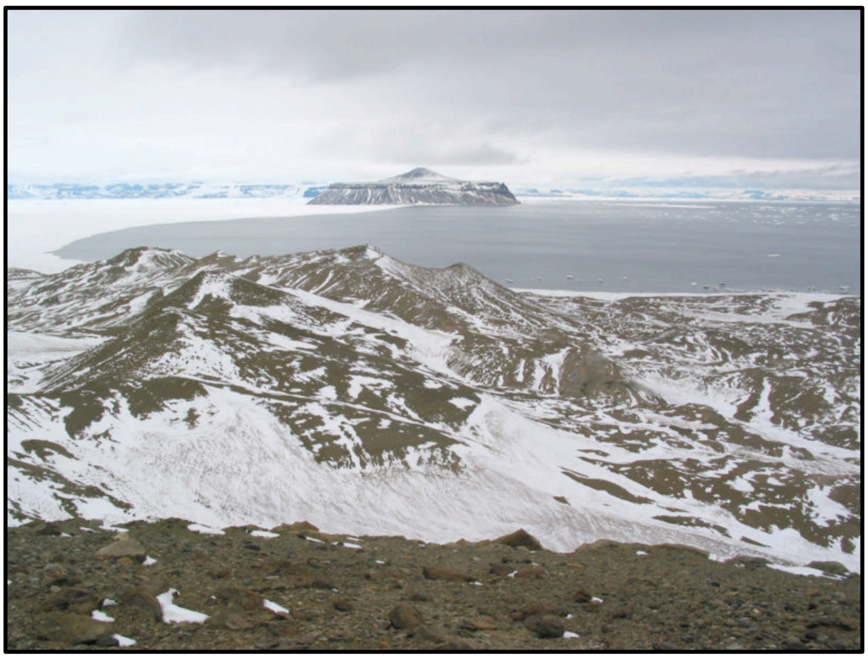
The invertebrate fossils of Seymour Island, Antarctic Peninsula, and their role in our understanding of the Eocene climate



Andrew Collins

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Kurtis Burmeister
National Science Foundation

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Abstract

The Eocene was an epoch of dramatic change in global climate, environment, and ecology. All of these changes are reflected in the fossil record of the La Meseta Formation on Seymour Island on the Antarctic Peninsula. Benthic extinctions and temporary protist excursion taxa indicate a period of climatic turbulence around the beginning of the Eocene, ~55.5 Ma. This thermal maximum negatively affected many groups of organisms but was followed by a diversification—especially of echinoderms, mollusks, bryozoans, and brachiopods—as temperatures cooled from the maximum to a stable, tropical, gradually warming level. The biota of Seymour Island was disturbed by two more major climatic extremes, the latter of which occurred ~48.5 Ma and coincided a major shift, represented by changes in preservation of bryozoans and other organisms, from a warming climate to a cooling climate, possibly due to (at least in part) an *Azolla* bloom in the opposite hemisphere. The cooling toward the end of the Eocene is reflected subtly in the La Meseta Formation, but it is no less evident. It is indicated by the lack of predators (exemplified by very little sublethal damage in crinoids and ophiuroids), lack of continued bivalve genetic transfer between the Antarctic and Australasia regions, and migration of numerous species of multiple phyla to lower-latitude habitats. All of these factors point to a shift and reorganization in community structures through the Eocene and into the Oligocene due to changes in habitability in the Antarctic region that are most likely the result of a cooling climate.

INTRODUCTION

The Eocene epoch was a very active one in geologic history. Broadly speaking, temperatures of the planet as a whole had been increasing since the Paleocene, hitting a maximum in the early Eocene (Zachos et al., 2001). These climatic conditions were exacerbated by sporadic, relatively brief (less than 200,000 years) spikes in temperature due to massive carbon increases in the atmosphere and oceans. Of particular note are the Paleocene-Eocene Thermal Maximum, which coincided with substantial development and diversification of mammalian groups and contemporaneous extinction of a number of benthic marine species (Weijers et al., 2007); the Eocene Thermal Maximum 2; and the Middle Eocene Climatic Optimum, which correlates directly with the formation of the Himalayan mountains (Zachos et al., 2001). However, the Eocene-Oligocene boundary marked the dramatic shift in climatic tendency toward the cooling that would eventually take us into the Pleistocene (Lear et al., 2008).

