., sharks, skates and rays) and certain odontaspidids (sand sharks), squatinids (angel sharks) and myliobatids (eagle rays) can be closely matched with warm temperate taxa from the modern Argentinean Province of central Argentina, Uruguay and southern Brazil (Cione et al., 2007). This in turn suggests that instead of becoming extinct when the climate cooled the Middle Eocene, neoselachian fish fauna was progressively displaced northwards along the eastern margins of South America (Cione et al., 2007).

A similar pattern can be detected in some of the infaunal bivalves missing from the modern Antarctic fauna. Veneridae today comprises one of the largest bivalve families globally, but is almost completely absent from Antarctica. It can, however, be detected in the Antarctic fossil record where the genus *Retrotapes* (subfamily Tapetinae) is particularly common in the Middle Eocene of Seymour Island (Beu, 2009; Crame et al., 2014; Stilwell & Zinsmeister, 1992). This genus can then be traced northwards along both the Pacific and Atlantic coasts of southern South America through the Late Eocene–Miocene, and into their respective modern faunas (Alvarez, 2019; Alvarez & del Rio, 2020; Beu, 2009). In this particular instance, *Retrotapes* also persisted in Antarctica until at least the Early Miocene (Beu & Taviani, 2014; Quaglio et al., 2008). A second infaunal bivalve genus, *Mulinia* (Mactridae), also appears to have spread northwards into modern southern South American waters from a Middle Eocene origin in Antarctica (Beu, 2009).

Strongly ribbed scallops of the genus *Austrochlamys* are particularly common in the Late Cenozoic fossil record of the northern Antarctic Peninsula region, but became extinct by the Late Pliocene (*c.* 2.5 Ma) (Berkman et al., 2004). However, one modern species, *Austrochlamys natans natans*, is present in southern Patagonia and it is likely that this genus too has been progressively displaced northwards through time (Jonkers, 2003). Contrary to widespread expectations, the islands of the Scotia Arc are permeable to benthic marine fauna through a number of channels and it is likely that significant faunal interchange between Antarctica and the Magellanic region still occurs at the present day (Brandt et al., 2007; Clarke et al., 2004; Dell, 1972).

Despite the incomplete nature of the later Cenozoic fossil record in Antarctica, there is no obvious evidence of excessive rates of faunal turnover linked to persistently high background extinction rates. It would seem more likely that benthic taxa responded to climate change through a pattern of northwards migration across the Scotia Arc into southern South America, in a manner similar to that recorded on other essentially north–south trending coastlines (Beu, 2004; Roy et al., 1995). In their comprehensive examination of global bivalve distribution patterns, Jablonski et al. (2006) could find little evidence of a variation in extinction rate with latitude; it may even be that polar rates are lower than those of temperate latitudes. Rates of origination, extinction and immigration into the polar regions may all have been comparatively low, giving an impression of relative stability through time (Fraser et al., 2012; Krug et al., 2009; Valentine et al., 2008).

5 | CONTINUITY IN TROPICAL DIVERSIFICATION THROUGHOUT THE CENOZOIC

There are some strong indications from the fossil record that the Early Cenozoic global pulse of tropical diversification continued throughout the era. This is particularly so in the benthic marine realm where major clades of both bivalves and gastropods have continued to diversify through to the present day (Close et al., 2020; Crame et al., 2018; Jablonski et al., 2003; Kantor

et al., 2021; Krug et al., 2009; Lemer et al., 2019; Stanley, 2007). In their review of global bivalve origination rates using backward survivorship curves derived from a series of modern regional faunas, Krug and Jablonski (2012) were able to show that Pliocene–Pleistocene origination rates were indistinguishable from those of the Early Cenozoic. There is also molecular phylogenetic evidence from the terrestrial tropics to show that at least one major passerine bird clade radiated continuously from c. 50 Ma onwards (Harvey et al., 2020; Jetz et al., 2012). Collectively, this evidence of continuous evolutionary radiations throughout the Cenozoic can be taken to indicate that tropical biotas have not reached any form of saturation. Any marked reduction of tropical diversification rates through the later Cenozoic could have served to inflate the relative importance of high-latitude and polar ones, but this does not appear to have been the case. Nevertheless, it should be emphasised that the topic of saturation and the imposition of ecological limits on regional biotas is a controversial one that is still not fully resolved (Harmon & Harrison, 2015; Marshall & Quental, 2016; Morlon, 2020; Rabosky, 2009). Jablonski et al. (2017) have suggested that, as other post-extinction rebounds have similarly reset diversification rates and achieved higher richness levels, and introduced species can often produce increases in regional diversity, saturation may not be a critical limiting factor.

Another important implication of the continuous pattern of diversification throughout the Cenozoic is that it casts further doubt as to the role of the tropics as a simple evolutionary museum (sensu Stebbins, 1974). While faster evolutionary rates could be attributed to the 'greater time and area' hypothesis in the Early Cenozoic (Fine & Ree, 2006; Jetz & Fine, 2012; Wiens & Donoghue, 2004), it is much less applicable after the onset of pronounced global cooling at c. 34 Ma and retraction in area of the tropics by as much as 40%–50% (Crame, 2020, and references therein). It is more likely that these high rates are linked to a Late Oligocene–Middle Miocene proliferation of coral reefs, particularly in the Indo-West Pacific region (Kiessling et al., 2010; Leprieur et al., 2016; Valentine et al., 2013; Williams & Duda Jr, 2008).

