Palaeontologia Electronica
http://palaeo-electronica.org

ENVIRONMENTAL CONTROL OF DIVERSITY, EVOLUTIONARY RATES AND TAXA LONGEVITIES IN ANTARCTIC NEOGENE RADIOLARIA

David B. Lazarus

David B. Lazarus. Museum für Naturkunde, Invalidenstrasse 43, 10115 Berlin.
david.lazarus@rz.hu-berlin.de

ABSTRACT

Antarctic Neogene deep sea sediments preserve excellent species-level records of faunal evolution that can be compared to equivalent records of environmental change from stable isotopes of carbon and oxygen, and to changes in the planktonic biota as recorded by carbonate/biosilica values in the sediment. A synthesis of paleoenvironmental data and radiolarian occurrence data from three authors analyses of ODP Legs 119 and 120 to the Kerguelen Plateau shows an inverse correlation between overall radiolarian diversity and the inferred productivity of the environment. Higher diversity, spumellarian (presumed partly symbiont bearing) faunas are seen in lower productivity, earlier Neogene carbonate phytoplankton rich sediment, but give way to lower diversity, presumably deeper dwelling, nassellarian dominated faunas (mostly without symbionts) in the later Neogene, in synchrony with the development of higher productivity in the late Neogene Southern Ocean. Major turnover events and increases in average extinction rates are associated with the mid-Miocene (ca. 15-13 Ma) and end-Miocene (ca. 7-4 Ma) increased glaciation and increased productivity shifts on or around Antarctica. Species longevities also decrease substantially during the Neogene, a phenomenon not previously reported for Cenozoic microfossils. In older sediments a bimodal distribution of taxon longevities is observed, although this latter phenomenon may be an artifact of the data analysis. Although environmental change appears to be the primary determinant of evolutionary change in these faunas, biologically mediated secondary effects caused by change in the physical environment (e.g., productivity and nutrient availability), are inferred to be the proximal causes driving evolution.

Submission: 7 January 2002 Acceptance: 7 May 2002
KEYWORDS: microfossils, extinctions, speciation, plankton, paleoceanography, Ocean Drilling Program

Lazaurus, David B. 2002. ENVIRONMENTAL CONTROL OF DIVERSITY, EVOLUTIONARY RATES AND TAXA LONGEVITIES IN ANTARCTIC NEOGENE RADIOLARIA. Palaeontologia Electronica 5(1):32pp, 1.9MB;
http://palaeo-electronica.org/paleo/2002_1/antarct/issue1_02.htm

INTRODUCTION

The factors driving evolutionary change in biotas are controversial. Both primarily internally driven and externally controlled evolutionary change have been proposed. At one end of the spectrum, the Red Queen model posits primarily internal, biologic interaction driven evolution (van Valen 1973; Stenseth and Maynard-Smith 1984), while at the other extreme, Stenseth and Maynard-Smith's (1984) stationary model, or Vrba's (1980, 1985) pulsed model posit that evolutionary change is dominantly driven by change in the external physical environment. Although numerous studies of biotic evolution have been published using macrofossil data, marine microfossil data offers, in principle, several advantages for this type of study, including relatively complete, species-level data sets, good chronology, and the widespread availability of independent, detailed paleoenvironmental information.

Marine micropaleontologists have only infrequently addressed this problem directly, being primarily concerned with research in biostratigraphy and paleoenvironmental reconstructions. Yet, at least in deep-sea plankton micropaleontology, these primary fields of inquiry suggest that both external and internal factors may be important. A close correlation between species distributions and external environmental factors has long been known and has been widely exploited by using fossil distributions as a proxy for past environmental parameters such as temperature (Imbrie and Kipp 1971; CLIMAP project members 1976; Kennett 1982). Yet in biostratigraphic work, it is generally assumed that species origins and extinctions occur more or less simultaneously throughout a broad geographic range (Bolli et al. 1985), despite the existence of environmental gradients in the oceans. Shifts in these gradients during the normal course of gradually changing global environments would cause critical absolute values of environmental thresholds to be crossed at noticeably different times in different locations. Biostratigraphic event isochroneity thus would seem to violate the basic assumption that a species' distribution, including the bounding value of zero abundance (local extinction), is closely controlled by specific combinations of external environmental parameters. Although detailed evaluation of biostratigraphic event isochroniety has shown this assumption sometimes to be wrong (Johnson and Nigrini 1985; Moore et al. 1993), there are also studies which have demonstrated that it is often correct (Hays and Shackleton 1976; Thierstein et al. 1977; Flores et al. 2000; Raffi, 2002).

Studies of macroevolutionary patterns in marine microfossil plankton do exist that have addressed the question of biotic vs abiotic controls on macroevolutionary change. Hoffman and Kitchell (1984) were among the first to examine macroevolutionary patterns with the explicit goal of testing biotic vs abiotic hypotheses. They studied several groups of Cenozoic marine plankton, but, due to the lack of comparisons to paleoenvironmental data, their results were inconclusive. Kitchell (1987) subsequently compared Hoffman and Kitchell's (1984) evolutionary patterns to the published literature of paleoceanographic change but was unable to detect significant correlations between evolution and environment. Most other work by contrast has demonstrated (or at least argued) for a strong link between environmental change and evolutionary change (e.g., Lipps 1970; Stehli et al. 1972; Hart 1980; Thunell 1981; Wei and Kennett 1983, 1986; Hallock 1987; Roth 1987; Stanley et al. 1988; Corfield and Shackleton 1988; Hallock et al. 1991; Pearson 1996). Several different environmental factors have been considered by these authors as possible pacesetters for evolutionary change, including changes in water temperature, global latitudinal gradients in the physical environment; water column stratification and productivity. In general, the results of these studies suggest that productivity and water column stratification play important roles in regulating rates of faunal change. Other more biologic or internal factors, such as the geographic extent of species, or the prior longevity of a species, by contrast, do not appear to play an important role. Nor has temperature been shown to be the most important direct factor. Differences in mean longevity and diversification history are, however, observed between individual clades within major taxonomic groups, suggesting that other, often poorly understood, biologic adaptations also play important roles.

The work done so far on macroevolutionary change in marine microplankton nonetheless still has some limitations. Most importantly, the vast majority of these studies are of one fossil group - the planktonic foraminifera - which, despite their enormous importance to paleoceanography and biostratigraphy research, are a relatively modest component of the modern plankton, measured either by taxonomic diversity (ca. 40 living morphospecies) or abundance in the plankton. Thus this group may not be fully representative of plankton organisms in general. Planktonic foraminifera are also primarily found in the 'warm water lid' of the ocean– (i.e., the low to mid latitude regions and only in the upper water column). This is significant, as within this environment many of the large environmental changes that have occurred elsewhere in the oceans over time have been muted. Most of the global temperature change signal in the Cenozoic, for example, has been concentrated in the higher latitude regions, as have the most dramatic changes in surface water-mass distribution and circulation, particularly the formation of the circumpolar Antarctic Current and the Southern Ocean in the Paleogene (Kennett 1982; Lazarus and Caulet 1994). The evolutionary effects of temperature and circulation change may be more apparent in faunas from these polar regions than in the lower latitude planktonic foraminifera studied so far. Thus, it is important to examine patterns of macroevolutionary change in other groups of organisms, particularly in regions outside the warm surface waters of the tropics to subtropics, to gain a more complete understanding of the relationship between environmental change and evolution. Understanding evolutionary processes in polar regions, particularly the Antarctic, is also of interest in itself, as these regions have played major roles in the evolution and maintenance of global biodiversity and global geographic biodiversity gradients, at least in Cenozoic times (Crame 1989; Crame and Clarke 1997).

Radiolarians are one group that can provide such data, as they are relatively diverse (globally, ca. 400 living morphospecies - Casey et al. 1979; Takahashi 1991) and have diverse polar faunas. Radiolarians also inhabit a broader range of water depths and occupy a broader range of ecological niches than do planktonic foraminifera (Casey et al. 1979; Casey 1993; Anderson 1980, 1993). Despite this potential, macroevolutionary studies of radiolarians are rare, and, to the author's knowledge, only two such studies have been published, both of low latitude Mesozoic faunas, that have directly examined the relationship between evolutionary change in radiolarians and environmental change. Erbacher et al. (1996) detected a close correlation between faunal turnover in late Cretaceous Tethyan radiolarian faunas and oceanic anoxic events. Danelian and Johnson (2001) compared patterns of faunal change in Tethyan Jurassic and early Cretaceous radiolarians to the general history of regional paleoceanographic change, and argued for an inverse relationship between oceanic productivity and faunal diversity.

Antarctic Neogene radiolarian faunas are employed in this investigation to explore these issues. These faunas are diverse and have been exposed to major changes in the environment due to long-term trends of cooling and glaciation of the Antarctic continent (Kennett 1982). The Neogene Antarctic radiolarian record is thought to closely reflect the original living diversity of the plankton. As is true for other regions of the ocean with good biosilica preservation, the great majority of living taxa in the Antarctic Ocean are also found in surface sediments, at least in regions not heavily influenced by glacial marine sedimentation (Lozano and Hays 1976; Nakaseko and Nishimura 1982; Abelmann 1992b). Furthermore, except for the earliest Miocene, Neogene dissolution has not been extensive enough to strongly affect preserved radiolarian diversity (Chen 1975; Lazarus 1990, 1992; Abelmann 1990, 1992a; Caulet 1991). Many Antarctic Neogene species are also endemic to the region, and, as is true for most Antarctic plankton, show little within-region geographic restriction (being instead distributed throughout the Southern Ocean, see Hays 1965; Lazarus and Caulet 1994). This is due to the circumpolar circulation system which, as in other plankton provinces, mixes biotas throughout the Antarctic water mass over decadal periods (Kennett 1979; McGowan 1986).

The fossil record of these faunas thus represents a relatively easily sampled, unusually complete history of the evolution of a distinct biota. Due to the availability of detailed records of regional environmental change, this fauna also provides useful test material for examining the role of environmental change in the evolution of faunas. Although our knowledge of these faunas' taxonomy and stratigraphic distribution are still incomplete, extensive study and recovery of new materials over the last decade by the Ocean Drilling Program (ODP) has provided a wealth of new material. This report presents the first quantitative, fauna-based macroevolutionary analysis of the Antarctic Neogene radiolarian record, or for that matter (so far as is known to this author), of any Cenozoic radiolarian fauna. This study is based on the range-chart data of three authors from ODP Legs 119 and 120 to the Kerguelen Plateau: Caulet (1991), Abelmann (1992a) and Lazarus (1992). The primary goal of this work is to document and interpret the correlations, if any, between known patterns of environmental change and evolution of the fauna.

A second, methodological goal is present as well. Many previous studies of macroevolution in the plankton cited above have relied on large compilations of literature data, and frequently on indirect representations of the primary observational data via major taxonomic syntheses (e.g., Kennett and Srinivasan 1983; Pearson 1993) as the base for analyses. Others (e.g., Corfield and Shackleton 1988) have carried out comprehensive surveys of faunas from selected sections as a base for analysis. Neither of these methods can yet be employed in radiolarian work. Major taxonomic/stratigraphic syntheses (at least below the family level) comparable to those for planktonic foraminifera are not yet available for radiolarians. Nor, given the highly incomplete species-level knowledge of fossil radiolarian diversity, is it possible to easily collect comprehensive faunal data from stratigraphic sections. These limitations must be overcome in order to use the data currently available: the original published marine micropaleontological biostratigraphic literature. Direct use of such primary range-chart data has been comparatively limited in macroevolutionary research, despite its richness (the Neptune database of selected DSDP/ODP range chart data for example currently has nearly 400,000 primary observational records in it for several thousand species of Cenozoic plankton (Lazarus 1994; http://www.unibas.ch/museum/nmb/21_FOR/MRC/NEPTUNE.htm). Given both the potential due to the vast extent of this primary data set and the difficulties that can occur in compiling such data, the secondary goal of this study is to explore methods that are appropriate for synthesizing this largely underutilized record of evolutionary change.

Prior Research

Current knowledge of radiolarian faunas in Antarctic Neogene sediments is derived from early taxonomic/stratigraphic studies (Hays 1965; Petrushevskaya 1967, 1975; Chen 1975) of piston and DSDP cores, and more extensive taxonomic, stratigraphic and distributional study from numerous ODP cores, which also generally have accurate geochronology based on both microfossils and paleomagnetic data (Gersonde et al. 1990; Barron et al. 1991; Harwood et al. 1992). However, this research has been done using the constraints imposed by the nature of Southern Ocean deep-sea drilling. The most important constraint has been that, when the drilling ship has been in the Antarctic, several legs have been run in quick succession, resulting in several researchers working on essentially the same radiolarian faunas simultaneously. In early DSDP work this frequently led to multiple, conflicting descriptions of the same species (e.g., Chen 1975; Petrushevskaya 1975, see also discussion in Lazarus 1990). Studies on the more recent ODP materials tended, by contrast, to be divided into individual studies of different, only slightly overlapping geologic time intervals. This reduced the degree of potential taxonomic confusion, given the largely non-overlapping ranges of time being examined, and also reduced the taxonomic scope of individual studies to more manageable levels. Essentially, each researcher compiled a checklist of taxa of interest for his or her geochronologic study interval. Advantageous as this has been for the taxonomic and stratigraphic goals of the original research, the largely non-overlapping time intervals of the published primary data creates a significant complication for later evolutionary analysis.

Despite the much improved knowledge of these faunas as the result of recent work, faunal lists are still very incomplete, with perhaps as many as half the preserved taxa not yet described or studied stratigraphically. This, in itself, is not necessarily a major limitation for study of faunal evolutionary patterns—most studies of macroevolutionary pattern, at least those based on multicellular taxa, are based on much less complete data than used here. What is important however, is that the taxa studied to date are a fair representation of the original total diversity. It is not believed that any major systematic bias exists in the choice of taxa studied so far, although the primary stratigraphic interest of research on these faunas may have somewhat biased the data collection in favor of short ranging taxa. Significantly, at least some taxa from each family-level group appear to have been included in published studies, with roughly similar numbers of taxa included from the two basic divisions of fossil radiolarians (Spumellaria and Nassellaria) as well. However, in the existing data, not all taxa have been studied in all stratigraphic intervals by all authors. In particular, each researcher selected a subset of the taxa available for his or her study, and these nonstandardized checklists are difficult to combine without creating a major compilation artifact: a species studied by one worker may not have been examined by another, despite its presence in the latter's material. This has the data compilation effect of artificially truncating the range of the taxon at the temporal boundary of the study intervals between the two workers. A second problem is the nonstandardization of species concepts. Researchers cooperated in creating standardized definitions for known or suspected stratigraphic indicator taxa, but for other taxa coordination was less rigorous, and the scope of taxon names (some still in open nomenclature) can differ significantly from one worker to the next. This can lead to substantially different reported stratigraphic occurrences for taxa, since many of the taxa studied are parts of anagenetically evolving phyletic lineages, and different morphologic boundaries between taxa divide the lineage into named taxa with different temporal ranges.

METHODS

To avoid these problems, data from each worker has been examined in this study as an independent data set. The estimates of evolutionary change (metrics) resulting from the analyses are compared to each other in intervals of overlap to check for consistency, and combined to create a composite record of evolutionary change over the entire Neogene.

Radiolarian stratigraphic occurrence data from each author, if available from more than one site, were combined to make composite range charts of taxa occurrences (Appendix 1 and Appendix 2). Data sources included the author's own files and ODP's online archives (http://www.ngdc.noaa.gov/mgg/mggd.html; http://www-odp.tamu.edu/download/index.htm). All samples were dated using age models developed by the Neptune project (Lazarus 1994) and MRC research center in Basel (http://www.unibas.ch/museum/nmb/21_FOR/MRC/NEPTUNE.htm) and are based on the published leg primary stratigraphic data sets (Barron et al. 1991; Harwood et al. 1992) and the Berggren et al. (1995) time scale. First and last occurrences of taxa were estimated for the most part using per taxon average stratigraphic gap size, which, in the absence of detailed information on preservation potential variation (Marshall 1990, 1994, 1997), appears to be a reasonable measure of potential age uncertainty for each event in sections with non-uniform discrete sampling.

The data was binned into 1 m.y. intervals for summary statistics. This binning interval was chosen as the maximum resolution that was compatible with the average age uncertainty in the placement of first and last occurrence events. With the 1 m.y. interval chosen, the event age uncertainty estimates largely fell within the bin intervals. Where they crossed a bin boundary the mid-point of the uncertainty interval was used. Diversity was estimated by range-through methods, and evolutionary change was represented by the metrics percent first occurrences, percent last occurrences and turnover (sum of the two former). Individual taxon longevities (with or without the inclusion of taxa whose ranges are truncated by the upper and lower limits of the sample sets) were also compiled for selected time intervals and higher taxonomic groups.