Scientists argue about the specific causes of these major events in Earth's history, but one thing is very much certain: these shifts and modifications within the Earth system resulted in a constantly changing and tremendously variable biosphere. Though the temperature gradient between the poles and the equator was much more gradual than it is now, temperature was still most variable toward the extreme ends of the planet, and so that is where the flora and fauna most representative of climatic variability during the Eocene can be found. The Antarctic Peninsula is one of the few places at the southern end of the planet that is ice-free enough for significant study to take place, and it has proven to be an excellent source of information for this turbulent epoch.

GENERAL LOCATION AND GEOLOGIC SETTING

Unfortunately (sort of), the end of the Eocene marks the time at which Antarctica began to glaciate (Zachos et al., 2001). Obviously it continued to do so and thus most of the fossil material that might allow us to most effectively examine this significant epoch is buried beneath quite a lot of ice. However, Seymour Island, located near the tip of the Antarctic Peninsula, east of the Ross Sea, and just west of the peninsula itself (see Figure 1), offers a reprieve for paleontologists from this conundrum. The island's climate ranges from close to freezing in the summer to far below freezing in the winter, but is dry enough that its rock formations (of which there are four) remain uncovered and accessible most of the time.

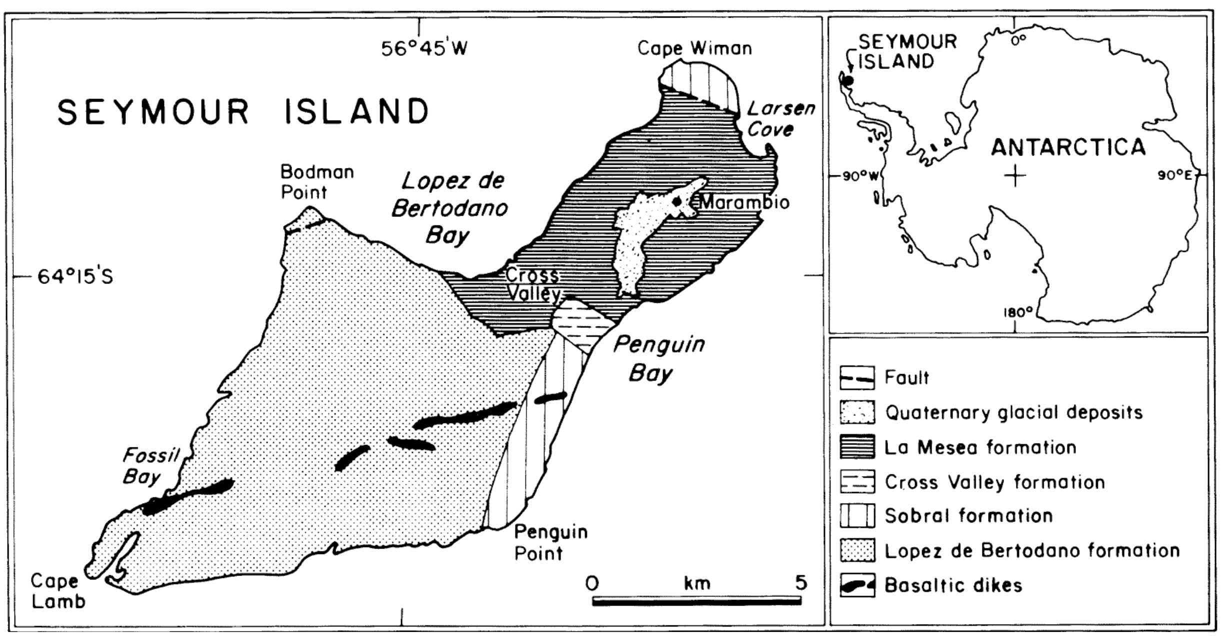

Figure 1. Location map and geologic map of Seymour Island, Antarctica (Zinsmeister, 1984, Fig. 1).

Spatially, the four formations on Seymour Island are arranged as shown in Figure 1, having been formed roughly *in situ*, as Antarctica was in roughly the same position in the Late Cretaceous and Paleogene as it is now. The formations range in time from the Late Cretaceous to the Eocene. The oldest, the López de Bertodano formation, consists mainly of Late Cretaceous fossils (including dinosaurs) and some early Paleocene specimens. The Sobral and Cross Valley formations both represent the Paleocene with their fossil record, with the Sobral Formation especially known for its wealth of fossils showing the development of life after the extinction of the non-avian dinosaurs. The La Meseta Formation is the youngest, containing a well-preserved and representative record of the Eocene epoch in the Antarctic region.

