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How synchronous are Neogene marine plankton events?

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Abstract. We analyzed the synchrony and diachrony of commonly used Neogene biostratigraphic events from data published in the Initial Reports of the Deep Sea Drilling Project (DSDP) and in the Proceedings of the Ocean Drilling Program (ODP). On the basis of the combined biostratigraphic and magnetostratigraphic evidence, new Neogene age models were constructed for 35 globally distributed DSDP and ODP holes. Biostratigraphic events from the four major plankton groups (calcareous nannofossils, diatoms, planktonic foraminifera, and radiolarians) were compiled from DSDP and ODP reports. After the elimination of possible sources of error such as stratigraphic hiatuses and reworking of specimens, 124 biostratigraphic events that occurred in at least four holes were analyzed in detail: for each event a biochronologic age estimate was derived by projection of the depth of the event onto the line of correlation of each hole, and from these a global mean age for each event was calculated, together with its standard deviation. Average standard deviations for event ages by fossil group are: calcareous nannofossil first appearance datums (FADs): 0.57 m.y. (21 events), calcareous nannofossil last appearance datums (LADs): 0.60 m.y. (25 events), diatom FADs: 0.57 m.y. (7 events), diatom LADs: 0.85 m.y. (14 events), planktonic foraminifera FADs: 0.88 m.y. (22 events), foraminifera LADs: 0.68 m.y. (16 events), radiolarian FADs: 0.30 m.y. (9 events), radiolarian LADs: 0.31 m.y. (10 events). Since the average sample spacing in the sites used for this analysis is only 0.185 m.y., we have examined the data for true patterns of diachrony and for other biases. Diachrony is more frequent among cosmopolitan than among endemic taxa, thus there is a general trade-off between the obtainable age precision and the geographic extent of a bioevent. Precision of age calibrations also decreases with increasing age. Although some of these features may be due to investigator bias, they appear in part to be real phenomena, and thus could also provide opportunities for further exploration of important paleobiological processes, such as change in environmental gradients through time, evolutionary adaptation of species populations and migration due to water mass changes.

Introduction

The general assumption on which traditional biostratigraphy is based is that first occurrences and last occurrences of taxa in various sedimentary sections represent synchronous events, thus justifying the biochronologic definition of first appearance datums (FADs) and last appearance datums (LADs). We use the FAD, LAD, and event as synonymous to the term "biohorizon" as defined in the *International Stratigraphic Guide* [Hedberg, 1976]. Synchrony of such biohorizons, demonstrated by globally distributed calibrations with other synchronous events, would elevate these units to chronologic rank (e.g., to "chronohorizons"). Ecologically, the assumption of synchrony of a biohorizon may be questionable, but the success of biochronology suggests that, within certain limits, the assumption is usually correct. Only with recent attempts to refine biochronologic resolution and in combination with other techniques, such as magnetostratigraphy

and chemostratigraphy, it has become possible to verify and quantify synchrony and diachrony. Although some biostratigraphic events are demonstrably synchronous to within a few thousand years [e.g., *Hays and Shackleton*, 1976; *Thierstein et al.*, 1977; *Backman and Shackleton*, 1983; *Wei*, 1993], many authors have also demonstrated diachrony of appearances and extinctions, sometimes ranging up to several million years [e.g., *Thierstein*, 1976; *Johnson and Nigrini*, 1985; *Barron*, 1985b; *Dowsett*, 1988; *Pujos*, 1988; *Hills and Thierstein*, 1989; *Wei and Wise*, 1992; *Wei*, 1993; *Spencer-Cervato et al.*, 1993].

As part of a larger project on the evolution of marine plankton in the Neogene, a recompilation and synthesis of biostratigraphic and magnetostratigraphic data has recently been performed on a large suite of Deep Sea Drilling Program (DSDP) and Ocean Drilling Program (ODP) sites [Lazarus et al., 1992; Spencer-Cervato et al., 1992]. Such an analysis is a necessary first step if macroevolutionary studies of speciation rates, extinction rates, and longevity analyses are to yield meaningful results. Knowledge of diachrony is also a prerequisite for microevolutionary studies of cladogenesis, because morphologic transitions can only be expected in the area of the earliest first appearance; in sections from other areas, speciation will likely appear punctuational, a pattern that is to be expected with any immigration event.