Paleoenvironmental data were compiled from several of the same sites used for radiolarian analysis, and samples ages were obtained using the identical age models for the sites. Stable isotopes of oxygen and carbon are from Leg 120 sites 747 and 751 (Mackensen et al. 1992; Wright and Miller 1992), while percent carbonate in the bulk sediment is from Site 751 (Mackensen et al. 1992). Neogene stable oxygen isotope data from these sites estimate both Southern Ocean near-surface water temperatures and ice sheet volume on Antarctica, while stable carbon isotope ratio data record both local and global changes in patterns of organic carbon storage, and thus indirectly indicate changes in ocean nutrient chemistry (Kennett 1982, Miller and Fairbanks 1985; Mackensen et al. 1992; Wright and Miller 1992). In the Antarctic Neogene, pelagic sediments such as those studied here consist of essentially only two major components - biogenic carbonate and biogenic opal (mostly diatoms). Although dissolution also affects the record, within the sites reported here changes in carbonate content primarily reflect changes in oceanic productivity - both absolute values and the nature of the dominant primary producers (Kennett and Barker 1990; Mackensen et al. 1992, Diester-Haass 1994; Diester-Haass and Zahn 1996; Diester-Haass et al. 2002).

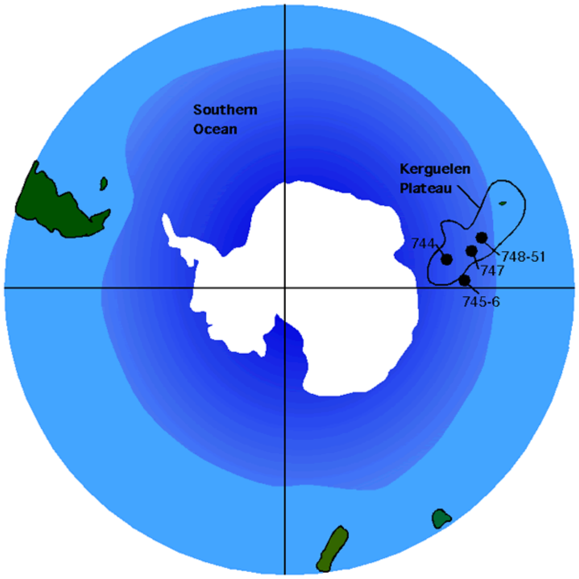


Figure 1. Location of ODP sites used in this study.

MATERIAL

A total of 168 named taxa from 6 sites (744, 745, 746, 747, 748, 751) from the Kerguelen Plateau were analyzed in the study (Figure 1).

Caulet (1991) provided a detailed record of faunal change (50 taxa, Figure 2A, Table 1) for the latest Miocene to late Pleistocene interval, based on 76 samples from Leg 119 Site 745. The mid Pliocene to Recent time interval is not well represented in most ODP sites recovered from the Southern Ocean and, in particular, was not studied

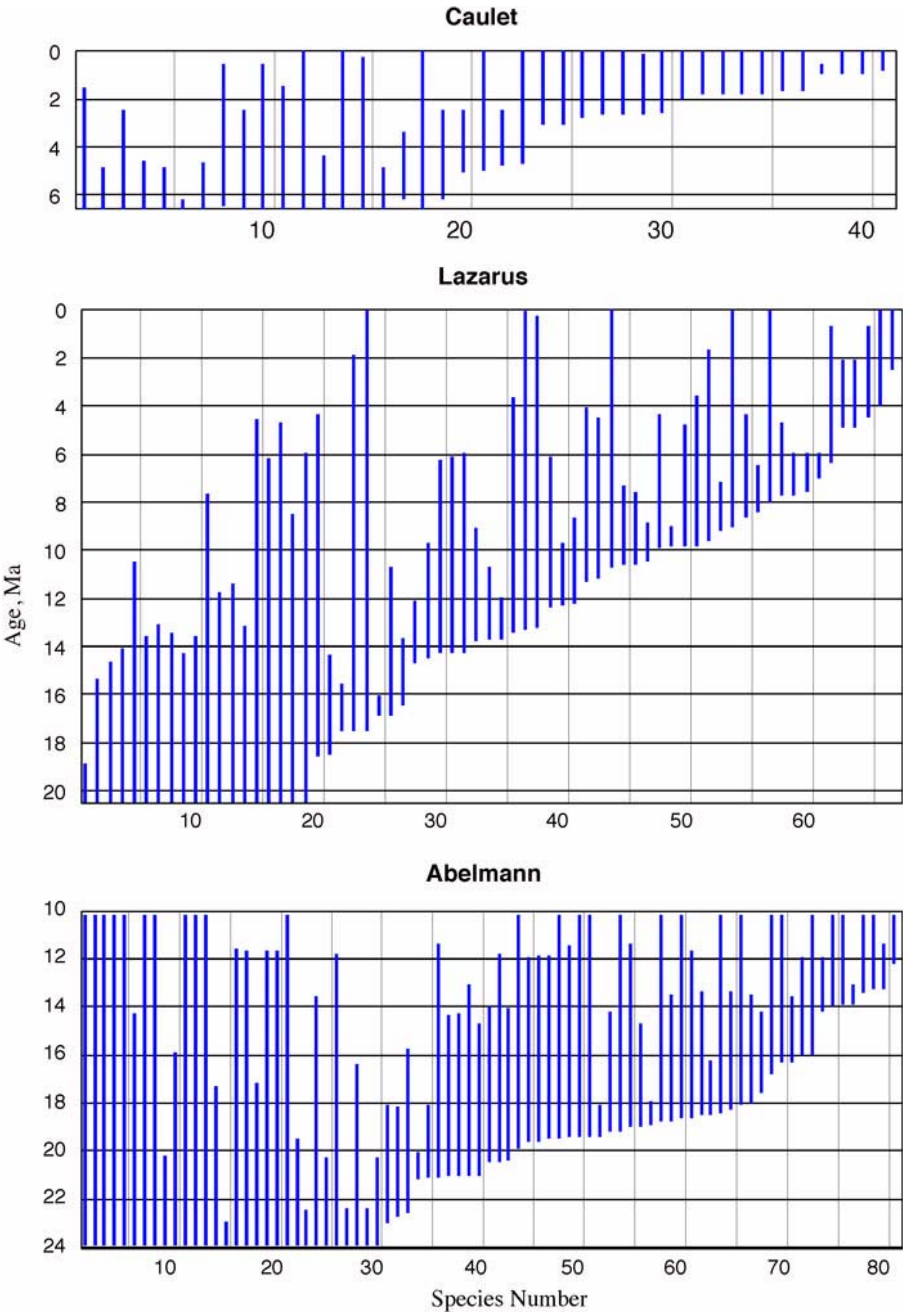


Figure 2. Stratigraphical distribution of taxa in the three studied data sets - Caulet (top), Lazarus (middle) and Abelmann (bottom). Vertical scale for age for all plots is the same, horizontal scale for taxa categories arbitrary. Names of species in each graph are given in the Figure 2 List (page 29).

in detail by either Lazarus (1992) or Abelmann (1992a). Although Caulet (1991) also provided less detailed data for the earlier Neogene as well, the bulk of his study is devoted to the very poorly known Southern Ocean faunas of Eocene age, that were well recovered by Leg 119 drilling. In this study, only the detailed Plio-Pleistocene data of Caulet are used, although its relative shortness (0-6 Ma, 6 m.y.) creates substantial problems in range truncation. Attempts to incorporate some of Caulet's results from older Neogene intervals were frustrated by the lack of well-resolved age models for these older sections.

Abelmann (1992a) studied radiolarian faunas from the middle and early Miocene interval of Leg 120 sediments, using 139 samples from three sites

Table 1. Stratigraphic-range information for species in the Caulet data set. Species marked with an asterisk had occurrences that are too rare or scattered to be used in this study. Dashes indicate a truncated first occurrence, bold values are FOs taken from the Lazarus data set. LOs with the value zero are taxa currently in existence. Longevities that are based on truncated values are given in italics.

Name	FO	LO	Range
Acanthodesmia viniculata	3	0	3
Actinomma popofskii	2.6	0	2.6
Antarctissa cylindrica	6.4	0.6	5.8
Antarctissa denticulata	2.6	0	2.6
Antarctissa robusta	-	2.5	
Antarctissa strelkovi	2.5	0	2.5
Anthocyrtella callopisma	-	0.6	
Botyropera triloba	4.6	0	4.6
Cycladophora bicornis	1.6	0	1.6
Cycladophora davisiana	2.7	0	2.7
Cycladophora pliocenica	9.6	1.6	8
Desmospyris rhodospyroides	20.5	4.9	15.6
Desmosypris spongiosa	5	2.5	2.5
Dictyophimus mawsoni	0.9	0.6	0.3
Eucyrtidium biconicum	-	2.5	
Eucyrtidium calvertense*			
Eucyrtidium cienkowski*			
Eucyrtidium inflatum	11.3	4.4	6.9
Eucyrtidium teuscheri orthoporus*			
Eucyrtidium teuscheri teuscheri	1.9	0	1.9
Gondwanaria dogieli	3	0	3
Haliometta miocenica*			
Helotholus praevema	-	4.6	
Lamprocyrtis heteroporos	6.1	2.5	3.6
Litharachnium tentorium	0.7	0	0.7
Lithelius nautiloides	1.7	0	1.7
Lychnocanium grande	9.9	4.9	5
Mitrocalpis araneafera	0.9	0	0.9

(747, 748 and 751). The total number of taxa reported (97, Figure 2B, Table 2) is relatively large, and the total time interval covered (ca. 24-10 Ma, or nearly 14 m.y.) is also substantial, but the data is complicated by the fact that many taxa were not examined in all three sites, leading to numerous range truncations, even within the composite range chart of this single author's results, due to the differing time intervals studied in each site. Preservation and abundance of radiolarians in this sample set are also relatively variable, and particularly in the earlier Miocene can be poor enough to affect observed diversity and taxon ranges.

The report of Lazarus (1992) on radiolarian faunas from both Legs 119 and 120 provides a relatively uniform data set from a large number of sites (744, 745, 746, 747, 748, 751) comprising in total 262 samples. A relatively fixed taxon checklist was used in this study which covers the entire Neogene interval, although the late Pliocene-Recent and early Miocene intervals were not as extensively examined as the early Pliocene to middle Miocene intervals. The number of taxa considered is moderately high (68 taxa were recorded, Figure 2C, Table 3), although noticably fewer taxa were recorded than in the study by Abelmann. Of the

Table 1 (continued)

Name	FO	LO	Range
Phormostichoartus pitomorphus*			
Phorticum clevei	4.9	0	4.9
Plectacantha sp.	0.9	0	0.9
Prunopyle antarctica	1.6	0	1.6
Prunopyle buspinigerum*			
Prunopyle frakesi	-	6.2	
Prunopyle tetrapila	-	1.5	
Prunopyle titan	6.1	3.4	2.7
Pseudocubus vema	4.7	2.5	2.2
Pterocanium trilobum	2.6	0.2	2.4
Pterocorys clausus*			
Rhizosphaera antarctica	-	0	
Saccospyris antarctica	1.7	0	1.7
Saccospyris conithorax	1.7	0	1.7
Saturnalis circularis	17.5	0	17.5
Spongotrochus glacialis	13.3	0	13.3
Stichocorys peregrina	9.8	4.7	5.1
Streblacantha circumtexta*			
Stylatractus universus	13.2	0.3	12.9
Theocorys redondoensis*			
Triceraspyris antarctica	1.7	0	1.7
Triceraspyris coronata	18.6	4.9	13.7

Notes: * -> not used as too rare, etc, bold - FAD taken from Laz data, italic - truncated range

three data sources used in this study, this one is also the least affected by truncation problems, due to the relatively long time interval covered (ca. 4-20 Ma, 16 m.y.) and consistency of data recording between sites.

RESULTS

Diversity

Diversity results for the three different data sources are shown in Figure 3 and summarized in Table 4. For Abelmann's data, two different curves are shown: a raw data curve (with higher diversity values) and a second, 'corrected' curve. This latter curve shows only data for taxa whose upper or lower ranges are not artificially truncated within the composite range chart by the lack of primary observational information in one or more sites. This correction was judged to be necessary as the observed diversity changes would otherwise be partially controlled by the arbitrary cutoff of ranges at the upper or lower boundaries of individual site sample sets used in Abelmann's study. This, of course, eliminates significant numbers of taxa from the author's data sets, but at least provides a method for recording and analyzing data that is consistent between different authors' data sets.

In all three authors' data sets, reported diversity declines near the beginning and end of their study intervals. Diversity, in both versions of Abelmann's curve and in Lazarus' data, increases gradually in the early Miocene and falls significantly near the early - middle Miocene boundary (ca., 15 Ma), although some of the drop in diversity at this time is due to the differences in overall diversity reported between the two authors. Diversity within Lazarus' data set rises from the middle Miocene into the late Miocene and falls significantly into the early Pliocene. Low diversity is also recorded in the early Pliocene by Caulet. Diversity recovers in the late Pliocene and Pleistocene within Caulet's data

Table 2. Stratigraphic-range information for species in the Abelmann data set. Data given separately for species whose ranges are complete, and for the full data set, including taxa with range truncations. Dashes in the former columns indicate truncated values. These are replaced with the ages of the base and top of the section studied by Abelmann in the latter columns. Some taxa could not be used due to scattered primary occurrence data, or because the taxon was a genus level grouping of several species – (see comments column in table).

Species	FO	LO	Range	FO w. truncs	LO w. truncs	Range w. truncs	Notes
Acrosphaera spp.	19.4	-		19.4	10.3	9.1	LO very uncertain. Genus level taxon.
Actinomma golownini	13.9	-		13.9	10.3	3.6	10.3 is truncated range - top of studied interval
Actinomma holtedahli	-	23.1		23.9	23.1	0.8	23.9 is truncated range - bottom of study interval
Actinomma medusa	-	20.3		23.9	20.3	3.6	range uncertain
Actinomma sp. A	18.5	16.4	2.1	18.5	16.4	2.1	
Actinomma sp. B	-	-		23.9	10.3	13.6	range has large gaps
Amphistylus angelinus	-	-		23.9	10.3	13.6	
Antarctissa deflandrei	14	-		14	10.3	3.7	
Antarctissa robusta	-	-		19.4	11.6	7.8	
Anthocyrtidium sp.	-	-		-	-		just 2 scattered occurrences - no range estimate possible
Artophormis gracilis	-	-		-	-		single trace occurrence
Calocyclas cf. **semipolita**	-	14.3		19.2	14.3	4.9	
Carpocanarium papillosum	-	-		23.9	10.3	13.6	
Cenosphaera sp. A	-	17.4		23.9	17.4	6.5	
Ceratocyrtis mashae	-	-		23.9	11.9	12	
Ceratocyrtis stigi	-	11.7		23.9	11.7	12.2	
Circodiscus ellipticus	20.5	-		20.5	11.9	8.6	
Collosphaerid sp. B	-	-		23.9	10.3	13.6	
Cornutella clathrata	13.3	11.5	1.8	13.3	11.5	1.8	
Cornutella profunda	-	-		-	-		3 scattered occurences only
Corythomelissa horrida	18.3	13.5	4.8	18.3	13.5	4.8	range has large gaps
Corythospyris fiscella	-	14.4		23.9	14.4	9.5	
Cycladophora antiqua	21.1	18.2	2.9	21.1	18.2	2.9	
Cycladophora conica	-	-		21.1	11.5	9.6	

Table 2 (continued).

Species	FO	LO	Range	FO w. truncs	LO w. truncs	Range w. truncs	Notes
Cycladophora golli golli	21	14.4	6.6	21	14.4	6.6	
Cycladophora golli regipileus	21	14.5	6.5	21	14.5	6.5	2 T values above LO interpreted as reworking
Cycladophora humerus	16	-		16	10.3	5.7	very gappy below 14.2 my
Cycladophora sp.	23	18.2	4.8	23	18.2	4.8	"FO could also be at base of section, truncated"
Cycladophora spongothorax	12.2	-		12.2	10.3	1.9	
Cyrtocapsella japonica	-	-		18.8	13.6	5.2	very gappy range
Cyclampterium milowi	-	-		-	-		single T occurrence
Cyrtocapsella cornuta	-	-		-	-		two T occurrences
Cyrtocapsella longithorax	20.4	14.2	6.2	20.4	14.2	6.2	
Cyrtocapsella robusta	-	22.6		23.9	22.6	1.3	
Cyrtocapsella tetrapera	21	13.2	7.8	21	13.2	7.8	1 T value above LO interpreted as reworking
Dendrospyris megalocephalis	14.2	12.1	2.1	14.2	12.1	2.1	
Dendrospyris rhodospyroides	18.8	-		18.8	10.3	8.5	
Dendrospyris stabilis	21	14.8	6.2	21	14.8	6.2	
Dictyophimus gracilipes	-	18.1		18.9	18.1	0.8	"base might be real, not truncated"
Didymocyrtis sp.	-	-		-	-		single rare occurrence
Disolenia spp.	-	-		-	-		"gappy range, genus taxon"
Druppatractus hastatus	19.6	12.1	7.5	19.6	12.1	7.5	
Eucyrtidium calvertense group	19.2	-		19.2	10.3	8.9	
Eucyrtidium cienkowskii group	-	[		23.9	10.3	13.6	
Eucyrtidium punctatum	17.6	14.3	3.3	17.6	14.3	3.3	
Eucyrtidium sp. A	16	12.1	3.9	16	12.1	3.9	
Eucyrtidium sp. B	-	-		-	-		just 2 scattered R occurrences
Gondwanaria deflandrei	-	-		23.9	10.3	13.6	
Gondwanaria japonica	-	-		23.9	10.3	13.6	range in upper part very gappy - could be only EMio species
Gondwanaria sp. A	19	14.8	4.2	19	14.8	4.2	

Table 2 (continued).