The La Meseta formation (Figure 2) is characterized by sandstone, reflective (because of the presence of marine organisms) of a shallow, near-shore environment. Studies on the La Meseta Formation on Seymour Island have revealed a number of invertebrate and vertebrate fossils in these sandstones that indicative a rich and diverse biota flourishing in the warm Eocene environment (see Figure 3). However, it is also evident in the fossil record that the members of this ecosystem were forced to adapt and shift due to major environmental changes near the end of the epoch. Because of these fossils and other corresponding evidence (e.g. $\delta^{18}O$), scientists have proposed that oceanic currents cooled and the near-surface climate closer to the poles became less bearable for these organisms, many of which had a relatively low tolerance for variation in temperature (stenothermal) and/or other related factors.

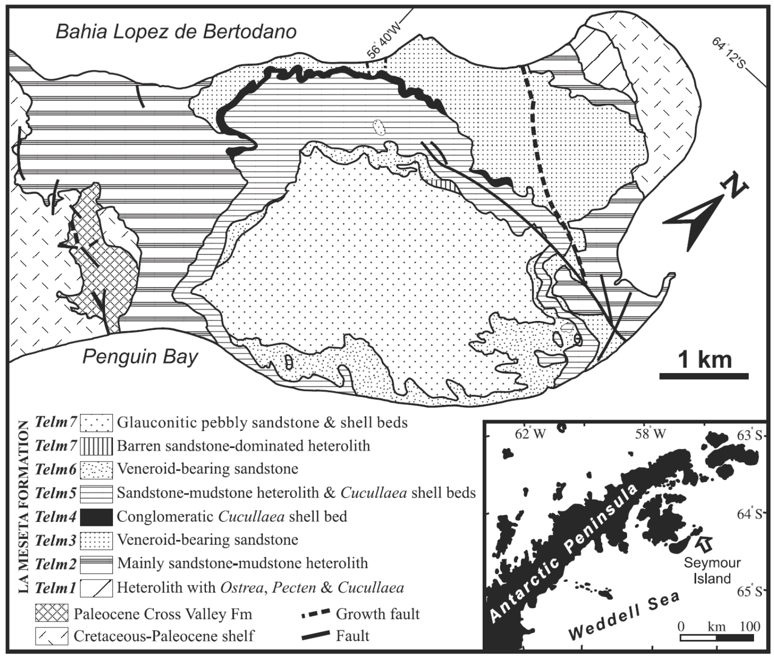

Figure 2. Location of Seymour Island (inset) and geologic map of northeastern part of island (modified from Sadler, 1988; Porebski, 2000, Fig. 1).

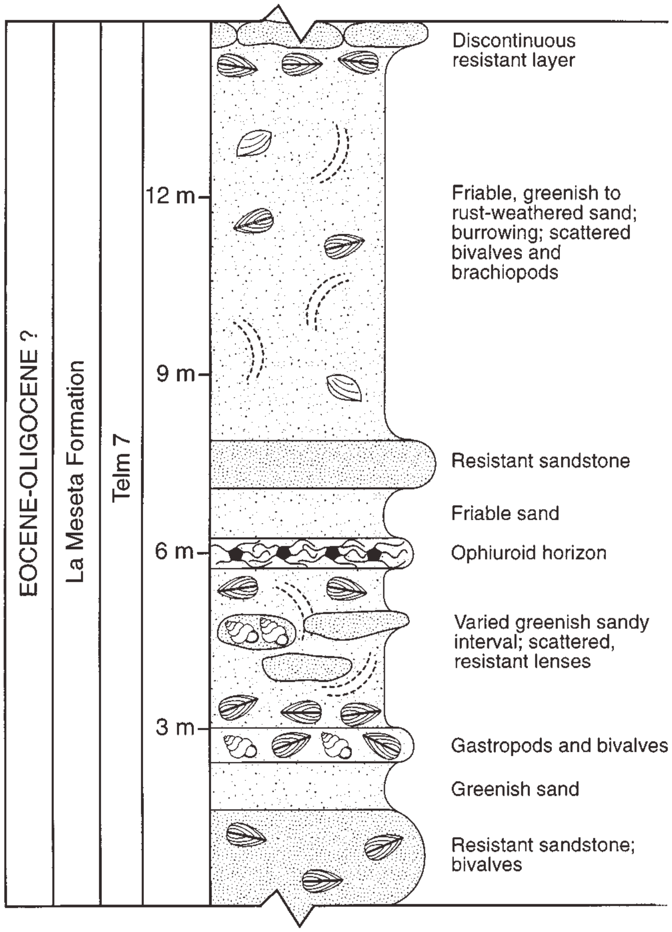

Figure 3. Sample column showing stratigraphic occurrence of an ophiuroid horizon. This and the other ophiuroid assemblages were surrounded by sandy layers, including locally fossiliferous horizons. All were found within the uppermost unit of La Meseta Formation (Aronson et al., 1997, Fig. 2).