In this article we discuss the biochronologic significance of our analyses and present a global synthesis of the age of occurrence of

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some of the most used biostratigraphic markers along with an analysis of their reliability. Our goal is to quantify the magnitude of error in current Neogene planktonic microfossil biostratigraphic data, to identify the possible mechanisms that produce this error, and to suggest strategies for improving Neogene biostratigraphic accuracy.

Methods

All of the 96 DSDP Initial Reports and the ODP Scientific Results up to leg 115 (available when we started this analysis in 1992) were examined and a first selection of 110 holes was made based on geographic location, recovery, lithology, preservation, and the availability of detailed biostratigraphic data for more than one plankton group. The limited number of sites used is a compromise between geographic and stratigraphic coverage, recovery, and the detail and quality of micropaleontological documentation. By using a uniform set of criteria for this selection we tried to avoid biases by including holes that were preferentially used for one or the other plankton group. Biostratigraphic data subsequently published in the literature could not yet be included. Thirty-five of these holes had an interpretable magnetostratigraphy, and these were selected for the analysis presented here. The 35 holes are globally distributed (Figure 1).

The record of geomagnetic reversals in deep-sea sediments can be assumed to be globally synchronous to within a few thousand years. Diachrony at that level is to be expected from differential bioturbation and early diagenetic processes [Verosub, 1977]. Magnetostratigraphic reversals therefore represent a fixed temporal sequence that, if properly identified, can be utilized as calibration for the associated biostratigraphic events. In this study we used the calibration of the geomagnetic polarity time scale proposed by Berggren *et al.* [1985]. As it is frequently necessary to apply biostratigraphic data to help identify magnetic polarity

intervals, there is the possibility of circular reasoning, when we subsequently determine the apparent local age of individual events from calibrated magnetic reversals. However, as we have considered the biostratigraphic evidence of all available plankton groups together with the magnetostratigraphic evidence for each hole in developing the individual age models, we consider circularity of age estimation for individual events as negligible.

More than 400 biostratigraphic events were identified, including the commonly used biostratigraphic markers previously correlated to the geomagnetic polarity timescale. These are for calcareous nannofossils and planktonic foraminifera: Berggren *et al.* [1985]; for radiolarians: Hays and Opdyke [1967], Hays [1970], Theyer *et al.* [1978], Johnson and Nigrini [1985], Goll and Bjørklund [1989], Nigrini [1991], Harwood *et al.* [1992]; for diatoms: Barron [1981, 1985a, b], Berggren *et al.* [1985], Koizumi and Tanimura [1985], Gersonde and Burckle [1990], Mikkelsen [1990], and Harwood and Maruyama [1992].

Data were extracted from the distribution range charts published in the DSDP Initial Reports and ODP Scientific Results. The depth of biostratigraphic events (such as first and last occurrence, evolutionary first occurrences, first and last abundant occurrence of a species) are given in meters below seafloor: for first occurrences the depth of the sample in which the species first occurs and the depth of the sample below it; for last occurrences the depth of the sample in which the species is last observed and the depth of the sample above it. Reworked specimens were often identified by the authors of the reports and were not considered for the definition of the depth of an event. In other cases it was not easily recognizable if an isolated or anomalous occurrence was due to reworking or downhole contamination or was real. In case of doubt we generally decided to be conservative and to include also possible outliers in the compilation of the data.

The usefulness of an event for our analysis depends on its frequency in the data set. We needed to stratigraphically organize the events, to check how often each event occurred in our record,