Species	FO	LO	Range	FO w. truncs	LO w. truncs	Range w. truncs	Notes
Heliodiscus ? sp. B	-	16		23.9	16	7.9	
Heliodiscus sp. A	18.5	13.5	5	18.5	13.5	5	
Hexacontium cf. **enthacanthum**	19.9	-		19.9	10.3	9.6	
Hexacontium spp.	-	-		-	-		good range but genus taxon
Hexastylus spp.	-	-		-	-		gappy range, genus taxon
Lamprocyclas sp.	-	20.4		23.9	20.4	3.5	"dup Lamprocyclas sp. in 748 removed, merged data in rc"
Lamprocyrtis ? cf. **hannai**	16.3	13.7	2.6	16.3	13.7	2.6	two entries in original rc - merged in this study
Lithocarpium polycantha	13.4	-		13.4	10.3	3.1	
Lithomelissa cf. **ehrenbergi**	20.5	14.1	6.4	20.5	14.1	6.4	
Lithomelissa robusta	-	22.5		23.9	22.5	1.4	
Lychnocanoma conica	-	20.4		23.9	20.4	3.5	
Lychnocanoma sp. B	16.8	-		16.8	10.3	6.5	
Lychnocanoma sp. C	-	-		-	-		single trace occurrence
Orosphaera sp. ?	-	-		-	-		4 concurrent occurrences but truncated base
Peripyramis circumtexta	-	-		19.4	10.3	9.1	almost entirely 751 occurrences given for cosmopol. species - fo may also be artifact.
Prunopyle hayesi	-	-		23.9	10.3	13.6	
Prunopyle sp. A	-	-		23.9	11.8	12.1	
Prunopyle sp. B	-	-		23.9	11.8	12.1	
Prunopyle sp. D	-	-		19.6	12	7.6	anomalously few occurrences in 747 data - fo may be truncated
Prunopyle tetrapila	18.6	-		18.6	11.8	6.8	
Prunopyle titan	-	-		23.9	11.8	12.1	
Pterocanium sp.	16.3	-		16.3	10.3	6	
Rhopalodictyum sp.	-	-		-	-		"just a few, disjunct occurrences"
Siphocampe sp.	-	15.9		22.6	15.9	6.7	
Saccospyris antarctica	-	-		18.6	10.3	8.3	"gappy range, only recorded in 751"

Table 2 (continued).

Species	FO	LO	Range	FO w. truncs	LO w. truncs	Range w. truncs	Notes
Siphocampe arachnea group	-	12		19.5	12	7.5	
Spongodiscus craticulatus	-	-		23.9	10.3	13.6	
Spongomelissa dilli	13.9	13.2	0.7	13.9	13.2	0.7	
Spongotrochus glacialis	-	-		-	-		range too scattered
Spongopyle osculosa	-	-		23.9	10.3	13.6	middle half of range mostly blank
Spongotrochus sp.	-	-		23.9	17.3	6.6	only recorded in 748
Stauroxiphos communis	19	11.5	7.5	19	11.5	7.5	
Stichophormis sp.	18	13.6	4.4	18	13.6	4.4	upper range too scattered to give accurate LO
Stylatractus santaeannae	-	18.3		22.7	18.3	4.4	
Stylodictya validispina	13.3	-		13.3	10.3	3	
Stylatractus neptunus	19.5	-		19.5	10.3	9.2	
Stylosphaera coronata laevis	-	22.5		23.9	22.5	1.4	
Stylosphaera radiosa	-	19.6		23.9	19.6	4.3	
Stylosphaera sp. A	18.1	-		18.1	10.3	7.8	
Stylosphaera sp. B	-	13.7		23.9	13.7	10.2	
Stylosphaera sp. C	21.2	20.2	1	21.2	20.2	1	
Tholoniid sp. B	-	-		-	-		single R occurrence
Thyrsocyrtis clausa	-	-		-	-		single R occurrence
Tripilidium clavipes	-	18.2		19.4	18.2	1.2	
Trissocylid sp. A	18.4	-		18.4	10.3	8.1	
Velicucullus altus	-	16.5		23.9	16.5	7.4	
Velicucullus cf. **oddgurneri**	-	-		23.9	10.3	13.6	
Averages:		No trunc:	4.468181818		W. truncs:	6.907407407	

Table 3. Stratigraphic-range information for species in the Lazarus data set. Same format as used for Abelmann data. Colors for individual species indicate higher taxonomic group membership (Spumellarian in red, Nassellarian in blue).

Species	FO	LO	Range no truncs	FO w. truncs	LO w. truncs	Range w. truncs
(blue - N, red - S)						
Acrosphaera ? **mercurius**	8.6	4.5	4.1	8.6	4.5	4.1
Acrosphaera australis	10.6	7.7	2.9	10.6	7.7	2.9
Acrosphaera labrata	7.7	4.8	2.9	7.7	4.8	2.9
Acrosphaera murrayana	12.3	9.8	2.5	12.3	9.8	2.5
Actinomma golowini	13.7	10.8	2.9	13.7	10.8	2.9
Actinomma magnifenestra	-	13.7		20.5	13.7	6.8
Amphistylus angelinus	-	11.9		20.5	11.9	8.6
Amphymenium challengerae	7.0	6.1	0.9	7.0	6.1	0.9
Antarctissa cylindrica	6.4	0.8	5.6	6.4	0.8	5.6
Antarctissa deflandrei	14.3	6.1	8.2	14.3	6.1	8.2
Antarctissa denticulata	7.9	-		7.9	0.0	7.9
Antarctissa strelkovi	9.0	-		9.0	0.0	9.0
Anthocyrtidium sp.	8.4	6.6	1.8	8.4	6.6	1.8
Calocyclas disparidens	16.9	16.2	0.7	16.9	16.2	0.7
Cenosphaera magnisphaera	14.5	9.8	4.7	14.5	9.8	4.7
Circodiscus microporus	-	10.6		20.5	10.6	9.9
Cycladophora antiqua	-	19.0		20.5	19.0	1.5
Cycladophora bicornis	10.7	-		10.7	0.0	10.7
Cycladophora davisiana	2.5	-		2.5	0.0	2.5
Cycladophora golli group	-	14.8		20.5	14.8	5.7
Cycladophora humerus	13.8	9.2	4.6	13.8	9.2	4.6
Cycladophora pliocenica	9.6	1.8	7.8	9.6	1.8	7.8
Cycladophora regipileus	-	15.5		20.5	15.5	5.0
Cycladophora spongothorax	12.2	8.8	3.4	12.2	8.8	3.4
Cyrtocapsella japonica	14.7	12.2	2.5	14.7	12.2	2.5
Cyrtocapsella longithorax	-	14.2		20.5	14.2	6.3
Cyrtocapsella tetrapera	-	13.6		20.5	13.6	6.9
Dendrospyris cf. **D. megalocephalis**	9.8	9.1	0.7	9.8	9.1	0.7
Dendrospyris megalocephalis	13.7	12.1	1.6	13.7	12.1	1.6
Dendrospyris rhodospyroides	-	6.1		20.5	6.1	14.4
Desmospyris spongiosa	4.9	2.2	2.7	4.9	2.2	2.7
Dictyophimus crisae	17.5	15.7	1.8	17.5	15.7	1.8
Didymocyrtis/Diartus sp.	14.3	6.2	8.1	14.3	6.2	8.1
Druppatractus hastatus	-	4.7		20.5	4.7	15.8
Eucyrtidium calvertense	17.5	2.0	15.5	17.5	2.0	15.5
Eucyrtidium cienkowski	-	6.3		20.5	6.3	14.2
Eucyrtidium pseudoinflatum	11.3	4.2	7.1	11.3	4.2	7.1
Eucyrtidium punctatum	18.5	14.5	4.0	18.5	14.5	4.0
Helotholus haysi	9.2	7.3	1.9	9.2	7.3	1.9

Table 3 (continued).

Species	FO	LO	Range no truncs	FO w. truncs	LO w. truncs	Range w. truncs
Helotholus vema	4.9	2.2	2.7	4.9	2.2	2.7
Hexalonche philosophica ?	-	14.4		20.5	14.4	6.1
Lamprocyclas aegles	7.6	6.1	1.5	7.6	6.1	1.5
Lampromitra sp.	13.4	3.8	9.6	13.4	3.8	9.6
Lithatractus timmsi	-	11.5		20.5	11.5	9.0
Lithatractus timmsi ?	7.7	6.1	1.6	7.7	6.1	1.6
Lithomelissa stigi	10.5	9.0	1.5	10.5	9.0	1.5
Lychnocanium grande	9.9	4.5	5.4	9.9	4.5	5.4
Lychnocanomma conica	-	13.2		20.5	13.2	7.3
Prunopyle hayesi	-	8.6		20.5	8.6	11.9
Prunopyle titan	9.8	3.7	6.1	9.8	3.7	6.1
Pterocanium charybdeum trilobum	4.5	0.8	3.7	4.5	0.8	3.7
Pterocanium korotnevi	12.4	6.2	6.2	12.4	6.2	6.2
Rhopalastrum sp.	14.3	6.4	7.9	14.3	6.4	7.9
Saturnalis circularis	17.5	-		17.5	0.0	17.5
Sethoconus sp.	-	7.8		20.5	7.8	12.7
Siphonosphaera vesuvius	10.6	7.4	3.2	10.6	7.4	3.2
Spongoplegma sp. **Chen**	not enough data					
Spongotrochus glacialis	13.3	-		13.3	0.0	13.3
Stichocorys peregrina	9.8	4.9	4.9	9.8	4.9	4.9
Stichopilium bicorne ?	16.9	10.8	6.1	16.9	10.8	6.1
Stylacontarium sp.	-	13.3		20.5	13.3	7.2
Stylatractus santaenae	-	4.8		20.5	4.8	15.7
Stylatractus transparum	11.2	4.6	6.6	11.2	4.6	6.6
Stylatractus universus	13.2	0.4	12.8	13.2	0.4	12.8
Thyrsocyrtis clausa	16.5	13.8	2.7	16.5	13.8	2.7
Triceraspyris antarctica	4.0	-		4.0	0.0	4.0
Triceraspyris coronata group	18.6	4.5	14.1	18.6	4.5	14.1
Velicucullus sp.	-	13.7		20.5	13.7	6.8

set but does not reach the levels seen by either Lazarus or Abelmann in earlier Miocene intervals.

FOs, LOs and Total Turnover

First occurrences (FOs), last occurrences (LOs) and total turnover (the sum of FOs and LOs) per 1 m.y. interval are shown for all three data sets in Figure 4(A-C) and are summarized in Table 4. Total turnover, which summarizes the relative intensity of faunal change, is given in Figure 4A. The overall pattern shows a trend from lower rates of change (ca. 20% turnover per m.y.) in the early Miocene to very high rates of change (as much as 50% turnover per m.y.) in the Plio-Pleistocene. The trend is far from monotonic, however, with major changes at a ca. 2-3 m.y. scale in the mid to early late Miocene, and at ca. 1 m.y. scales in the latest Miocene to Recent. As 1 m.y. is the sampling scale , the true scale of variability in the latter interval may even be shorter.

First and last occurrence data (Figures 4B and C) reveal that two contrasting patterns contribute to the overall pattern of turnover. First occurrences vary substantially on short time scales, but over the entire interval studied show no discernible trend, although there are two broad intervals of low

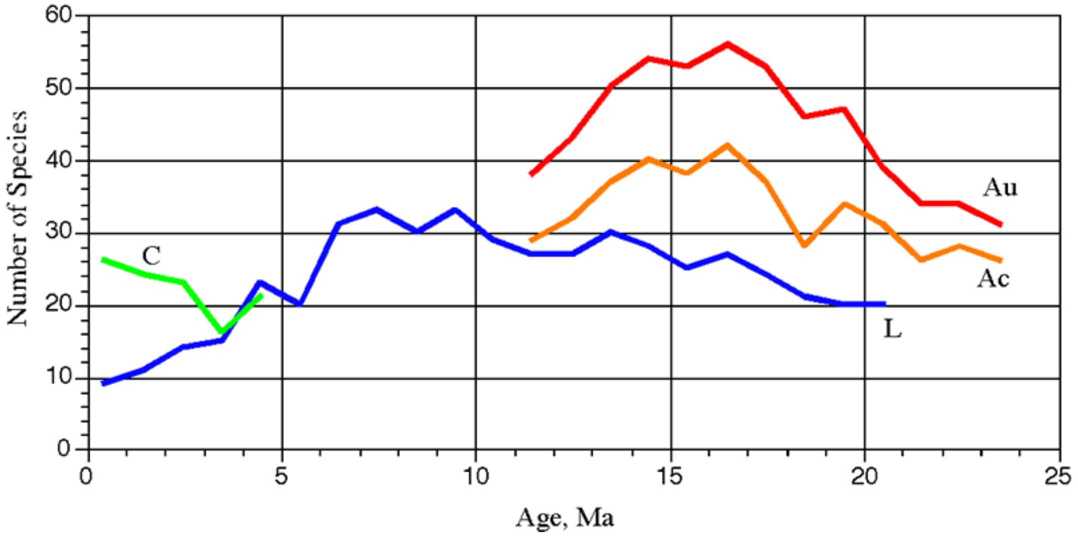


Figure 3. Species-level taxonomic diversity for the three data sets using the range-through method. Two curves are shown for the Abelmann data - with (Ac) and without (Au) correction for taxa whose ranges are truncated internally in the data set.

FO rates in the late middle Miocene and latest Miocene. Last occurrence rates, by contrast, are more clearly non-uniform, being low in the early Miocene, higher in the mid-Miocene to Recent, and with distinct peaks in between 15-13 Ma and near the Miocene-Pliocene boundary. These two differing faunal change characteristics are compared in Figure 4D, which is the percent net change of the faunal data. This statistic, being a difference value and thus inherently more noisy than other measurements, nonetheless shows broadly positive net rates of change for the early Miocene and late Pliocene-Recent, with substantial net negative rates of change between 15-13 Ma and the near Miocene-Pliocene boundary.

Longevity Distributions

Given that the time intervals studied by the authors are similar to the average taxon longevity, truncation of ranges—and thus truncated longevities—are a major problem. Analyzing only non-truncated taxa is not in itself an adequate solution to this problem, as it preferentially excludes long ranging taxa. Including truncated ranges avoids this problem, although of course it adds artificially shortened ranges as well. Thus, the analysis was done for both truncated and non-truncated taxon ranges. The distribution of taxon longevities is given in Figure 5A-G and Tables 1-3, beginning with data from Lazarus (1992), the data set least affected by truncation problems. Non-truncated taxon longevities in this data set (Fig. 5A) show a noticeably non-Gaussian distribution, with both skew towards short longevities (mode at 2-4 m.y.) and a suggestion of bimodality with a gap at 10-12 m.y. This latter gap, however, is based on too few data to be convincing in itself. When truncated taxon ranges are included (Fig. 5B), the general pattern largely remains. The distribution is still non-Gaussian, with a clearly bimodal distribution of long ranging taxa (mode 14-16 m.y.), short ranging taxa (the mode at 6-8 m.y. now shifted towards larger values), and a distribution minimum at 10-12 m.y.

The data of Abelmann (1992a), covering only the older Miocene, also shows these patterns, although the numerous truncations in her data set, due to the lack of specific taxon data from some of her study sites, makes the analysis less robust. For her non-truncated ranges, the distribution of longevities (Fig. 5C) is similar to that for Lazarus with truncated ranges included, although the total number of taxa is very limited, and no longer ranging species were observed. When truncated range data are included (Fig. 5D) the longevity distribution matches that of Lazarus, although, due to the limited total time of her study interval, long-ranging species in the second distributional mode (>10-12 m.y.) are all recorded in a single—and thus artificially high-valued—bin at 12-14 m.y.

Too few non-truncated species ranges were available in Caulet's (1991) data set to make a distributional analysis of non-truncated taxa ranges worthwhile. Given the very short time interval studied and the apparent presence of significant numbers of much longer-ranging species, Caulet's data

Table 4. Raw and calculated values for diversity, FO, LO, and Turnover for all data sets. Column headings abbreviated for compactness, key in lower left corner of table.