CLIMATIC AND ECOLOGICAL CONDITIONS IN THE CRETACEOUS AND PALEOCENE

To fully understand the implications of the Eocene fossil record on Seymour Island, it is first necessary to examine the elements of the biosphere left behind during the Paleocene, and even during the Cretaceous. The record from these times is substantial and diverse. At this point, Gondwanaland had almost completely ripped apart, and the planet and its oceans were continuing to warm. However, despite what were hypothesized to be relatively stagnant conditions (that is, consistently increasing temperatures, steadily occurring variation in groups of organisms), a mass extinction at the end of the Cretaceous stirred the genetic pool substantially. It is here that the fossil record of Antarctica and surrounding environs begins to prove its worth.

The infamous Cretaceous-Tertiary (or K/T) boundary, where the Cretaceous ends relatively abruptly and is superseded by the Tertiary, is an oft-studied and well-known event. Zinsmeister et al. (1989) studied the boundary on Seymour Island and encountered a problem: the boundary occurred over as much as 50 meters, and many extinction-bound taxa did not disappear stratigraphically until after new members appeared. The diversity of mollusks, for example, gradually decreased over the course of the interval, but over the same interval an influx of mollusk species was occurring, developing as (not after) other species were dying out. Ammonites also contribute to the puzzle, occurring at varying intervals above and below one evident extinction horizon defined by dinocysts (Olivero and Zinsmeister, 1989). This implies either that the substrate was reworked in the process of the transition (one possible explanation for the multitude of species discrepancies within the boundary), or simply that some ammonites survived into the Tertiary in the high southern latitudes. In general, though, the absence of a definitive extinction horizon carries heavy implications concerning climate and its relationship to the K/T boundary. Zinsmeister et al. (1989, p. 737) wrote:

> *The absence of an extinction horizon argues strongly against a sudden catastrophic event as the direct cause of the biotic turnover at the end of the Cretaceous in the high southern latitudes. At the very least, there is no evidence for an abrupt extinction event. The transitional nature of the biotic change leaves open the possibility that, perhaps, global climatic change or changes in chemistry of the oceans may have been the cause of the faunal turnover. Whether such a change resulted from an asteroid impact or from increased volcanism during this period of time remains to be determined.*

The end of the Cretaceous, wherever exactly it occurred, was followed directly by a wide diversification of a number of organisms, including marine invertebrates, and gastropods especially. Oleinik and Zinsmeister (1996) note specifically the diversification of the bucciniform gastropods, identifying the appearance of four new species, all of the correspondingly new genus *Seymourosphaera*, within the relatively short time frame observed. The authors point to the fact that no evidence of these organisms or their ancestors was found below the K/T boundary, indicating perhaps that they migrated from another continental mass shortly after the beginning of the Cretaceous. Harasewych et al. (2009) reference another group of gastropods, Pleurotomariids (Vetigastropoda). This group also has no ancestry in or around Antarctica, but found its way there and diversified to an impressive degree. The authors note, however, that their diversity does not match that of older, established continents like Africa, but more closely aligned with smaller, newer island regions such as Australia and New Zealand. The theories of both of these papers suggest a common cause for the isolation and diversification of these groups: the final break-up of Gondwanaland (Harasewych et al., 2009; Oleinik and Zinsmeister, 1996), and geographical and biological isolation of the Antarctic continent and surrounding minor land masses. These associated events contributed extensively to the continued development of invertebrate (and vertebrate) ecology in this region throughout the Paleocene and into the Eocene.

THE EARLY EOCENE: DIVERSIFICATION

At the Paleocene-Eocene boundary, the first of a small number of climatic events occurred that served as an indicator of geological and environmental change. The Paleocene-Eocene thermal maximum (PETM, ~55.5 Ma) was relatively brief, lasting only approximately

170 Ka, including warming time and recovery time (Wiejers et al., 2007). During this time, ocean temperatures (deep and surface) rose by as much as 5°C around equatorial latitudes and as much as 8°C at higher latitudes, leading to diminished latitudinal temperature gradients across the globe. In the invertebrate fossil record, this maximum was characterized by massive benthic extinctions (Kennett and Stott, 1991) as a result of lowered dissolved oxygen levels in deep water (Kelly et al., 1996). This was possibly due to a shift in currents so that the source area for deep water temporarily transitioned to low-altitude regions rather than high-altitude ones. This hypothesis is supported by evidence for a number of non-native, "excursion" taxa of foraminifera (that is, taxa that appear in the fossil record only over the interval of the PETM). Figure 4 shows some of these excursion taxa and a proposed sequence of evolution, which would rank among the fastest known in pelagic protista, of members of the genus *Morozovella*. Kelly et al. (1996) attribute these rapid changes to increased preservation of organic matter on the sea floor due to the decreased oxygen levels there, which would have resulted in significant carbon fluctuation and a need to adapt quickly.