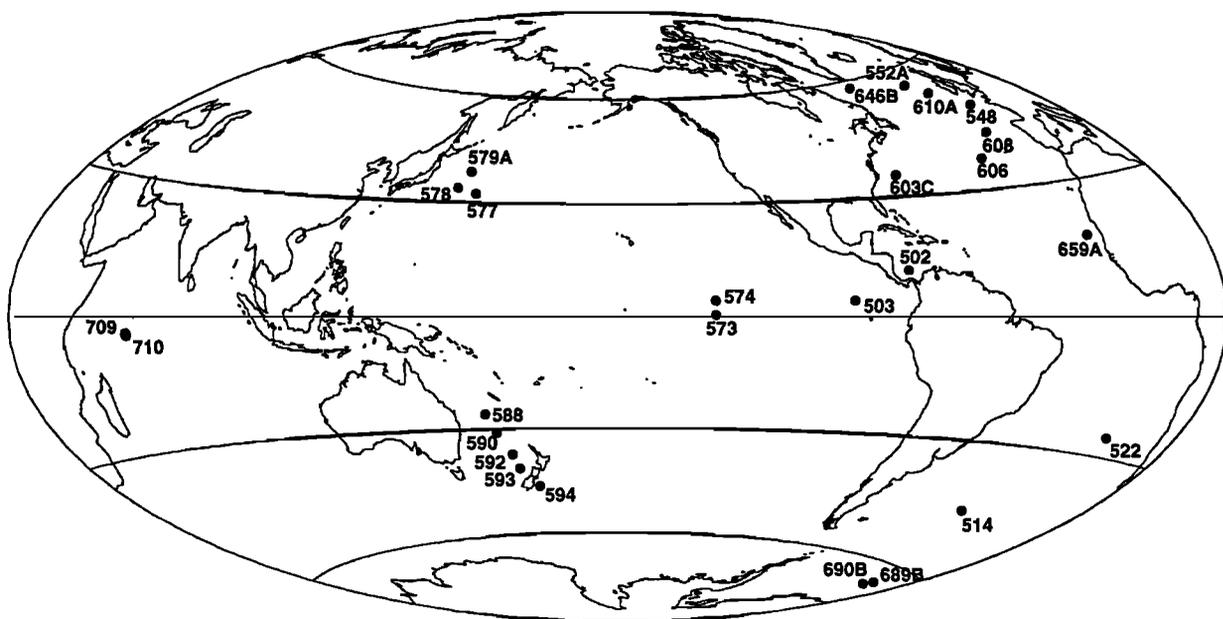


Figure 1. Map with locations of the 35 Deep Sea Drilling Project (DSDP) and Ocean Drilling Program (ODP) holes considered in this study. Locations where two or more holes, part of the same site, were present, are marked only with the site number. The geographic projection is cylindrical Hammer.

and to test whether a particular stratigraphic succession was globally valid and if it coincided with the chronological order proposed in the published calibrations. The data were therefore analyzed using a probabilistic approach first suggested by Hay [1972], applying a modification of the program described by Hills and Thierstein [1989]. The method consists of a compilation of the frequency of particular event successions in the analyzed sections and results in a most frequently occurring sequence of events observed in those sections. Using the computed probability matrix as a guide, the events were then reorganized after examination of the obtained probability distributions, taking into account successional inconsistencies which occurred occasionally [Agerberg and Gradstein, 1988].

The probabilistic stratigraphy analysis gave us the most probable succession of events without any chronological data. To characterize the reliability of each event, we needed to obtain absolute age estimates for each event in each hole. For this purpose we used an age/depth plotting program [Lazarus, 1992] to

obtain age estimates for the events in each of the 35 magnetostratigraphically calibrated holes considered. Except for a few short intervals, we based our age/depth plots on the published paleomagnetic age models. This program plots all the available biostratigraphic and magnetostratigraphic events, using the two sample depths bracketing each event in meters below seafloor (mbsf) (Figure 2). The published age calibrations cited previously are used for the magnetostratigraphic and biostratigraphic events in these files. A line of correlation is graphically constructed by interpolation between the geomagnetic reversal boundaries, taking into account also the biostratigraphic data. The biostratigraphic events are then "projected" by the program onto the line of correlation (arrows in Figure 2) and their apparent ages in that hole are then written into a new file. Two projected ages are given for each event, which bracket the uncertainty caused by sample spacing in the fossil distribution charts. In this phase of the analysis it was possible to identify hiatuses of sedimentation which interrupted the stratigraphic sequence. Events that occurred