6 | THE EMERGENCE OF A TWO-PHASE LDG THROUGH THE CENOZOIC

A widespread view is that the onset of pronounced global cooling at the Eocene–Oligocene boundary (34 Ma) led to a steepening of the global LDG that has continued unabated to the present day. This was linked to a contraction in area of the tropics and inability of many taxa to deal with significantly lower temperatures at high latitudes (Archibald et al., 2010; Hawkins et al., 2007; Mannion et al., 2014). Nevertheless, the emerging evidence of a reverse latitudinal gradient in diversification rates in both the marine and terrestrial realms over at least the last 10–20 Myr now casts this theory into some doubt. Extensive polar radiations over this time span would work against the formation of the LDG rather than enhance it. This strongly suggests that at some time between c. 40 Ma and 20 Ma, the classical LDG, with more species in the tropics than

at the poles, and the processes that underpin this pattern, began to change. The locus of species origination began to expand from the tropics to the poles, but there has not yet been enough time for this to affect the form of the long-established LDG. The latter is now essentially a fossil feature of Early Cenozoic origin (Powell & Glazier, 2017; Schluter, 2016).

This leads directly to an alternative way of looking at the formation of these phenomena whereby speciation rates are seen not so much as a cause but a consequence of the latitudinal diversity gradient (Schluter, 2016; Schluter & Pennell, 2017; Weir & Price, 2011). As the latitudinal diversity gradient formed through the Cenozoic progressively more ecological opportunities became available in the expanding high latitudes, and these in turn boosted speciation rates. Schluter (2016) suggested that bursts of speciation in depauperate temperate environments are just like other episodes of rapid diversification in the history of life. However, something else is involved in this process besides an increase in the area of the high-latitude and polar regions. For example, a major radiation of diatoms in the Southern Ocean over approximately the last 15 Myr was very probably due to the conjunction of a mid-Miocene intensification of the Antarctic Circum-Polar Current and the introduction of silicon-rich North Atlantic Deep Water (Crame, 2018, and references therein). Diatoms are in turn a major food source for krill and other plankton and this undoubtedly led to the diversification of whales, penguins, seals and fishes from the late Middle Miocene onwards (Crame, 2018). In all probability, it also resulted in an intensification of pelago-benthic coupling, enabling enriched organic material to reach the seafloor.

7 | NO SIMPLE LINK BETWEEN TAXONOMIC DIVERSITY PATTERNS AND TEMPERATURE

If we work forward through time from the K-Pg boundary, then for approximately the next 25 Myr there is comprehensive evidence to suggest that a steep LDG was formed by a higher net rate of diversification in the tropics than at the poles (Crame, 2020; Crame & McGowan, 2022; Gillman & Wright, 2014; Jablonski et al., 2006; Martin et al., 2007; Mittelbach et al., 2007). And even though the precise mechanisms linking higher temperatures with higher rates of diversification are still uncertain, the link between the two has been a consistently strong one. This is what Worm and Tittensor (2018) have termed 'the evolutionary primacy of temperature', a 'time-invariant feature that underpins the ever-present latitudinal diversity gradient'.

Nevertheless, although temperature may be shown to be a first-order predictor of taxonomic diversity at various geographic scales in both the marine and terrestrial realms (Worm & Tittensor, 2018), it is far from certain that this relationship is directly causal (Clarke, 2017; Valentine et al., 2013). For example, there is a considerable volume of evidence to show that there is a steep LDG at the present day in the deep sea where there is a negligible latitudinal temperature gradient (Bouchet et al., 2009; Cairns, 2007; O'Hara et al., 2019; Rex & Etter, 2010). In their

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investigation of modern molluscan diversity gradients along four major north–south trending coastlines, Valentine et al. (2013) found a strong correlation between taxonomic diversity and sea surface temperature in each case, but the diversity values were far higher in the tropical West Pacific than the tropical East Pacific. Although latitudinal diversity patterns correlate with temperature at the present day, longitudinal ones do not. When examining the Cenozoic evolution of the LDG, it is difficult to evaluate roles played by present day variables and historical factors (Clarke, 2017; Crame, 2020; Erwin, 2009; Jablonski et al., 2017).

8 | A CLOSER LOOK AT THE NATURE OF TROPICAL HIGH DIVERSITY

One feature that is becoming steadily more apparent from both phylogenetic and palaeontological studies is the very uneven distribution of tropical species richness. In many taxa and regions, only a comparatively small number of component clades or families are hyper-diverse, and many others are just as species-poor as in the high-latitude and polar regions. The cause of the LDG might involve faster net rates of origination within just a small number of component clades (Rabosky, 2020; Rabosky et al., 2015). For example, global bird diversity at the present day reaches a peak in the New World tropics and is due in large part to the spectacular radiation of just two clades, the suboscine passerines and the tanagers (Harvey et al., 2020; Rabosky et al., 2015). In the same way, tropical freshwater fish diversity is underpinned by the very large otophysan clade (Rabosky, 2020), and the Amazonian peak in global snake diversity by the family Dipsadidae (Grazziotin et al., 2012); other vertebrate taxa almost certainly show very similar patterns (Alfaro et al., 2009). Within the marine realm, the fossil record of two of the largest benthic clades, Imparidentia (bivalves) and Neogastropoda, also shows consistent tropical patterns of dominance by just a small number of component families throughout the Cenozoic (Crame & McGowan, 2022; Data S1).