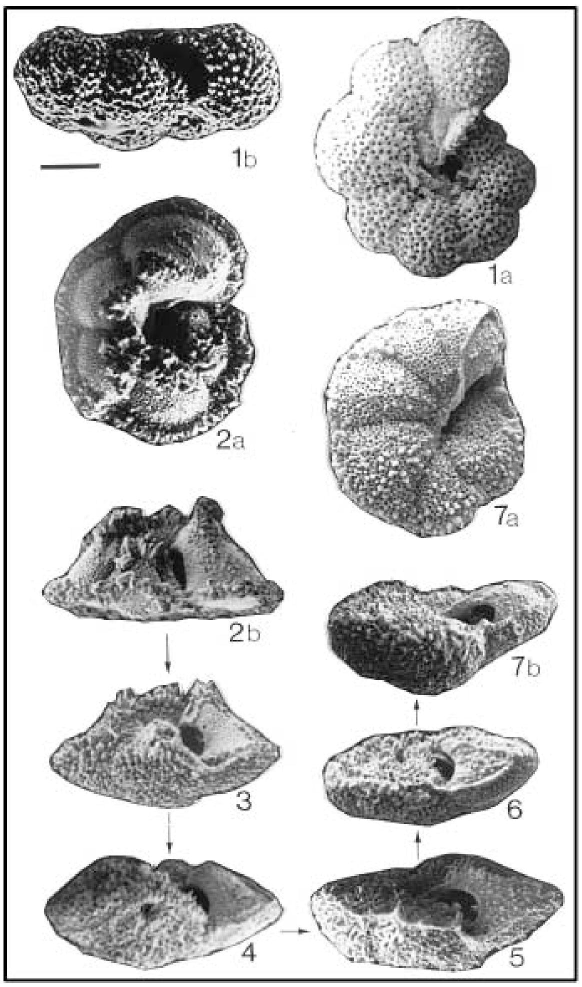

Figure 4. Scanning electron micrographs of excursion taxa *Acarinina sibaiyaensis* (1a, 1b), and proposed evolutionary sequence (2a-7b) from *Morozovella velascoensis* (2a, 2b) to *Morozovella allisonensis* (7a, 7b). Scale represents 100 μm (Kelly et al., 1996, Figure 2).

The end of this maximum marked the beginning of the Eocene, which was characterized in the high latitudes of the southern hemisphere by a relatively cool climate and an abundance of numerous invertebrates. Some of these invertebrates, such as some types of ammonites, survived the climatic maximum, while some groups (such as the gastropods) saw incumbent replacement of species through the course of the interval (which may have occurred more gradually than suddenly; Zinsmeister et al., 1989). Many other species appear for the first time after the boundary and are in existence even today. A number of echinoderm species were found by Blake and Aronson (1998) to be new in the La Meseta formation, including *Sclerasteriasz insmeisteri* (Asteriidae), *Paragonasterc larkae*, *Tesselasterc larki* (both Goniasteridae), and the new ophiuroid *Ophiurah endleri*. Additionally, both common and uncommon groups were found with varying degrees of abundance (Blake and Aronson, 1998).

The La Meseta formation also hosted a small number of crinoids groups, including a new species, *Notocrinus rasmusseni* (see Figure 5), which, as an isocrinoid (a group which is only found in deep water today), had a relatively unusual stalk-less lifestyle in these shallow waters (Meyer and Oji, 1993). Its existence in the shallow-water facies may be attributable, state Meyer and Oji (1993), to reduced (but not absent) predation and a favorable temperature regime *prior* to the beginning of the cooling period toward the close of the Eocene. Aronson et al. (1997) suggest that this anomalous pattern is, in fact, representative of community structures as a whole during the early Eocene. Low predation, low sediment resuspension, and a high flux of particulate