	Lazarus							Caulet							
Age	**DivL**	**FOL**	**LOL**	**PctFOL**	**PctLOL**	**PctTL**	**PctNetTL**	**DivC**		**FOC**	**LOC**	**PctFOC**	**PctLOC**	**PctTC**	**PctNetTC**
0.5	9	0	3	0	33.3	33.3	-33.3	26		4	5	15.4	19.2	34.6	-3.8
1.5	11	0	1	0	9.1	9.1	-9.1	24		6	2	25	8.3	33.3	16.7
2.5	14	1	3	7.1	21.4	28.6	-14.3	23		8	5	34.8	21.7	56.5	13
3.5	15	0	2	0	13.3	13.3	-13.3	16		0	1	0	6.3	6.3	-6.3
4.5	23	4	8	17.4	34.8	52.2	-17.4	21		3	6	14.3	28.6	42.9	-14.3
5.5	20	0	1	0	5	5	-5								
6.5	31	2	10	6.5	32.3	38.7	-25.8	19		2	1	10.5	5.3	15.8	5.3
7.5	33	5	4	15.2	12.1	27.3	3								
8.5	30	2	2	6.7	6.7	13.3	0	Abelmann							
9.5	33	7	5	21.2	15.2	36.4	6.1	**DivAu**	**DivAc**	**FOAc**	**LOAc**	**PctTAc**	**PctFOAc**	**PctLOAc**	**PctNetTA**
10.5	29	4	3	13.8	10.3	24.1	3.4								
11.5	27	2	2	7.4	7.4	14.8	0	38	29	3	3	20.7	10.3	10.3	0
12.5	27	3	2	11.1	7.4	18.5	3.7	43	32	1	3	12.5	3.1	9.4	-6.3
13.5	30	6	6	20	20	40	0	50	37	5	6	29.7	13.5	16.2	-2.7
14.5	28	5	4	17.9	14.3	32.1	3.6	54	40	2	8	25	5	20	-15
15.5	25	0	2	0	8	8	-8	53	38	0	0	0	0	0	0
16.5	27	2	1	7.4	3.7	11.1	3.7	56	42	5	3	19	11.9	7.1	4.8
17.5	24	3	0	12.5	0	12.5	12.5	53	37	1	1	5.4	2.7	2.7	0
18.5	21	2	0	9.5	0	9.5	9.5	46	28	6	3	32.1	21.4	10.7	10.7
19.5	20	0	1	0	5	5	-5	47	34	6	1	20.6	17.6	2.9	14.7
20.5	20	0	0	0	0	0	0	39	31	3	4	22.6	9.7	12.9	-3.2
21.5								34	26	3	0	11.5	11.5	0	11.5
22.5								34	28	1	4	17.9	3.6	14.3	-10.7
23.5								31	26	1	0	3.8	3.8	0	3.8

Key: L-Lazarus, u-uncorrected, Div-Diversity, C-Caulet, c-corrected, FO-First Occurences, A-Abelmann, Pct-Percent, LO-Last Occurences, T-Turnover

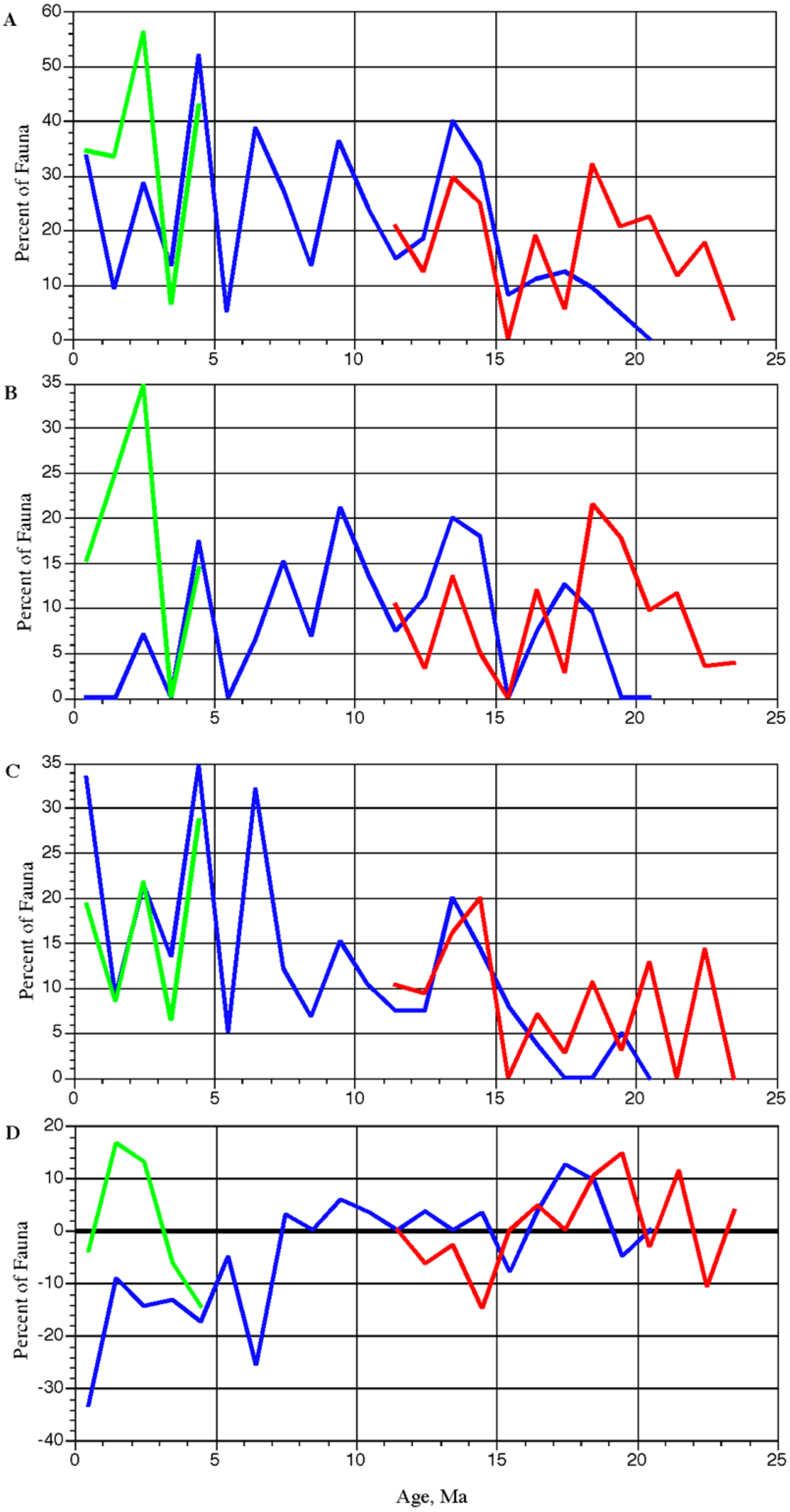


Figure 4. Evolutionary patterns in Antarctic Neogene radiolarian faunas. All values normalized to per sample diversity. Data from Caulet in green, from Lazarus in blue, from Abelmann in red. A - total turnover, B - first occurrences, C - last occurrences, D - net change in diversity.

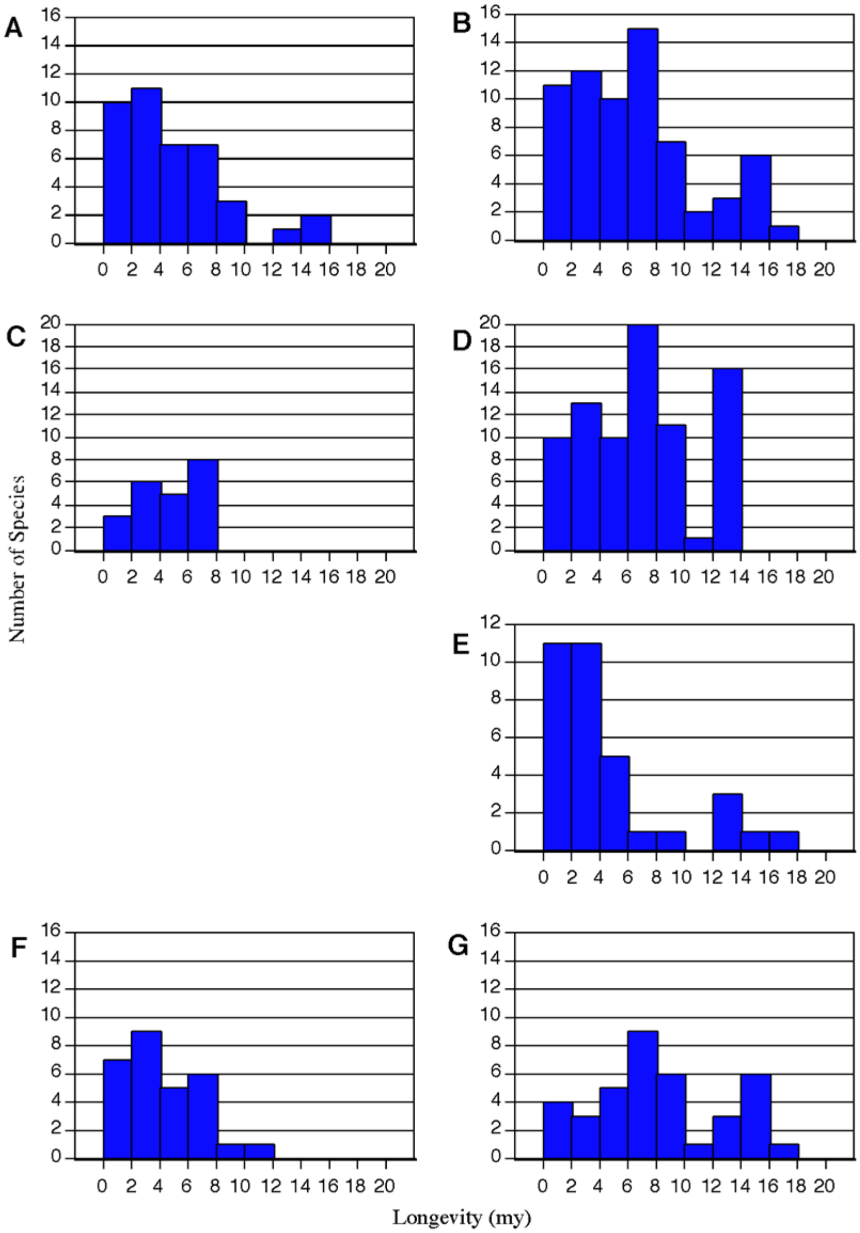


Figure 5. Histograms of species longevities. Horizontal scales (longevity in m.y.) are the same for all plots, vertical scales are the same for data for one author. A - Lazarus, complete ranges only. B - Lazarus, with truncated ranges. C - Abelmann, complete ranges only. D - Abelmann, with truncated ranges. E - Caulet, including truncated range tops and extended range bases determined from Lazarus' data. F - Lazarus, species originating after 13 Ma (includes truncated ranges). G - Lazarus, species originating before 13 Ma (includes truncated ranges).

on truncated species ranges was supplemented by locating in Lazarus' data the FO for as many of his taxa as possible that range below the base of his study interval. Given the taxonomic differences between the authors, this approach (as noted in the introduction) is risky, and only a few taxa could be matched with some degree of confidence in the uniformity of taxonomic concept. The result is shown in Figure 5E, which very closely resembles that of Lazarus' (1992) for untruncated ranges.

Lastly, longevity distributions were summarized for taxa originating in two different time intervals within Lazarus' data (including truncated range taxa): prior to, and after, 13 Ma. Figure 5F shows the data for species originating prior to 13 Ma. Here the distribution is very bimodal, and, barring the absence of an upper value limit effect, is very similar to the pattern seen in Abelmann's data. The longevity distribution for species originating after 13 Ma is given in Figure 5G. Here there is no

Table 5. Number of species and calculated average longevity values for species in the Lazarus data set.

	Complete ranges only		With truncated ranges	
	N	Ave., my	N	Ave. my
Neogene, all species	41	4.8	68	6.5
>13 Ma, all species	17	6.34	38	8.2
<13 Ma, all species	24	3.65	29	4.2
Neogene, Nassellaria	27	4.8	42	5.8
Neogene, Spumellaria	14	4.8	25	7.6
>13 Ma, Nassellaria	12	5.95	22	6.92
<13 Ma, Nassellaria	15	3.79	20	4.55
>13 Ma, Spumellaria	5	7.28	16	9.89
<13 Ma, Spumellaria	9	3.42	9	3.42

indication of bimodality, and the distribution is skewed towards short-ranging taxa (mode at 2-4 m.y.)

Taxonomic Group Effects

Radiolarians are a diverse group of organisms with a wide range of ecologic preferences and preferred habitats, which is presumed to be reflected in their taxonomic structure. Basic data on the longevity of taxa are given for different time intervals in Table 5, where the longevities (drawn from the Lazarus data set) are presented not only for radiolarians as a whole, but also for each of the two major taxonomic subgroups within them—the Nassellaria and Spumellaria. Although at first glance there seems to be no major difference between these two groups (average longevity for both Nassellaria and Spumellaria over the entire Neogene interval studied is 4.8 m.y. for those taxa whose ranges are not truncated), more detailed comparisons reveal substantial differences in the longevity characteristics for the two groups. Spumellarians tend to be longer lived than nassellarians in the older part of the study interval (mean longevities of 7.28 vs. 5.95 m.y., untruncated ranges only), and are relatively more important as a fraction of the total diversity (42% of the taxa in >13 Ma sediments, vs. only 31% in <13 Ma sediments). There is also a clear difference between older and younger intervals which affects both nassellarians and spumellarians - younger taxa in both groups are shorter ranging than they are in the same taxonomic group in older intervals (3.79 vs. 5.95 for Nassellaria, 3.42 vs. 7.28 for Spumellaria). In fact, in <13 Ma sediments the average longevity of the two groups is very similar, or possibly even reversed, with nassellarians being (albeit only slightly) more long lived than spumellarians (3.79 vs. 3.42 m.y.).

DISCUSSION

Coherence Between Data Sets and Validity of Patterns

The observed decline of diversity near the beginning and end of each author's study interval is, of course, to be expected, given the way the data were collected. As the beginning and the end of the study interval was reached, fewer taxa characteristic of the core of the study interval are found. An increasing proportion of the taxa present do not belong to the list of taxa used by the author and are thus not recorded. When interpreting data of this sort it is therefore necessary to distinguish the bias towards lower diversity of this 'edge' effect and place most reliance on the data from within the main study interval of each author. However, in those intervals where data of different authors overlap, shorter-term trends may still be of interest. In particular, they can be compared between data sets to check the consistency of patterns as seen by different authors, and thus provide an indication as to how accurately the data reflect a primary biologic signal instead of only artifacts in recording of data. The intervals in which the data of different authors overlap (early Pliocene, late early/early mid-Miocene, Fig. 3) show a high degree of similarity to each other.

Data from different authors also show a high degree of coherence in most other estimates of evolutionary change. Although there are some differences in absolute values, first and last occurrence patterns and total turnover (Fig. 4), as well as average longevity values for taxa (Table 5) from different time intervals, all show similar results. Most remarkably, even the bimodal distribution of taxon longevities is seen in both Lazarus' and Abelmann's data sets (Fig. 5).