Speciation rates vary widely across tropical lineages and there is no simple or uniform rate for tropical taxa. If we are to understand the nature and origin of tropical high diversity hotspots, then we need to know why only a comparatively small number of taxa are hyper-diverse. One immediate possibility might be that biotic interactions are higher in the tropics than temperate and polar regions (Brown, 2014; Schemske et al., 2009), but it is still unclear whether these are a cause or a consequence of higher species diversity (Schluter, 2016). It may be that the expansion of these clades in the marine realm is simply a response to the later Cenozoic proliferation of tropical coral reefs (Leprieur et al., 2016).

9 | THE CRITICAL ROLE OF ECOLOGICAL OPPORTUNITY

The wave of recent time-calibrated molecular phylogenetic studies demonstrating high-latitude and polar origination rates equal to or

higher than those of the tropics has forced us to reconsider some of the fundamental principles governing the formation of LDGs. In particular, we may now have to consider that a significant change in the balance of global origination rates occurred around approximately the 30 Ma mark. It is not so much that tropical rates slowed at this time as extra-tropical ones accelerated as the temperate and polar regions expanded. This in turn led to greater ecological opportunities within the latter and consequently higher rates of origination (Schluter, 2016). One of the most spectacular examples of such a radiation in the polar regions is that of the notothenioid fishes whose rate of radiation exceeds that of contemporary coral reef taxa (Rabosky et al., 2018). However, there has simply been insufficient time for Late Cenozoic evolutionary radiations to radically alter a LDG with roots in the Early Cenozoic, or even earlier (Crame, 2020; Mannion et al., 2014; Powell, 2009).

10 | SYNOPSIS

1. A revised chronology for the Cenozoic evolution of the LDG is presented in Table 1. It should be emphasised that the various dates given in the table are provisional, but in essence they serve to divide the era into two approximately equal parts. In the first of these, the LDG develops in what may be described as the conventional way, with significantly higher origination rates in the tropics than at the poles. Then from *c.* 30 Ma onwards a subtle change occurs with the latitudinal gradient in origination rates becoming much shallower or even reversed. If this interpretation is correct, then the modern LDG is fundamentally a fossil feature that formed in the Early Cenozoic.

TABLE 1 An outline chronology for the Cenozoic evolution of the latitudinal diversity gradient.

1. **66 Ma**: The K-Pg mass extinction event 'levels the playing field' and paves the way for a radical expansion of the modern biota.

2. **66 to *c.* 41 Ma**: For at least 25 Myr, this expansion occurs at a significantly higher rate in the tropics than at the poles; this forms the basis of the steep LDG seen at the present day.

3. **34 Ma**: The greenhouse–icehouse transition at the Eocene–Oligocene boundary was not accompanied by a mass extinction in the polar regions; as elsewhere in the world, climate change was accommodated by serial range expansions and contractions. There is no evidence that polar marine faunas were subject to exceptionally high turnover rates at this or any other interval in the Cenozoic.

4. ***c.* 30 Ma to present**: Instead of evolutionary rates determining the LDG, it might be the other way round. After 30+ Myr of a well-established LDG, significant ecological opportunities began to appear in the extra-tropical regions; this is particularly so after the onset of global cooling at 34 Ma. These led to a significant increase in origination rates in a wide range of taxa, but there has simply been insufficient evolutionary time for these increases to affect the form of the well-established LDG.

5. ***c.* 15 Ma to present**: This process may have been particularly intense in the marine realm in the polar regions.

2. Evidence from molecular phylogenetics indicates that as the extra-tropical regions expanded through the Cenozoic, they provided increasingly more ecological opportunities for a wide variety of taxa. Significantly lower temperatures in the high-latitude and polar regions were clearly not an obstacle to substantial evolutionary radiations, and these findings corroborate earlier studies which suggested that there was no simple relationship between latitudinal temperature and diversity gradients.

3. High–low latitude diversity comparisons to date indicate that tropical high diversity is very much concentrated in a small number of hyper-diverse clades. How and when these taxa formed may hold important clues as to the generation and maintenance of LDGs.

CONFLICT OF INTEREST STATEMENT
There are no conflicts of interest to report.

DATA AVAILABILITY STATEMENT
No quantitative data are used in this study.

ORCID
J. Alistair Crame https://orcid.org/0000-0002-5027-9965

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AUTHOR BIOGRAPHY

J. Alistair Crame is a geologist/palaeontologist at the Natural Environment Research Council (NERC) British Antarctic Survey with a long-standing research interest in the evolutionary history of the polar regions.

SUPPORTING INFORMATION

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