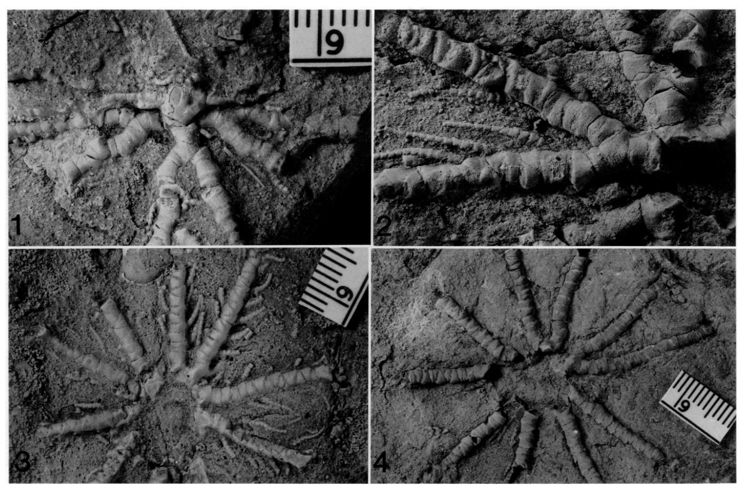

Figure 5. *Notocrinus rasmusseni*, aboral sides of 4 specimens with scale in mm, La Meseta Formation, Seymour Island, Antarctica (Meyer and Oji, 1993, Fig. 5).

organic matter invited or encouraged the "counterevolution" (Aronson et al., 1997, p. 905) of deeper-sea invertebrate suspension feeders toward shallower waters in the early part of the epoch, creating retrograde communities. These ecosystems may have been common in the southern hemisphere before the onset of cooling, but the most vibrant example of such a community appears to have been that in the vicinity of Seymour Island.

The Middle Eocene: Thermal Anomalies

As the Eocene progressed, it was subjected to more transient thermal maxima. Most of these were less intense than the PETM, characterized by smaller temperature increases and, in almost every case, only affecting populations and ecosystems locally rather than on a global scale. This lack of effect was evident especially in the early middle Eocene, when the climate was still in a warming stage and these temperature excursions were less of a departure from the norm. The second substantial event of the Eocene (after the PETM) occurred approximately 53.5 Ma. Known as the Eocene Thermal Maximum 2 (ETM2), this excursion was characterized by a rise in sea surface temperatures of 3-5°C and occurred as a result of a rapid increase in atmospheric CO_2 levels (Sluijs et al., 2009) that could have been associated with orbital infrequencies of the planet at that time.

At ~48.5 Ma a major shift in climatic trend occurred. It is not known definitely what triggered this event, which correlated roughly with the Early Eocene Climatic Optimum (EECO—also known as the Eocene Thermal Maximum 3, or ETM3; see Figure 4). However, it coincides with a very active bloom of the floating freshwater fern *Azolla* in the Arctic Ocean. Numerous researchers have suggested that at this time, *Azolla* began to reproduce rapidly in situ, creating large blooms that contributed locally to a very substantial CO_2 drawdown of up to 470 ppm from the atmosphere (which, at the time, contained 760-1910 ppm CO_2) as a result of burial of *Azolla*-derived organic material (e.g. Speelman et al., 2009).

Despite the reversal of climatic trends, warming events still periodically affected the Eocene climate. The last major event of the Eocene was the Middle Eocene Climatic Optimum (MECO) at ~41.5 Ma, which was suggested to be the result to increased volcanism and accelerated plate tectonic activity in the Indian Ocean and Himalayan regions (Bohaty and Zachos, 2003). During this optimum the temperature increased by up to 4°C. Bohaty and Zachos (2003) suggest that this represents one of the most rapid warming events in the Cenezoic (see Figure 6), and propose that it would have drastically affected ecosystems everywhere, especially communities on the Australian and Antarctic coasts. However, none of the isotope data used to identify this climatic event can yet be correlated directly with the fossil record.