These similarities strongly suggest that the patterns shown in Figures 3 to 5 are not just artifacts of different authors' observational methods, but instead reflect primary patterns of the actual fossil record. Given the well-preserved nature of the faunas and the lack of obvious bias in the choice of taxa studied, it seems reasonable to believe that the patterns observed also reflect original patterns of faunal change in the living faunas. It is therefore valid to compare the patterns of faunal change to those of environmental change to answer the question posed at the beginning of this article: are faunal changes in these planktonic

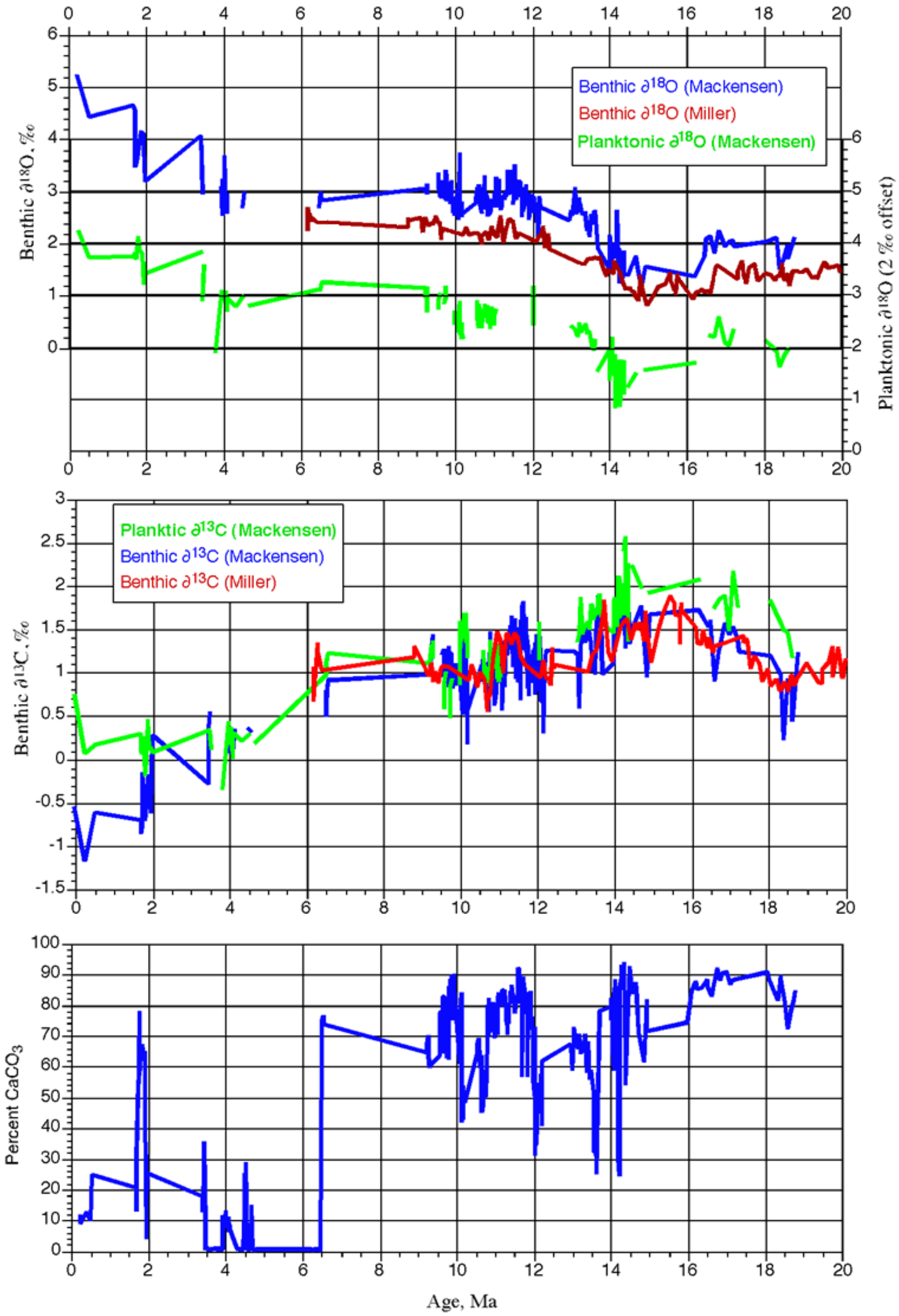


Figure 6. Paleoenvironmental data, Antarctic Neogene, replotted from data given in Mackensen et al. (1992) (green and blue) and Wright and Miller (1992) (red). Top - planktonic and benthic foraminiferal $\delta^{18}O$ values. Note that for clarity, planktonic values are plotted with a 2‰ offset to the benthic data. Middle - $\delta^{13}C$ values for planktonic and benthic foraminifera. Bottom - percent $CaCO_3$ in Site 751 sediments. Gaps in data in all three plots reflect either hiatuses or unmeasured intervals.

organisms strongly correlated to those of environmental change?

Correlation Between Evolutionary and Paleoenvironmental Change

Figure 6 summarizes Kerguelen Plateau Neogene environmental data. Although there are gaps in these records due both to hiatuses in the sections and occasional lack of sufficient foraminifera for isotopic analysis (particularly in the late Neogene), clear patterns are nonetheless apparent. Prior to 15 Ma, oxygen isotopes were fairly stable and percent sedimentary carbonate values were uniform and high. Carbon isotope values were increasing, and planktonic values tended to be heavier than benthic ones. The period between 15 and 13 Ma was one of major change, with short-term, large-amplitude fluctuations appearing in both isotope and carbonate records. Oxygen isotopes shifted towards heavier values, carbon isotopes became more negative, and the offset between benthic and planktonic values decreased. This new regime persisted to approximately 6.5 Ma, at which point there was a dramatic drop in carbonate values. There was also renewed change in both oxygen and carbon isotopes, with both indicators shifting again in the same direction as in the prior shift at 15-13 Ma. These changes reflect the well-known Neogene history of the Southern Ocean, which is dominated by two major events, each of which shifted the system into a new state (Kennett 1982). The changes between 15 and 13 Ma reflect the mid-Miocene increase of glaciation on the Antarctic continent, together with cooling of both surface and deep waters in the Southern Ocean, and an increase in biologic productivity (Flower and Kennett 1993, 1994). The ca. 6.5-4.5 Ma shift reflects further increases in Southern Ocean productivity, a shift towards diatom-dominated primary production, and is associated with a (poorly understood) interval of major glaciation of the Antarctic continent near the Miocene -Pliocene boundary (Van Couvering et al. 1976; Kennett 1982).

Selected evolutionary metrics and environmental records are compared to each other in Figure 7. A clear correlation can be seen between the evolutionary (Fig. 7A-C) and environmental (Fig. 7D-F) data. The overall trends in diversity (Fig. 7C) are correlated to the carbon isotope records (Fig. 7D), particularly that of the planktonic foraminifera, while there is a good general match between levels of turnover (primarily via stepwise increases in last occurrences, Fig. 7B) and the three major phases of Southern Ocean development that are delineated by the two major intervals of rapid environmental change at 15-13 Ma and near the Miocene-Pliocene boundary. Faunal diversity thus appears to be inversely correlated to productivity, as indicated by stable carbon isotope values, and by the increase in biogenic silica in sediments (indicated by the decrease in carbonate content in Fig. 7E). This correspondence is reinforced when other estimates of regional productivity are considered. Sedimentation rates in Antarctic Neogene pelagic sections for example tend to reflect water-column productivity, particularly in those later Neogene biosiliceous sections where carbonate is nearly absent, and thus changes in carbonate dissolution are not important. Although no comprehensive synthesis of regional data is available, sedimentation rates in the Antarctic Neogene have tended to increase from fairly low values in the early Miocene, to moderately high values in many sections in the late Miocene, reaching a peak in the early Pliocene before declining into the later Pliocene and Pleistocene (Brewster 1980; Gersonde et al. 1990; Froelich et al. 1991; Barron et al. 1991; Harwood et al. 1992). This pattern, in inverse form, is also reflected in the biodiversity curve (Fig. 7C).

There is no evidence for a pattern of near uniform, continuous change as predicted by models of evolution driven primarily by biotic interactions (Stenseth and Maynard-Smith 1984; Hoffman and Kitchell 1984). Rates of evolutionary change vary dramatically and are clearly linked temporally to changes in the environment. Environmental change, directly or indirectly, thus appears to play a major role in the evolution of Southern Ocean Neogene radiolarian faunas, with the primary timing and general magnitude of evolutionary change being driven by external environmental forces. These results may also be relevant to understanding factors driving the evolution of Antarctic biotas in general. As noted by Clarke (1990), temperature change and cold absolute values for temperature, do not by themselves seem to be sufficient explanations for extinctions of taxa in the historical development of Antarctic faunas. It may be instead that for much of the Antarctic biota, and not just for radiolarians, extinction has been caused by changes—primarily increases—in oceanic productivity, which according to Hallock's (1987) model, decreased the range of habitats in the 'trophic resource continuum', and thus led to the loss of biodiversity.

Changes in Evolutionary Rate Characteristics with Time

One of the more interesting, and quite unexpected, results of this study are the patterns of lon-

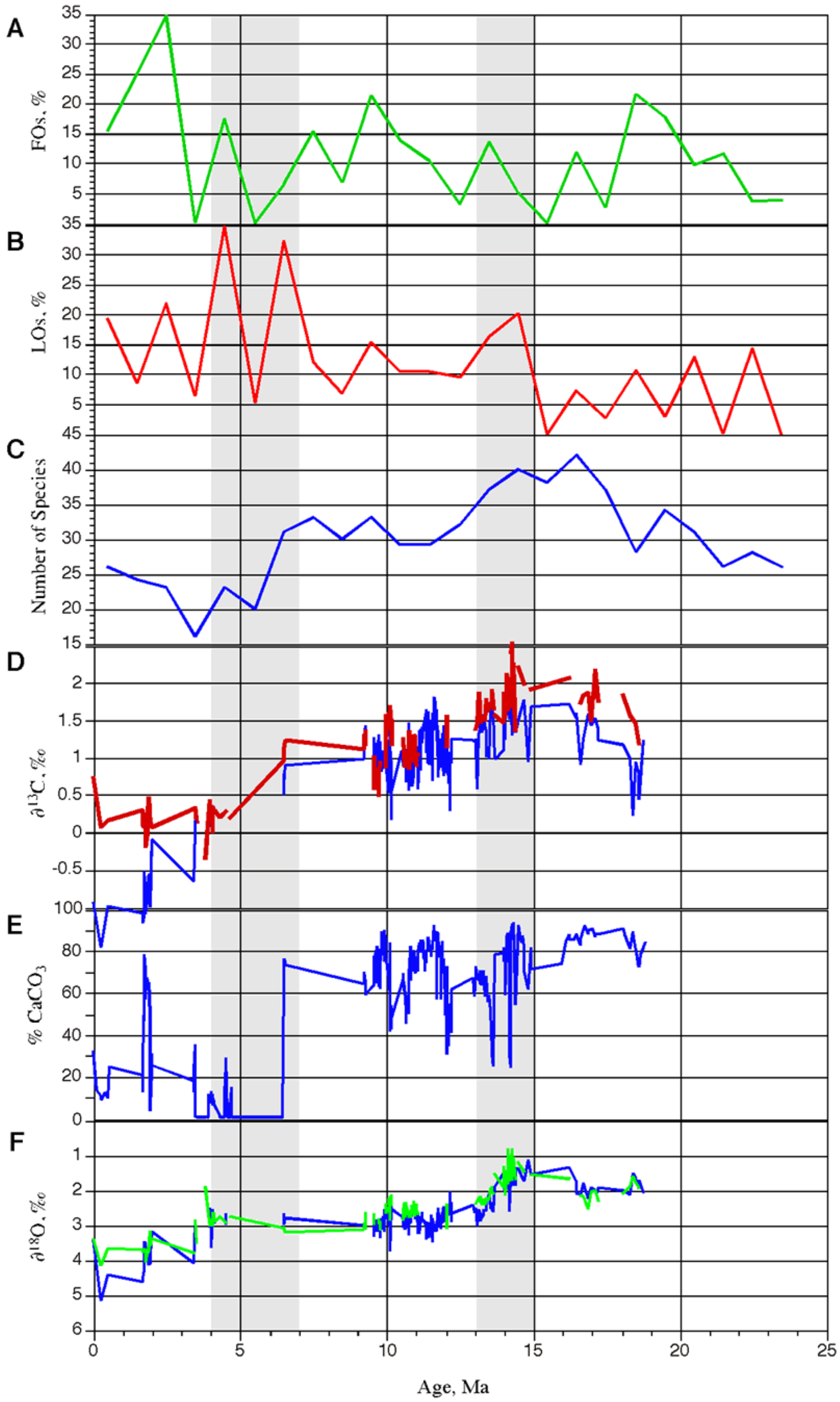


Figure 7. Comparison of radiolarian evolutionary (A-C) and environmental history (D-F, Mackensen et al. 1992 data only) in Antarctic Neogene. Evolution curves are composites of the different authors' data sets, with cut-points of 5 and 11 Ma. Gray shading indicates the two major episodes of environmental change between 15-13 Ma and 7-4 Ma. A - first occurrences in radiolarian faunas. B - last occurrences. C - Diversity. D - δ^{13}C of planktonic (red) and benthic (blue) foraminifera . E - Percent $CaCO_3$ in sediment. F - δ^{18}O of planktonic (green) and benthic (blue) foraminifera.

gevity data for species. All data show a similar pattern of bimodal longevities, separated by the relative dearth of taxa with longevities in the range 10-12 m.y. The subpopulation of long-lived taxa seems to be found primarily in species that originate in the older part of the study interval, below 13 Ma, while species of more recent origin are notably shorter lived. One possible explanation for such a bimodal pattern would be the existence of two distinct evolutionary sub-groups within the radiolarian plankton, such as might hypothetically exist between surface and deep-dwelling faunas. Radiolarians in many parts of the modern ocean include both shallower dwelling forms and deeper-dwelling species (Casey et al. 1979; Takahashi 1991; Casey 1993). The Southern Ocean, however, is different from lower latitude environments in that modern radiolarian faunas are most abundant in deeper waters (>150 m to 1,000 m or more) (Abelmann and Gowing 1996). In the early Neogene, prior to the mid-Miocene climate shift, surface waters in the Antarctic may have more closely resembled those of modern cool-temperate regions, with relatively more radiolarian taxa living in the uppermost layers of the water column. The observed bimodality in evolutionary rates in the older Neogene data would thus reflect differences in characteristic evolutionary rates between these two depth environments. Depth-related differences in evolutionary rates are also known from lower latitude planktonic foraminifera (Stanley et al. 1988), where deeper dwelling forms were found to have shorter mean longevities than the shallower taxa, possibly due to the lower abundances (population sizes) of deeper dwelling taxa. Extending this idea to the current study would suggest that the longer lived mode seen in the older Neogene radiolarian longevity data reflect near-surface dwelling forms. With the loss of this near-surface water environment in the mid-Miocene, later Neogene radiolarian faunas became primarily deeper dwellers. The longevity data reflect this shift in that only shorter lived forms are seen in the late Neogene longevity histograms. Some support for this interpretation also comes from the changes in taxonomic abundance between Nassellaria and Spumellaria (see below).

The observed pattern, however, can also be explained in at least two other ways. First, the bimodality must—at least partly—reflect the time-windowed nature of these data, plus the substantial extinction that occurred between 15 and 13 Ma. Many of the taxa lost at the mid-Miocene event exhibit truncated ranges at the base of the study and thus are constrained to have longevities <10 m.y. The distribution of the survivors' longevities suggests that many that do survive then continue to near the second, Miocene-Pliocene boundary, extinction event, before becoming extinct, thus creating a second mode of long-lived taxa. However, the same type of explanation cannot be used to describe the longevity pattern of taxa originating after 13 Ma, as they show a significantly different distribution of longevities, with no evidence of a large number of long-lived taxa that go through the end-Miocene event and continue into the Recent. The post mid-Miocene fauna therefore consists of (on average) significantly shorter ranging species, implying an increase in evolutionary rates in the region during the Neogene interval studied.

A second possible alternate explanation is that not all Southern Ocean taxa are in fact endemic, and in particular, significant numbers of the post-Miocene taxa appear to be bipolar, with records of occurrence as well in the Norwegian-Greenland Seas (Bjørklund 1976). Some of the turnover, particularly in the late Neogene, may thus represent immigration of taxa. This is still of interest but represents a different biological process for diversity regulation than *in situ* evolution (see also discussion in Hoffman and Kitchell 1984).

It should also be noted that both the overall rates of change (up to more than 50% species turnover/m.y.) and the average longevity of species (4.8 m.y.) are comparable to, or exceed, rates that have been previously reported for marine microplankton groups (ca. 7-16 m.y. for cladogenetically delimited lineages of planktonic foraminifera (Stanley et al. 1988); 5.6 and 9.5 m.y. mean longevity for Cretaceous to Recent keeled and non-keeled species of planktonic foraminifera (including both cladogenetic and anagenetic evolution, Norris 1991), and ca. 5-10 m.y. for species of planktonic foraminifera, coccolithophores and radiolarians, based on the survival decay curves given in Hoffman and Kitchell (1984).

Biological Causes

Although external environmental change appears to be the primary factor driving evolution of Antarctic Neogene radiolarian faunas, biology does seem to play an important role. This is suggested by two aspects of the results. First, diversity and evolutionary turnover metrics appear to correlate more closely to productivity (carbon isotopes, sedimentation rates), and the composition of the primary producer flora (carbonate/biogenic silica ratio), than to temperature itself (oxygen isotopes). This result is similar to those from the study of the warm water Cenozoic planktonic foraminifera, (e. g., Corfield and Shackleton 1988; Lipps 1986; see also discussion in Norris 1991) and Tethyan Mesozoic radiolaria (Erbacher et al. 1996; Danelian and Johnson 2001), and lends general support to Hallock's (1987) trophic model of biodiversity regulation. Second, the shift from a lower productivity, carbonate phytoplankton ocean to a higher productivity, biogenic silica phytoplankton ocean is accompanied by a shift in the ecological nature of the radiolarian fauna (Table 5). Spumellarians are more common in the older Neogene but are less common in the later Neogene. Spumellarians are, as a group, more likely to host symbiotic algae and to live in near-surface waters than are Nassellaria, which tend to be deeper dwelling, non-symbiotic forms (Casey et al. 1979; Takahashi 1991; Anderson 1980, 1993; Abelmann 1992b). The shift from spumellarian dominated to nassellarian dominated faunas suggests a shift from faunas more adapted to lower productivity, silica-rich surface waters, to faunas living in deeper waters, below a relatively silica poor surface water layer dominated by highly productive, silica depleting diatoms. Diatoms are known to be particularly efficient in removing available biogenic silica in surface waters, and thus are thought to have a potential negative effect on radiolarian growth (Anderson 1980; Takahashi 1991). On a much broader scale, Harper and Knoll (1975) suggested that the Cenozoic evolution of both diatoms and radiolaria has been influenced by competition for silica. However, it should be noted that in the modern Southern Ocean, biogenic silica is not a limiting nutrient - light and water column stability play instead more important roles (Siegfried et al. 1985). Whether this condition was also true for earlier intervals in the Neogene is not known.

Conclusions and Suggestions for Future Research

Antarctic Neogene radiolarian faunal occurrence data drawn from several recent ODP studies have been used to reconstruct the diversity and evolutionary turnover history of this group, and to compare the patterns to that of environmental change. A clear correlation exists between overall radiolarian diversity and proxies for ocean productivity, such as stable carbon isotopes, regional sedimentation rates, and abundant biogenic silica in sediments. Higher rates of inferred productivity characterize the later Neogene and are associated with lower radiolarian diversity, and an increased dominance of Nassellarians, a predominantly deeper dwelling group of radiolarians with fewer photosymbiont taxa.

Overall rates of evolutionary turnover, and particularly rates of extinction, are not uniform, but are also closely linked to environmental change, with shifts towards increased turnover and extinction rates being associated with the shifts in the environment marked by the mid-Miocene and end Miocene glacial events that affected the Antarctic region.

The average longevity of species also has been affected by environmental change, with post mid-Miocene species having significantly shorter stratigraphical ranges than older taxa. This seeming acceleration of evolution is a phenomenon that has not been reported, or at least much emphasized in previous studies of warmer water microplankton. Norris (1991), for example, presents data suggesting that longevity distributions in Cretaceous to Recent planktonic foraminifera have remained largely unchanged for the last ca. 100 m.y.

These results together suggest that changes in the environment, not internal biologic interactions, primarily regulate overall rates of faunal change in Antarctic Neogene radiolarians. This largely confirms prior results from study of lower latitude faunas of planktonic foraminifera and radiolaria, although changing average longevity distributions in Antarctic Neogene radiolarian faunas suggest that important differences may exist as well, and that the environmental history of polar and low-latitude regions may differ in evolutionarily significant ways. Lastly, biology, although not the ultimate pacesetter of evolutionary change, nonetheless plays an important role in mediating changes in the physical environment through mixed physical-biologic mechanisms such as change in marine productivity.

This study is a preliminary analysis, as the available taxonomic, stratigraphic and biologic data on these faunas are still very incomplete. Clearly, more complete surveys of the faunas using existing taxonomy, as well as a more complete taxonomy, would be desirable. So would a better knowledge of the ecology of the taxa studied, particularly the relationship between different taxa and marine productivity, including the distribution of symbionts among species. The relative importance of *in situ* evolution *vs.* immigration from other cold water regions also needs to be resolved. However, despite these limitations, it appears that useful evolutionary signals can be extracted even from relatively incomplete data such as that recorded in normal DSDP/ODP radiolarian biostratigraphic range charts. Given that few studies of evolution have been carried out with such data sets, despite their abundance in the published literature, it is hoped that additional studies may be possible which will yield further insights into patterns and processes of evolution in the pelagic realm.

ACKNOWLEDGMENTS

The author acknowledges support for his recent work on these faunas from DFG grants La 1191/1-1 and -2. This article was partly inspired by participation in meetings on evolutionary change: Geoscience 2000, Manchester; Geological Society London Lyell meeting, 2001; NAPC Berkeley, 2001; The author wishes to thank these meetings' organisers, fellow participants, and the DFG for travel support for attending the NAPC. A. Mackensen (AWI, Bremerhaven) generously provided computer readable versions of his data for use in this study. B. Mohr, D. Unwin and M. Apel are thanked for discussions which assisted the writing of this article and two anonymous reviewers for suggestions on how to improve it.

REFERENCES

Abelmann, A. 1990. Oligocene to Miocene radiolarian stratigraphy of southern high-latitudes from ODP Leg 113, Sites 689 and 690, Maud Rise, p. 675-708. In Barker, P. F. and Kennett, J. P. (eds.) **Proceedings of the Ocean Drilling Program, Scientific Results, Leg 113.** ODP, College Station, Texas.

Abelmann, A. 1992a. Early to mid-Miocene radiolarian stratigraphy of the Kerguelen Plateau (ODP Leg 120), p. 757-784. In Wise, S. W. and Schlich, R., **Proceedings of the Ocean Drilling Program, Scientific Results, Leg 120**. ODP, College Station, Texas.

Abelmann, A. 1992b. Radiolarian taxa from Southern Ocean sediment traps (Atlantic Sector). **Polar Biology**, 12:373-385.

Abelmann, A., Gersonde, R. and Spiess, V. 1990. Pliocene-Pleistocene paleoceanography in the Weddell Sea - siliceous microfossil evidence, p. 729-759. In Bleil, U. and Thiede. J. (eds.), **Geological History of the Polar Oceans: Arctic versus Antarctic**. Kluwer, Dordrecht.

Abelmann, A. and Gowing, M. M., 1996. Horizontal and vertical distribution pattern of living radiolarians along a transect from the Southern Ocean to the South Atlantic subtropical region. **Deep-Sea Research I, Oceanographic Research Papers**, 43(3):361-382.

Anderson, O. R., 1980. **Radiolaria**. Academic Press, New York.

Anderson, O. R. 1993. The trophic role of planktonic foraminifera and radiolaria. **Marine Microbiol. Food Webs**, 7:31-51.

Barron, J. A., Baldauf, J. G., Barrera, E., Caulet, J.-P., Huber, B. T., Keating, B. H., Lazarus, D., Sakai, H., Thierstein, H. R. and Wei, W. 1991. Biochronologic and magnetochronologic synthesis of Leg 119 sediments from the Kerguelen Plateau and Prydz Bay, Antarctica, p. 813-848. In Barron, J. A. and Larsen, B. (eds.), **Proceedings of the Ocean Drilling Program, Scientific Results, Leg 120**. ODP, College Station, Texas.

Berggren, W. A., Kent, D. V., Aubry, M. P. and Hardenbol, J. 1995. **Geochronology, Time Scales and Global Stratigraphic Correlation**. SEPM, Tulsa, Oklahoma.

Bjørklund, K. R., 1976. Radiolaria from the Norwegian Sea, Leg 38 of the Deep Sea Drilling Project , p. 1101-1168. In **Initial Reports of the Deep Sea Drilling Project, Leg 38**. U. S. Government Printing Office, Washington, D. C.

Bolli, H. M., Saunders, J. B. and Perch-Nielsen, K. (eds.) 1985. **Plankton Stratigraphy.** Cambridge Earth Science Series. Cambridge University Press, Cambridge, UK.

Brewster, N. A. 1980. Cenozoic biogenic silica sedimentation in the Antarctic Ocean, **GSA Bulletin**, Part 1, 91:337-347.

Casey, R., Gust, L., Leavesley, A., Williams, D., Reynolds, R., Duis T. and Spaw, J. M. 1979. Ecological niches of radiolarians, planktonic foraminiferans and pteropods inferred from studies on living forms in the Gulf of Mexico and adjacent waters. **Transactions-Gulf Coast Association of Geological Societies.** 29:218-223.

Casey, R. E. 1993. Radiolaria, p. 249-284. In Lipps, J. E. (ed.) **Fossil Procaryotes and Protists**. Blackwell, Boston, Massachusetts.

Caulet, J. P. 1991. Radiolarians from the Kerguelen Plateau, ODP Leg 119, p. 513-546. In Barron, J. and Larsen, B. (eds.) **Proceedings of the Ocean Drilling Program, Scientific Results, Leg 119.** ODP, College Station, Texas.

Chen, P. H. 1975. Antarctic Radiolaria, p. 437-513. In Hayes, D. E and Frakes, L. (eds.), **Initial Reports of the Deep Sea Drilling Project, Leg 28.** U. S. Government Printing Office, Washington, D. C.

Clarke, A. 1990. Temperature and evolution: Southern Ocean cooling and the Antarctic marine fauna, p. 9-22. In Kerry, K. R. and Hempel, G. (eds.) **Antarctic Ecosystems: Ecological Change and Conservation**. Springer-Verlag, Berlin.

CLIMAP project members 1976. The surface of the ice-age earth. **Science**, 191:1131-1137.

Corfield, R. M. and Shackleton, N. J. 1988. Productivity change as a control on planktonic foraminiferal evolution after the Cretaceous/Tertiary boundary. **Historical Biology**, 1:323-343.

Crame, J. A. (ed.) 1989. **Origins and Evolution of the Antarctic Biota**. Geological Society of London, Bath.

Crame, J. A. and Clarke, A. 1997. The historical component of marine taxonomic diversity gradients, p. 258-273. In Ormond, R. F. G., Gage, J. D. and Angel, M. V. (eds.) **Marine Biodiversity Patterns and Processes**. United Kingdom.

Danelian, T. and Johnson, K.G. 2001. Patterns of biotic change in Middle Jurassic to Early Cretaceous Tethyan radiolaria. **Marine Micropaleontology,** 43:239-260.

Diester-Haass, L. 1994. Middle Eocene to early Oligocene paleoceanography of the Antarctic Ocean (Maud Rise, ODP Leg 113, Site 689): change from a low to a high productivity ocean. **Paleogeography, Paleoclimatology, Paleoecology**, 113:311-334.

Diester-Haass, L., Meyers, P. A. and Vidal, L. 2002. The Late Miocene onset of high productivity in the Benguela Current upwelling system as part of a global pattern. **Marine Geology**, 180: 87-103.

Diester-Haass, L. and Zahn, R. 1996. Eocene-Oligocene transition in the Southern Ocean: History of water mass circulation and biological productivity. **Geology**, 24:163-166.

Erbacher, J., Thurow, J. and Littke, R. 1996. Evolution patterns of radiolaria and organic matter variations: A new approach to identify sea-level changes in mid-Cretaceous pelagic environments. **Geology**, 24:499-502.

Flores, J.-A., Gersonde, R., Sierro, F. J. and Niebler, H.-S. 2000. Southern Ocean Pleistocene calcareous nannofossil events: calibration with isotope and geomagnetic stratigraphies. **Marine Micropaleontology**, 40:377-402.

Flower, B. and Kennett, J. P. 1993. Middle Miocene ocean-climate transition: high resolution oxygen and carbon isotopic records from Deep Sea Drilling Project Site 588A, Southwest Pacific. **Paleoceanography**, 8:811-843.

Flower, B. and Kennett, J. P. 1994. The middle Miocene climatic transistion: East Antarctic ice sheet development, deep ocean circulation and global carbon cycling. **Palaeogeography**, **Palaeoclimatology, Palaeoecology**, 108:537-555.

Froelich, P. N., Malone, P. N., Hodell, D. A., Ciesielski, P. F., Warnke, D. A., Westall, F., Hailwood, E. A., Nobes, D. C., Fenner, J. and Mienert, J. 1991. Biogenic opal and carbonate accumulation rates in the subantarctic South Atlantic: the late Neogene of Meteor Rise Site 704, p. 515-550. In Ciesielski, P. F. and Kristoffersen Y. (eds.), **Proceedings of the Ocean Drilling Program, Scientific Results, Leg 119.** ODP, College Station, Texas.

Gersonde, R., Abelmann, A., Burckle, L., Hamilton, N., Lazarus, D., McCartney, K., O'Brien, P., Spiess, V. and Wise, S. W. 1990. Biostratigraphic synthesis of Neogene siliceous microfossils from the Antarctic Ocean, ODP Leg 113 (Weddell Sea), p. 915-936. In Barker, P. and Kennett, J. P. (eds.) **Proceedings of the Ocean Drilling Program, Scientific Results, Leg 113.** ODP, College Station, Texas.

Hallock, P. 1987. Fluctuations in the trophic resource continuum: a factor in global diversity cycles?. **Paleoceanography**, 2:457-471.

Hallock, P., Premoli Silva, I. and Boersma, A. 1991. Similarities between planktonic and larger foraminifera evolutionary trends through Paleogene paleoceanographic changes. **Paleogeography, Paleoclimatology, Paleoecology**, 83:49-64.

Harper, H. E. and Knoll, A. H. 1975. Silica, diatoms and Cenozoic radiolarian evolution. **Geology**, 3:175-177.

Harwood, D., Lazarus, D. B., Aubry, M., Berggren, W. A., Heider, F., Inokuchi H. and Maruyama , T. 1992. Neogene stratigraphic synthesis, ODP Leg 120, p. 1031-1052. In Wise, W., Schlich, R. and O'Connell S. (eds.), **Proceedings of the Ocean Drilling Program, Scientific Results, Leg 120**. ODP, College Station, Texas.

Hart, M. B. 1980. A water depth model for the evolution of the planktonic Foraminiferida. **Nature**, 286:252-254.

Hays, J. D. 1965. Radiolaria and late Tertiary and Quaternary history of Antarctic Seas, p. 125-184. In Llano, D. (ed.), **Biology of Antarctic Seas**, Antarctic Research Series 5, AGU, Washington, D.C.

Hays, J. D. and Shackleton, N. J. 1976. Globally synchronous extinction of the radiolarian **Stylatractus universus. Geology**, 4:649-652.

Hoffman, A. and Kitchell, J. A. 1984. Evolution in a pelagic planktic system: a paleobiologic test of models of multispecies evolution, **Paleobiology**, 10:9-33.

Imbrie, J. and Kipp, N. G. 1971. A new micropaleontological method for quantitative paleoclimatology: application to a late Pleistocene Carribean core, p. 71-181. In Turekian, K. K. (ed.), **Late Cenozoic Glacial Ages**. Yale University Press, New Haven.

Johnson, D. A. and Nigrini, C. A. 1985. Synchronous and time-transgressive Neogene radiolarian datum levels in the equatorial Indian and Pacific Oceans. **Marine Micropaleontology**, 9:489-523.

Kennett, J. P. 1979. Recent zoogeography of Antarctic plankton microfossils, p. 328-355. In van der Spoel, S. and Pierrot-Bults, A.C. (eds.), **Zoogeography and Diversity of Plankton**. Halstead, New York.

Kennett, J. P. 1982. **Marine Geology**. Prentice-Hall, Englewood Cliffs, New Jersey.

Kennett, J. P. and Barker, P. F. 1990. Latest Cretaceous to Cenozoic climate and oceanographic developments in the Weddell Sea, Antarctica: an ocean-drilling perspective, p. 937-962. In Barker, P.F. and Kennett, J. P. (eds.), **Proceedings of the Ocean Drilling Program, Scientific Results., Leg 113**. ODP, College Station, Texas.

Kennett, J. P. and Srinivasan, M. S. 1983. **Neogene Planktonic Foraminifera , A Phylogenetic Atlas**. Hutchinson Ross, Stroudsburg, Pennsylvania.

Kitchell, J. A. 1987. The temporal distribution of evolutionary and migrational events in pelagic ecosystems: episodic or continuous? **Paleoceanography,** 2:473-488.

Lazarus, D. B. 1990. Middle Miocene to Recent radiolarians from the Weddell Sea, Antarctica, ODP Leg 113, p. 709-728. In Barker, P. F. and Kennett , J. P. (eds.), **Proceedings of the Ocean Drilling Program, Scientific Results, Leg 113**. ODP, College Station, Texas.

Lazarus, D. B. 1992. Antarctic Neogene radiolarians from the Kerguelen Plateau, ODP Legs 119 and 120, p. 785-810. In Wise, S. W. and Schlich, R. (eds.), **Proceedings of the Ocean Drilling Program, Scientific Results, Leg 120.** ODP, College Station, Texas.

Lazarus, D. B. 1994. The Neptune Project - a marine micropaleontology database, **Mathematical Geology**, 26:817-832.

Lazarus, D. and Caulet, J. P. 1994. Cenozoic Southern Ocean reconstructions from sedimentologic, radiolarian, and other microfossil data, p. 145-174. In Kennett, J. P. and Warnke, D. A. (eds.), **The Antarctic Paleonvironment: A Perspective on Global Change. Part 2, Antarctic Research Series**. AGU, Washington, D. C.

Lipps, J. H. 1970. Plankton evolution. **Evolution**, 24:1-22.

Lipps, J. H. 1986. Extinction dynamics in pelagic ecosystems, p. 87-104. In Elliot, D. K. (ed.), **Dynamics of Extinction**. Wiley, New York.