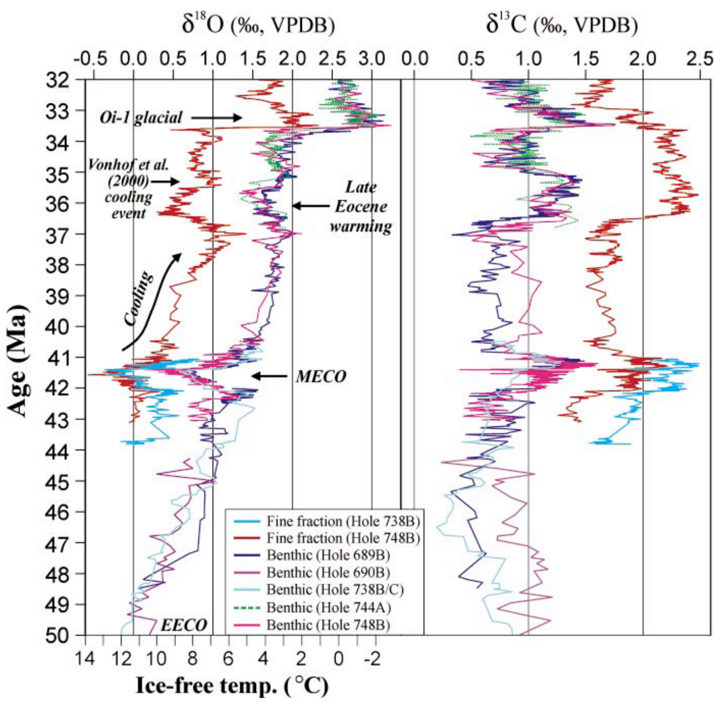

Figure 6. Compilation of Southern Ocean stable isotope data between 50 and 32 Ma. The MECO is identified at ~41.5 Ma, interpreted as an interval of significant transient warming. This event was followed by gradual increase in $\delta^{18}O$ values between ca. 41 and 37 Ma, representing significant cooling of both surface and deep waters. Also shown is the EECO at ~49 Ma (Bohaty and Zachos, 2003, Fig. 2).

The Late Eocene: Accelerated Cooling and Associated Adaptations

Despite these numerous excursions and the major trend reversal, a large number of taxa persisted in their evolutionary development and occupation of the communities around Seymour Island. Crinoids and ophiuroids, which flourished at the beginning of the Eocene, continued to do so later, and to an even higher degree (see Figure 7). Research by Aronson and Blake (2001) shows a very low level of sublethal damage to these organisms (i.e. any damage that would necessitate the regenerations of arms, etc.). In echinoderms, because predators aim for appendages first, this is indicative of a very low level of predation by bone-breaking predators such as fish or crustaceans. According to Aronson and Blake (2001), this is because the global cooling trend at the time both directly and indirectly reduced predation pressure. There are shark fossils in relative abundance in the lower (earlier) units of the La Meseta Formation. Isolated teleost bones and crabs can also be found throughout most of the formation. However, these fossils all but disappear by the Eocene-Oligocene boundary. Though it is clear that this decline is attributable in part to climatic change, it is unclear exactly how it relates, because predation of the sort that existed among these organisms still exists today in the Arctic. Nevertheless, this lack of predators benefited not only echinoderms, but other invertebrates as well, such as mollusks and bryozoans.

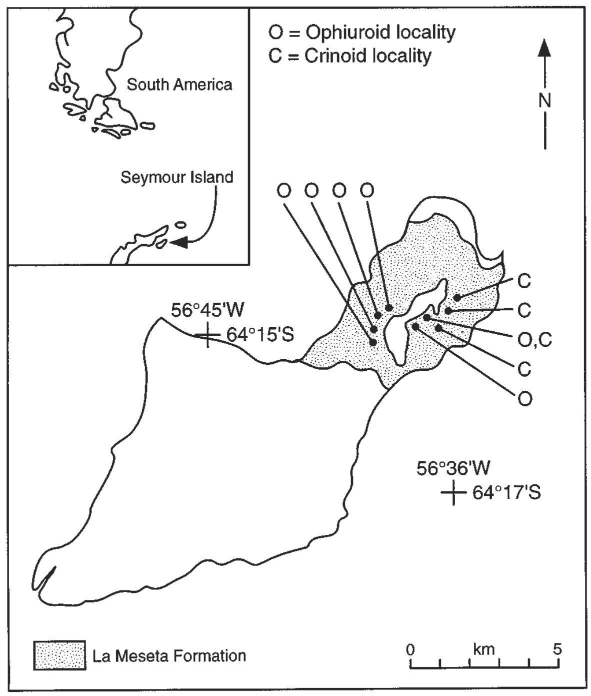

Figure 7. Map of Seymour Island, showing locations of six dense ophiuroid assemblages and four crinoids assemblages within the La Meseta Formation (Aronson et al., 1997, Fig. 1)

Mollusks, specifically bivalves, were only slightly less successful (according to the fossil record), with at least 3 new genera and 22 new species found in the La Meseta formation. These species (in addition to previously known varieties in the formation) provide a number of interesting insights into the Eocene conditions. Some of the known species represented had previously only been found in the Neogene and earlier. Some scientists (e.g. Zinsmeister, 1984) have suggested that their presence at high latitudes in the Paleogene and at low latitudes later indicates shifting of currents and displacement of cold-water facies to those areas closer to the equator. This would be further evidence of substantial cooling during the late Eocene and subsequent epochs. Some of the bivalves show clear species interchange with species in Australasia, but this interchange ceases by the late Eocene (Zinsmeister, 1984), indicating either that the distance between the continental areas became too great for the species to traverse or that the deep sea channels between the regions became too cold to cross.