Lozano, J. A. and Hays, J. D. 1976. Relationship of radiolarian assemblages to sediment types and physical oceanography in the Atlantic and western Indian Ocean sectors of the Antarctic Ocean, p. 303-336. In Cline, R. M. and Hays, J. D. (eds.), **Investigation of Late Quaternary Paleoceanography and Paleoclimatology.** GSA, Boulder, Colorado.

Mackensen, A., Barrera, E. and Hubberten, H.-W. 1992. Neogene circulation in the Southern Indian Ocean: evidence from benthic foraminifers, carbonate data, and stable isotope analyses, p. 867-880. In: Wise, S.W. and Schlich, R. (eds.), **Proceedings of the Ocean Drilling Program, Science Results, Leg 120**. ODP, College Station, Texas.

Marshall, C. R. 1990. Confidence intervals on stratigraphic ranges. **Paleobiology**, 16:1-10.

Marshall, C. R. 1994. Confidence intervals on stratigraphic ranges: partial relaxation of the assumption of randomly distributed fossil horizons. **Paleobiology**, 20:459-469.

Marshall, C. R., 1997. Confidence intervals on stratigraphic ranges with nonrandom distributions of fossil horizons. **Paleobiology**, 23: 165-173.

McGowan, J. A. 1986. The biogeography of pelagic ecosystems, p. 191-200. In Pierrot-Bults, A. C. van der Spoel, S. Zahuranec B. J. and Johnson, R. K. (eds.), **Pelagic Biogeography.** UNESCO, Paris.

Miller, K. G. and Fairbanks, R. G. 1985. Oligocene to Miocene carbon isotope cycles and abyssal circulation changes. In Sundquist, E. J. and Broecker, W. S. (eds.), **The Carbon Cycle and Atmospheric CO2: Natural Variations Archean to Present**. Geophysical Monographs. AGU, Washington, D. C. Moore, T. C., Shackleton, N. J. and Pisias, N. G. 1993. Paleoceanography and the diachrony of radiolarian events in the eastern equatorial Pacific. **Paleoceanography**, 8:567-586.

Nakaseko, K. and Nishimura, A. 1982. Radiolaria from the bottom sediments of the Bellingshausen Basin in the Antarctic Sea. **Reports of the Technology Research Center of Japan National Oil Corporation**, 16:91-244.

Norris, R. D. 1991. Biased extinction and evolutionary trends. **Paleobiology**, 17:388-399.

Pearson, P. N. 1993. A lineage phylogeny for the Paleogene planktonic foraminifera. **Micropaleontology**, 39:193-232.

Pearson, P. 1996. Cladogenetic, extinction and survivorship patterns from a lineage phylogeny: the Paleogene planktonic foraminifera. **Micropaleontology**, 42:179-188.

Petrushevskaya, M. G. 1967. Radiolarians of the orders Spumellaria and Nassellaria of the Antarctic region, **Issled. Fauny morei** 4:5-186.

Petrushevskaya, M. G. 1975. Cenozoic radiolarians of the Antarctic Deep Sea Drilling Project Leg 29, p. 541-676. In Kennett J. P. and Houtz, R. E. (eds.), **Initial Reports of the Deep Sea Drilling Project, Leg 29**. U. S. Government Printing Office, Washington, D. C.

Raffi, I. 2002. Revision of the early-middle Pleistocene calcareous nannofossil biochronology (1.75 to 0.85 Ma). **Marine Micropaleontology**, 45: 25-56.

Roth, P. H. 1987. Mesozoic calcareous nannofossil evolution: relation to paleoceanographic events. **Paleoceanography**, 2:601-611.

Siegfried, W. R., Condy, P. R. and Laws, R. M. (eds.) 1985. **Antarctic Nutrient Cycles and Food Webs**. Springer, Berlin.

Stanley, S. M., Whetmore, K. L. and Kennett, J. P. 1988. Macroevolutionary differences between the two major clades of Neogene planktonic foraminifera. **Paleobiology**, 14:235-249.

Stehli, F. G., Douglas, R. G. and Kafesioglu, I. A. 1972. Models for the evolution of planktonic foraminifera, p. 116-128. In Schopf, T. J. M. (ed.), **Models in Paleobiology**. Freeman, Cooper, San Francisco, California.

Stenseth, N. C. and Maynard-Smith, J. 1984. Coevolution in ecosystems: Red Queen evolution or stasis? **Evolution**, 38:870-880.

Takahashi, K. 1991. **Radiolaria: Flux, Ecology, and Taxonomy in the Pacific and Atlantic.** Woods Hole Oceanographic Institution, Woods Hole, Massachusetts.

Thierstein, H., Geitzenauer, K. R., Molfino, B. and Shackleton, N. J. 1977. Global synchroneity of late Quaternary coccolith datum levels: validation by oxygen isotopes. **Geology**, 5:400-404.

Thunell, R. C. 1981. Cenozoic palaeotemperature changes and planktonic foraminiferal speciation. **Nature**, 289:670-672.

Van Couvering, J. A., Berggren, W. A., Drake, R. E., Aguirre, E., and Curtis, G. H. 1976. The terminal Miocene event. **Marine Micropaleontology**, 1:263-286.

van Valen, L. 1973. A new evolutionary law. **Evol. Theory**, 1:1-30.

Vrba, E. S. 1980. Evolution, species and fossils: how does life evolve? **South African Journal of Science**, 76:61-84.

Vrba, E. S. 1985. Environment and evolution: alternative causes of the temporal distribution of evolutionary events. **S.-Afr. Tydskr. Wet**., 81:229-236.

Wei, K. Y. and Kennett, J. P. 1983. Non-constant extinction rates of Neogene planktonic foraminifera. **Nature**, 305:218-230.

Wei, K. Y. and Kennett, J. P. 1986. Taxonomic evolution of Neogene planktonic foraminifera and paleoceanographic relations. **Paleoceanography**, 1:67-84.

Wright, J. D. and Miller, K. G. 1992. Miocene stable isotope stratigraphy, Site 747, Kerguelen Plateau, p. 855-866. In Wise, S.W. and Schlich, R. (eds.), **Proceedings of the Ocean Drilling Program, Science Results, Leg 120**. ODP, College Station, Texas.

Figure 2 List.

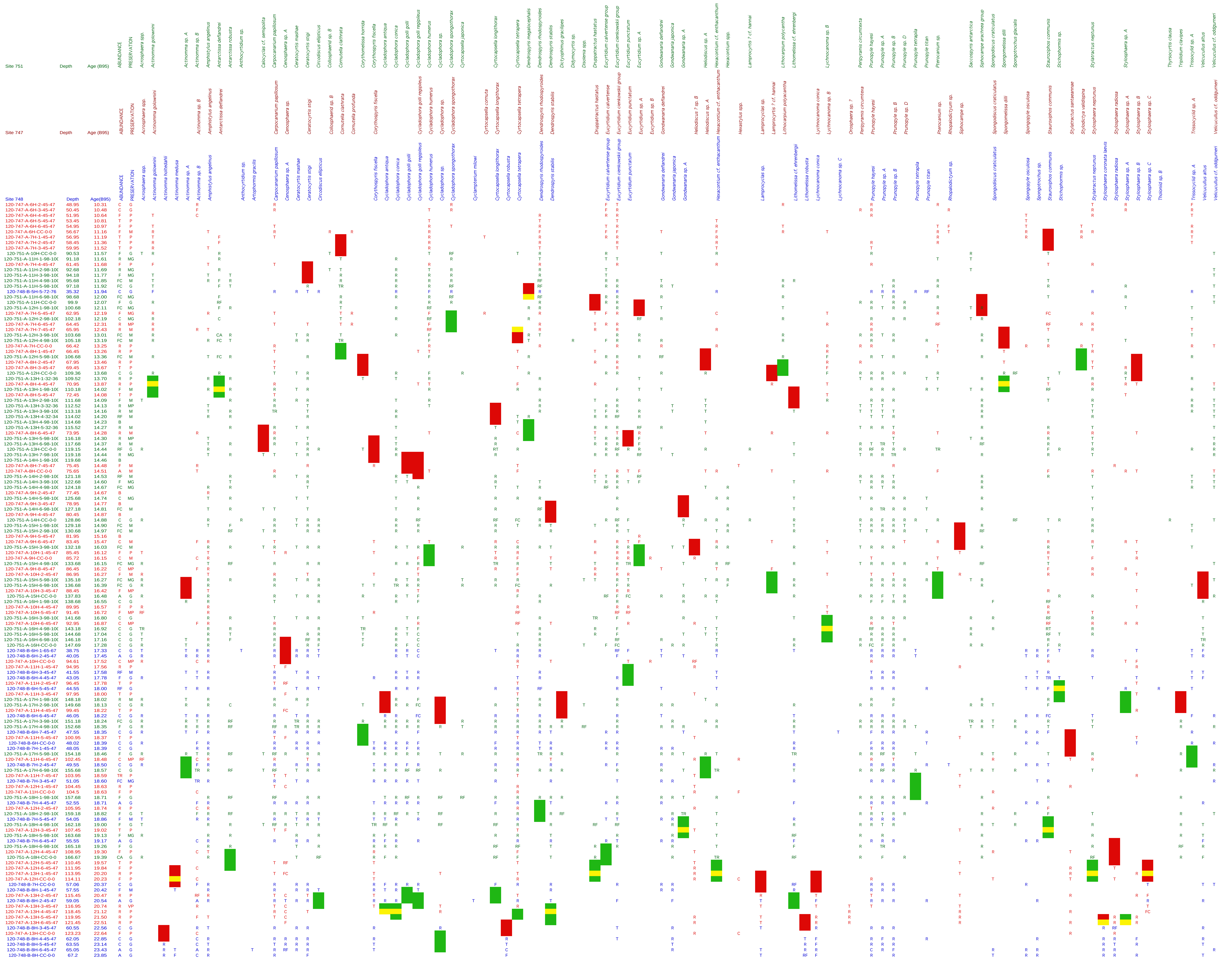
Number	Lazarus list	Abelmann list	Caulet list
1	**Velicucullus** sp.	**Gondwanaria deflandrei**	**Cycladophora pliocenica**
2	**C. antiqua**	**Prunopyle hayesi**	**Desmospyris rhodospyroides**
3	**C. regipileus**	**Gondwanaria japonica**	**Eucyrtidium biconicum**
4	**C. golli group**	**Collosphaerid** sp. **B**	**Helotholus praevema**
5	**S. santaenae**	**Spongodiscus craticulatus**	**Lychnocanium grande**
6	**C. longithorax**	**Corythospyris fiscella**	**Prunopyle frakesi**
7	**L. conica**	**Actinomma** sp. **B**	**Stichocorys peregrina**
8	**Stylacontarium** sp.	**Amphistylus angelinus**	**Antarctissa cylindrica**
9	**C. microporus**	**Actinomma medusa**	**Antarctissa robusta**
10	**A. magnifenestra**	**Heliodiscus** ? sp. **B**	**Anthocyrtella callopisma**
11	**Sethoconus** sp.	**Spongopyle osculosa**	**Prunopyle tetrapila**
12	**C. tetrapera**	**Carpocanarium papillosum**	**Spongotrochus glacialis**
13	**H. philosophica ?**	**Velicucullus** cf. **oddgurneri**	**Eucyrtidium inflatum**
14	**D. hastatus**	**Cenosphaera** sp. **A**	**Saturnalis circularis**
15	**L. timmsi**	**Actinomma holtedahli**	**Stylatractus universus**
16	**E. cienkowski**	**Ceratocyrtis stigi**	**Triceraspyris coronata**
17	**A. angelinus**	**Prunopyle** sp. **A**	**Prunopyle titan**
18	**D. rhodospyroides**	**Spongotrochus sp.**	**Rhizosphaera antarctica**
19	**P. hayesi**	**Prunopyle titan**	**Lamprocyrtis heteroporos**
20	**T. coronata** group	**Prunopyle** sp. **B**	**Desmosypris spongiosa**
21	**E. punctatum**	**Eucyrtidium cienkowskii** group	**Phorticum clevei**
22	**D. crisae**	**Stylosphaera radiosa**	**Pseudocubus vema**
23	**S. circularis**	**Cyrtocapsella robusta**	**Botyropera triloba**
24	**E. calvertense**	**Stylosphaera** sp. **B**	**Acanthodesmia viniculata**
25	**C. disparidens**	**Lamprocyclas** sp.	**Gondwanaria dogieli**
26	**S. bicorne** ?	**Ceratocyrtis mashae**	**Cycladophora davisiana**
27	**T. clausa**	**Stylosphaera coronata laevis**	**Actinomma popofskii**
28	**C. japonica**	**Velicucullus altus**	**Antarctissa denticulata**
29	**C.magnisphaera**	**Lithomelissa robusta**	**Pterocanium trilobum**
30	**Rhopalastrum** spp.	**Lychnocanoma conica**	**Antarctissa strelkovi**
31	**Didymocyrtis/Diartus** spp.	**Cycladophora** sp.	**Eucyrtidium teuscheri teuscheri**
32	**A. deflandrei**	**Stylatractus santaeannae**	**Lithelius nautiloides**
33	**C. humerus**	**Siphocampe** sp.	**Saccospyris antarctica**
34	**D. megalocephalis**	**Stylosphaera** sp. **C**	**Saccospyris conithorax**
35	**A. golowini**	**Cycladophora antiqua**	**Triceraspyris antarctica**
36	**Lampromitra** sp.	**Cycladophora conica**	**Cycladophora bicornis**
37	**S. glacialis**	**Cycladophora golli regipileus**	**Prunopyle antarctica**
38	**S. universus**	**Cycladophora golli golli**	**Dictyophimus mawsoni**
39	**P. korotnevi**	**Cyrtocapsella tetrapera**	**Mitrocalpis araneafera**
40	**A. murrayana**	**Dendrospyris stabilis**	**Plectacantha** sp.
41	**C. spongothorax**	**Lithomelissa** cf. **ehrenbergi**	**Litharachnium tentoriu**
42	**E. pseudoinflatum**	**Circodiscus ellipticus**	

Figure 2 List (continued).

Number	Lazarus list	Abelmann list	Caulet list
43	**S. transparum**	**Cyrtocapsella longithorax**	
44	**C. bicornis**	**Hexacontium** cf. **enthacanthum**	
45	**S. vesuvius**	**Druppatractus hastatus**	
46	**A.australis**	**Prunopyle** sp. **D**	
47	**L. stigi**	**Siphocampe arachnea** group	
48	**L. grande**	**Stylatractus neptunus**	
49	**P. titan**	**Antarctissa robusta**	
50	**S. peregrina**	**Acrosphaera** spp.	
51	**D.** cf. **megalocephalis**	**Peripyramis circumtexta**	
52	**C. pliocenica**	**Tripilidium clavipes**	
53	**Helotholus haysi**	**Calocyclas** cf. **semipolita**	
54	**A. strelkovi**	**Eucyrtidium calvertense** group	
55	**A.** ? **mercurius**	**Stauroxiphos communis**	
56	**Anthocyrtidium** sp.	**Gondwanaria** sp. **A**	
57	**A. denticulata**	**Dictyophimus gracilipes**	
58	**A. labrata**	**Dendrospyris rhodospyroides**	
59	**L.timmsi** ?	**Cyrtocapsella japonica**	
60	**L. aegles**	**Saccospyris antarctica**	
61	**A.challengerae**	**Prunopyle tetrapila**	
62	**A. cylindrica**	**Heliodiscus** sp. **A**	
63	**H. vema**	**Actinomma** sp. **A**	
64	**D. spongiosa**	**Trissocylid** sp. **A**	
65	**P. c. trilobum**	**Corythomelissa horrida**	
66	**T. antarctica**	**Stylosphaera** sp. **A**	
67	**C. davisiana**	**Stichophormis** sp.	
68	**Eucyrtidium punctatum**		
69	**Lychnocanoma** sp. **B**		
70	**Pterocanium** sp.		
71	**Lamprocyrtis** ? cf. **hannai**		
72	**Eucyrtidium** sp. **A**		
73	**Cycladophora humerus**		
74	**Dendrospyris megalocephalis**		
75	**Antarctissa deflandrei**		
76	**Actinomma golownini**		
77	**Spongomelissa dilli**		
78	**Lithocarpium polycantha**		
79	**Stylodictya validispina**		
80	**Cornutella clathrata**		
81	**Cycladophora spongothorax**		