Bryozoans managed to show a rather stunning resilience over the course of the Eocene. At least 30 genera and 43 species are represented in the La Meseta formation, of which 15 are cyclostomes and 28 are cheilostomes. In 2001, Hara identified nineteen of these species and three genera as new taxa, indicating a very quick start following the Cretaceous for this particular phylum. Bryozoa, especially this many, can be powerful indicators of climatic conditions in a given area. Hara (2001, p. 33) suggests: “the relationships between colony form, growth pattern, inferred associated biota and sedimentary structure point to a nearshore, shallow−marine−estuarine, and wave−dominated environment for the La Meseta Formation.” She ponders further, noting that there is a distinct separation between the upper and lower assemblages of bryozoans within the formation, represented by differences in preservation (poor in the upper section, good in the lower) which are indicative of climatic change during the

Eocene. These differences point, more specifically, to the boundary between warming and cooling in the middle Eocene (Hara, 2001).

All of these evidences of cooling are corroborated by stable oxygen isotope ratios in abundant foraminifera. Changes in deep-sea benthic $\delta^{18}O$ in the southern hemisphere are an excellent indicator of changing temperatures, and in the case of the values derived from very well-preserved foraminifera around New Zealand, suggest cooling near the Eocene-Oligocene boundary (Liu et al., 2009). Models and proxies show discrepancies here, however, with proxies more often depicting more drastic changes. Lear et al. (2008) propose that this is probably due to the sweeping analysis of proxies such as $\delta^{18}O$ (i.e. assuming they apply over a very broad regional area), whereas it may be the case that cooling occurred differentially over different continents and bodies of water, meaning that there may have been a $\delta^{18}O$ change of 0.5% around Antarctica (as models suggest) at the same time as another region recorded a change 1.5% (as proxies suggest). Regardless of specifics, however, it is nearly indisputable that cooling occurred in the Eocene beginning ~48.5 Ma and continued to the point where Antarctica began to glaciate. That event marked the beginning of a new epoch, the Oligocene. The trend has continued to the present day, though the current state of the climate is in question to some degree.

There are some lines of evidence that interrupt this hypothesis to a degree, such as the presence of warm-water brachiopod genera such as *Lingula* and *Bouchardia* in the upper part of the La Meseta formation (Bitner, 1996), but this can generally be explained by evolution to suit different environmental conditions—i.e. the brachiopods, which can be found in cooler environments at depth today, may have made the transition between warm/shallow and cool/deep habitats during this period of time when currents and climate were shifting.

Conclusion

The Eocene was an epoch of dramatic change in global climate, environment, and ecology. All of these changes are readily reflected in the fossil record of the La Meseta Formation on Seymour Island on the Antarctic Peninsula. Benthic extinctions and temporary protist excursion taxa indicate a period of climatic turbulence around the beginning of the Eocene. This thermal maximum negatively affected many groups of organisms but was followed by a diversification—especially of echinoderms, mollusks, bryozoans, and brachiopods—as temperatures cooled from the maximum to a stable, tropical level. The biota of Seymour Island was disturbed several more times but showed a major shift, represented by changes in preservation of bryozoans and other organisms, around 48.5 Ma from a warming climate to a cooling climate, possibly due to (at least in part) an *Azolla* bloom at the opposite hemisphere.

The cooling toward the end of the Eocene is reflected more subtly in the La Meseta Formation, but it is nonetheless evident. It is indicated by the lack of predators (exemplified by lack of sublethal damage in crinoids and ophiuroids), lack of continued bivalve genetic transfer between the Antarctic and Australasia regions, and migration of numerous species of multiple phyla to lower-latitude habitats. Of course, there is much more to discuss about the La Meseta Formation of Seymour Island, specifically in relation to the Eocene, the advent of the age of mammals, and the global climate; this, however, would involve delving further into the vertebrate fossil record, which is not within the scope of this paper. There is more than enough information present in the marine invertebrate fossil record on this island to piece together a cohesive climatic history of the Eocene, complete with its thermal anomalies, climatic trends, and biological intricacies.

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