	A	B	C	D	E
1	Age	mbsf	Sample Name	Abunda	Preservation
2	Age	mbsf	Sample Name	Abundanc	Preservation
3	Age	mbsf	Sample Name	Abundanc	Preservation
4	Age	mbsf	Sample Name	Abundan	Preservation
5	Age	mbsf	Sample Name	Abundan	Preservation
6	0.007	0.45	747A-1H-1,45-47	C-A	G
7	0.174	1.95	747A-1H-2, 45-47	C	G
8	0.34	3.45	747A-1H-3,45-47	A	M-G
9	0.357	0.98	751A-1H-1,98-102	A	G
10	0.487	0.10	748B-1H,CC	A	G
11	0.507	4.95	747A-1H-4, 45-47	A	G
12	0.55	1.50	751A-1-1,'BOTTOM'	A	G
13	0.655	0.55	748B-2H-1,45-47	A	G
14	0.673	6.45	747A-1H-5,45-47	A	M-G
15	0.84	7.95	747A-1H-6, 45-47	A	G
16	0.956	9.00	747A-1H, CC	C	G
17	1.006	9.45	747A-2H-1,45-47	A	G
18	1.037	3.53	744A-1H-3,53-55	A	G
19	1.173	10.95	747A-2H-2, 45-47	A	G
20	1.195	4.73	744A-2H-1,53-55	A	G
21	1.213	2.05	748B-2H-2,45-47	A	M-G
22	1.34	12.45	747A-2H-3,45-47	A	G
23	1.393	6.23	744A-2H-2,53-55	A	G
24	1.456	13.95	747A-2H-4, 45-47	A	G
25	1.591	7.73	744A-2H-3,53-55	A	G
26	1.673	15.45	747A-2H-5,45-47	A	G
27	1.739	2.56	751A-1H-2,106-110	A	G
28	1.789	9.23	744A-2H-4,53-55	A	G
29	1.789	3.45	751A-1H-3,45-50	A	G
30	1.839	16.95	747A-2H-6, 45-47	A	G
31	1.915	5.68	751A-2H-1,98-102	A	G
32	2	7.18	751A-2H-2,98-102	A	G
33	2.006	18.45	747A-2H-7,45-47	A	G
34	2.011	18.50	747A-2H, CC	A	G
35	2.061	18.95	747A-3H-1,45-47	A	G
36	2.228	20.45	747A-3H-2, 45-47	A	G
37	2.448	14.23	744A-3H-1,53-55	C-A	G
38	2.631	3.10	748B-2H-3,'TOP'	A	G
39	2.718	15.73	744A-3H-2,53-55	A	M-G
40	2.801	4.60	748B-2H-3,BOTTOM	C	G
41	3.022	6.55	748B-2H-5,45-47	A	G
42	3.192	8.05	748B-2H-6,45-47	A	G
43	3.368	9.60	748B-2H,CC	A	G
44	3.486	8.68	751A-2H-3,98-102	C-A	G
45	3.555	14.20	751A-2H,CC	C-A	G
46	3.698	21.95	747A-3H-3,45-47	A	G
47	3.753	23.45	747A-3H-4, 45-47	A	G
48	3.806	15.18	751A-3H-1,98-102	C-A	G
49	3.807	24.95	747A-3H-5,45-47	A	G
50	3.861	26.45	747A-3H-6, 45-47	A	G
51	3.879	16.68	751A-3H-2,98-102	A	G
52	3.953	18.18	751A-3H-3,98-102	C	G
53	4.027	19.68	751A-3H-4,98-102	A	G
54	4.1	21.18	751A-3H-5,98-102	C	G
55	4.142	23.70	751A-3H,CC	A	G
56	4.346	26.18	751A-4H-2,98-102	C	G
57	4.419	27.68	751A-4H-3,98-102	A	M
58	4.467	28.00	747A-3H, CC	A	G
59	4.493	29.18	751A-4H-4,98-102	A	G
60	4.512	150.53	745B-18-2,53-55		
61	4.567	30.68	751A-4H-5,98-102	C-A	G
62	4.597	153.53	745B-18-4,53-55	C-A	VG
63	4.64	32.18	751A-4H-6,98-102	A	G
64	4.649	29.10	747A-4H-1,110-112	A	G
65	4.649	29.95	747A-4H-2, 45-47	A	G
66	4.682	156.53	745B-18-6,53-55	A	G
67	4.69	33.20	751A-4H,CC	A	G
68	4.739	34.18	751A-5H-1,98-102	C	E
69	4.78	159.96	745B-19-2,46-48	C	G
70	4.788	35.19	751A-5H-2,49-51	A	G
71	4.858	164.46	745B-19-5,46-48	C	M-G
72	4.872	165.96	745B-19-6,46-48	A	G
73	4.903	169.53	745B-20-2,53-55	C-A	G
74	4.93	175.53	745B-20-6,53-55	A	G
75	4.957	182.03	745B-21-4,53-55	A	G
76	5.967	188.53	745B-22-2,53-55	F	G
77	6.018	191.53	745B-22-4,53-55	A	G
78	6.07	194.53	745B-22-6,53-55	F-C	G
79	6.079	32.10	747A-4H-3,110-112	F-C	M
80	6.13	198.03	745B-23-2,53-55	C	G
81	6.141	32.95	747A-4H-4, 45-47	F	P
82	6.189	33.60	747A-4H-4,110-112	F	M
83	6.233	204.03	745B-23-6,53-55	F	G
84	6.251	34.45	747A-4H-5,45-47	C-A	P-M
85	6.273	36.69	751A-5H-3,49-51	C-A	VG
86	6.293	207.53	745B-24-2,53-55	C	G
87	6.306	37.18	751A-5H-3,98-102	A	G
88	6.361	35.95	747A-4H-6, 45-47	C	P-M
89	6.373	38.18	752A-5H-4,48-50	A	VG-E
90	6.406	38.68	751A-5H-4,98-102	A	
91	6.408	36.60	747A-4H-6,110-112	F-C	P
92	6.44	165.33	746A-4-1,53-55	A	G
93	6.506	166.83	746A-4-2,53-55	C-A	M-G
94	6.506	40.18	751A-5H-5,98-102	A	G
95	6.571	168.33	746A-4-3,53-55	C-A	M-G
96	6.573	41.18	751A-5H-6,48-50	A	G
97	6.594	42.70	751A-5H,CC	A	G
98	6.636	169.83	746A-4-4,53-55	A	G
99	6.702	171.33	746A-4-5,53-55	C	G
100	6.767	172.83	746A-4-6,53-55	C	VG
101	6.854	174.83	746A-5-1,53-55	A	VG
102	6.985	177.83	746A-5-3,53-55	C	M
103	7.01	213.53	745B-24-6,53-55	C-A	G
104	7.05	179.33	746A-5-4,53-55	F	M?
105	7.115	180.83	746A-5-5,53-55	A	G
106	7.18	182.33	746A-5-6,53-55	C	M-G
107	7.329	185.83	746A-6-2,53-55	A	G
108	7.394	187.33	746A-6-3,53-55	A	G
109	7.458	188.83	746A-6-4,53-55	F-C	G
110	7.585	191.83	746A-6-6,53-55	C	M
111	7.643	192.96	746A-6-7,53-55	C-A	M-G
112	7.72	195.33	746A-7-2,53-55	A	G
113	7.835	198.33	746A-7-4,53-55	C-A	M-G
114	7.95	201.33	746A-7-6,53-55	A	G
115	8.027	203.33	746A-8-1,53-55	C-A	G
116	8.122	206.33	746A-8-3,53-55	C	G
117	8.197	209.10	746A-8-CC,20-22	C-A	M-G
118	8.36	215.78	746A-9-5,48-50	A	G
119	8.424	218.33	746A-10-1,53-55	C	G
120	8.499	221.33	746A-10-3,53-55	R	G
121	8.575	224.33	746A-10-5,53-55	C	G
122	8.663	227.83	746A-11-1,53-55	A	G
123	8.738	230.83	746A-11-3,53-55	C-A	G
124	8.825	37.50	747A-4H, CC	A	G
125	8.999	10.05	748B-3H-1,45-47	A	M
126	9.036	232.33	746A-11-4,53-55	C	M
127	9.088	11.55	748B-3H-2,45-47	C	G
128	9.113	233.83	746A-11-5,53-55	A	G
129	9.177	13.05	748B-3H-3,45-47	A	G
130	9.182	41.62	747A-5H-3,112-114	A	G
131	9.236	43.23	751A-6H-1,53-55	A	G
132	9.254	42.45	747A-5H-4, 45-47	C	M-G
133	9.259	43.68	751A-6H-1,98-102	A	G
134	9.312	44.70	751A-6H-2,50-52	C-A	G
135	9.442	43.12	747A-5H-5,112-114	C	M
136	9.475	45.45	747A-5H-6, 45-47	A	M-G
137	9.581	45.18	751A-6H-2,98-102	C	G
138	9.625	46.68	751A-6H-3,98-102	F-C	G
139	9.648	47.00	747A-5H, CC	F	M
140	9.65	244.23	746A-13-2,53-55	A	G
141	9.684	49.20	751A-6H-5,50-52	C	G
142	9.719	23.72	744A-4H-1,52-54	A	G
143	9.737	25.22	744A-4H-2,59-61	A	G
144	9.754	26.72	744A-4H-3,52-54	C	G
145	9.76	52.20	751A-6H,CC	C	G
146	9.771	28.23	744A-4H-4,59-61	C-A	G
147	9.796	19.10	748B-3H,CC	C	G
148	9.805	247.23	746A-13-4,53-55	A	G
149	9.808	19.55	748B-4H-1,45-47	C	G
150	9.811	54.20	751A-7H-2,50-52	C-A	G
151	9.829	33.23	744A-5H-1,53-55	A	M-G
152	9.863	36.23	744A-5H-3,53-55	A	M-G
153	9.879	37.60	744A-5H-4,36-38	A	G
154	9.926	58.70	751A-7H-5,50-52	C	G
155	10.002	61.70	751A-7H-7,50-52	C	VG
156	10.002	61.70	751A-7H,CC	A	G
157	10.065	64.16	751A-8H-2,98-102	C-A	G
158	10.068	252.33	746A-14-1,53-55	C	G
159	10.103	65.68	751A-8H-3,98-102	C	G
160	10.141	67.18	751A-8H-4,98-102	A	G
161	10.18	68.68	751A-8H-5,98-102		
162	10.214	71.20	751A-8H,CC	C-A	G
163	10.312	48.95	747A-6H-2, 45-47	C-A	M
164	10.477	50.45	747A-6H-3,45-47	A	M
165	10.569	262.03	746A-15-1,53-55	F-C	M
166	10.6	72.18	751A-9H-1,98-102	C	G
167	10.642	51.95	747A-6H-4, 45-47	C	M
168	10.679	73.68	751A-9H-2,98-102	C	G
169	10.759	75.18	751A-9H-3,98-102	C-A	G
170	10.838	76.68	751A-9H-4,98-102	C	G
171	10.918	78.18	751A-9H-5,98-102	A	G
172	10.971	54.95	747A-6H-6, 45-47	A	G
173	10.997	79.18	751A-9H-6,98-102	A	G
174	11	271.64	746A-16-1,53-55	A	G
175	11.052	80.70	751A-9H,CC	A	G
176	11.103	81.68	751A-10H-1,98-102	C-A	G
177	11.141	56.50	747A-6H, CC	F	M
178	11.169	42.73	744A-6H-1,53-55	C-A	G
179	11.183	83.18	751A-10H-2,98-102	A	G
180	11.212	21.05	748B-4H-2,45-47	A	G
181	11.262	84.68	751A-10H-3,98-102	F-C	G
182	11.288	22.55	748B-4H-3,45-47	C	G
183	11.342	86.18	751A-10H-4,98-102	A	G
184	11.355	58.45	747A-7H-2, 45-47	F-C	M
185	11.365	24.05	748B-4H-4,45-47	C	G
186	11.421	87.68	751A-10H-5,98-102		
187	11.501	89.18	751A-10H-6,98-102	A	G
188	11.52	59.95	747A-7H-3,45-47	C	P
189	11.555	90.20	751A-10H,CC	A	G
190	11.596	28.66	748B-4H,CC	C	G
191	11.607	91.18	751A-11H-1,98-102	C	G
192	11.684	61.45	747A-7H-4, 45-47	R-F	P
193	11.695	30.55	748B-5H-2,45-47	A	G
194	11.766	94.18	751A-11H-3,98-102	C	M
195	11.806	45.73	744A-6H-3,53-55	A	M-G
196	11.845	95.68	751A-11H-4,89-102	A	M-G
197	11.847	33.55	748B-5H-4,45-47	C	G
198	11.925	97.18	751A-11H-5,98-102	A	G
199	11.999	36.55	748B-5H-6,45-47	A	G
200	12.004	98.68	751A-11H-6,98-102	C-A	G
201	12.058	99.70	751A-11H,CC	A	M
202	12.078	38.10	748B-5H,CC	C	G
203	12.11	100.68	751A-12H-1,98-102	C-A	G
204	12.124	47.23	744A-6H-4,60-62	C-A	G
205	12.309	64.45	747A-7H-6, 45-47	C-A	M-G
206	12.435	66.00	747A-7H, CC	F	P
207	13.006	103.68	751A-12H-3,98-102	A	M
208	13.185	105.18	751A-12H-4,98-102	A	M
209	13.257	66.45	747A-8H-1,45-47	C	P
210	13.275	52.65	744A-7H-1,95-97	A	P-M
211	13.364	106.68	751A-12H-5,98-102	A	M
212	13.461	67.95	747A-8H-2, 45-47	F	P
213	13.543	108.18	751A-12H-6,98-102	A	G
214	13.665	109.20	751A-12H,CC	A	M
215	13.823	55.23	744A-7H-3,53-55	A	P-M
216	13.871	70.95	747A-8H-4, 45-47	C	M
217	14.141	56.73	744A-7H-4,60-62	A	M
218	14.28	73.95	747A-8H-6, 45-47	C	M
219	14.415	118.70	751A-13-CC	A	M-G
220	14.46	58.23	744A-7H-5,53-55	A	P-M
221	14.491	75.50	747A-8H, CC	C	M
222	14.664	59.19	744A-7H-6,46-48	A	P-M
223	14.67	76.40	747A-9H-2, 40-42	C	M
224	14.772	77.40	747A-9H-3, 45-47	F-C	P-M
225	14.852	128.20	751A-14-CC	A	M
226	14.87	79.04	747A-9H-4, 45-47	C	P-M
227	15.165	80.54	747A-9H-5, 45-47	C	M
228	15.469	82.04	747A-9H-6, 45-47	A	M-G
229	15.559	63.23	744A-8H-2,60-62	A	M
230	15.783	85.00	747A-9H, CC	C	M
231	15.894	64.73	744A-8H-3,53-55	A	P-M
232	16.219	85.04	747A-9H-8, 45-47	A	M
233	16.27	86.95	747A-10H-2, 45-47	C	M
234	16.474	137.70	751A-15-CC	A	M
235	16.57	89.95	747A-10H-4, 45-47	C	P
236	16.798	66.23	744A-8H-4,60-62	C	P
237	16.87	92.95	747A-10H-6, 45-47	C	P
238	17.242	147.20	751A-16-CC	C-A	M
239	17.279	71.30	744A-9H-1,60-62	A	M
240	17.327	38.75	748B-6H-1,65-67	A	M
241	17.445	40.05	748B-6H-2,45-47	C	M
242	17.499	94.50	747A-10H, CC	R	P
243	17.779	43.05	748B-6H-4,45-47	C	M
244	17.783	96.45	747A-11H-2, 45-47	F	P
245	18.22	99.45	747A-11H-4, 45-47	R-F	P
246	18.22	46.05	748B-6H-6,45-47	A	M
247	18.356	47.60	748B-6H,CC	A	G
248	18.479	102.45	747A-11H-6, 45-47	F	P
249	18.496	49.55	748B-7H-2,45-47	A	M
250	18.594	80.73	744A-10H-1,60-62	A	P-M
251	18.597	104.00	747A-11H, CC	F	P
252	18.639	156.70	751A-17-CC	A	M-G
253	18.711	52.55	748B-7H-4,45-47	A	M
254	18.744	105.95	747A-12H-2, 45-47	F	P
255	19.02	107.50	747A-12H-3, 45-47	F	P-M
256	19.077	83.75	744A-10H-3,60-62	A	P-M
257	19.175	55.55	748B-7H-6,45-47	A	M
258	19.256	85.25	744A-10H-4,60-62	A	M
259	19.301	108.45	747A-12H-4, 45-47	C	P
260	19.571	110.50	747A-12H-5, 45-47	F	P
261	19.613	88.25	744A-10H-6,60-62	A	M
262	19.75	89.40	744A-10H-7,16-18	A	P-M
263	19.8	166.20	751A-18-CC	C-A	P-M
264	19.84	111.95	747A-12H-6, 45-47	F	P
265	20.119	113.50	747A-12H, CC	F	P
266	20.374	57.10	748B-7H,CC	A	M
267	20.541	59.05	748B-8H-2,45-47	A	M
268					

S19 S23 S53 N33 N82 S16 N73 S55 N42


Site 751
Depth
Age (B95)
Site 747
Depth
Age (B95)
Site 748
Depth
Age(B95)
ABUNDANCE
PRESERVATION