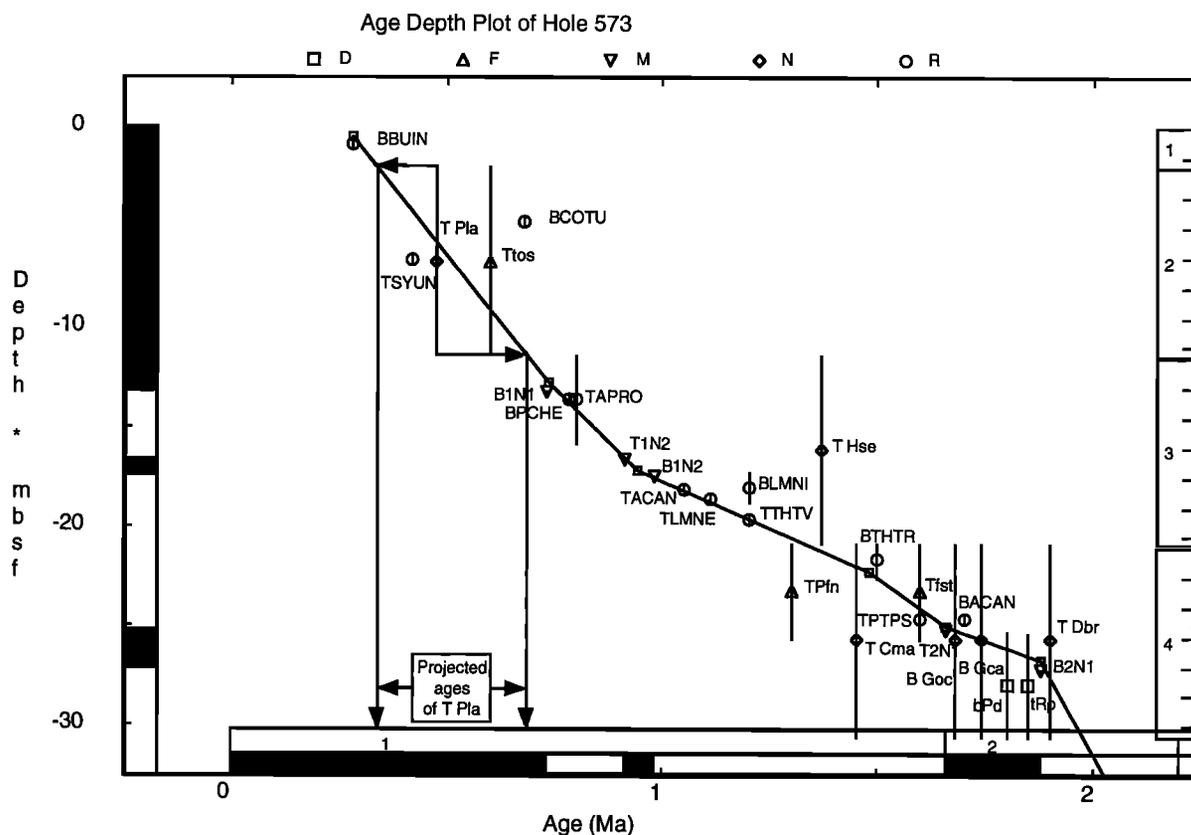


Figure 2. Example of age/depth plot. The x axis represents the age in million years. There is also a reproduction at the bottom of the Berggren *et al.* [1985] magnetostratigraphic scale. On the left y axis is the depth in meters below seafloor (mbsf), on the right a representation of the cores (numbered boxes, with heights proportional to actual recovery) and (short lines on right side of boxes) 1.5-m section breaks. The white and black bars on the left-hand side by the y axis represent magnetic polarity intervals as interpreted from measured paleomagnetic data in the section: black, normal; white, reverse. The symbols corresponding to the microfossil groups are on the top of the plot: D, diatoms; F, foraminifera; M, magnetostratigraphy; N, nanofossils; R, radiolarians. Each event is labelled only with a short plotcode to reduce visual clutter in the figure. Error bars for the depth level of each event are represented as vertical lines crossing the symbols, but sometimes the error bars are not visible because they are smaller than the symbol itself. To illustrate the projection of the data onto the line of correlation, we used as example the "T Pla" (Top of the nanofossil *P. lacunosa*) which has a large error bar. The horizontal arrows represent the projections of the error bar onto the line of correlation, which give two ages, projected with the two vertical arrows onto the age scale.

during or in proximity of a hiatus and whose projected age could therefore be affected by it, were identified on the age/depth plots and eliminated from the data set.

The remaining data were sorted by plankton group and event. To prevent subsequent analyses from being too strongly affected by datasets containing only a few data points, we eliminated all events which had been magnetostratigraphically calibrated in less than four holes. This reduced our original 400 events to 124 events for analysis. The reduction indicates that there are a large number of potentially valuable and commonly used Neogene plankton events for which too little data is available for evaluation of their synchronous or diachronous character. For each of the remaining 124 events we calculated a mean age in each hole (mean of the two projected ages derived from the sampling interval), which we designated as local first occurrence (FO) and local last occurrence (LO), and a local error bar, representing the difference between the two age estimates for the samples bracketing the event (see example, illustrated with arrows in Figure 2). The error bars mostly reflect sample spacing but may also be influenced by sedimentation rate, recovery, preservation, and possibly differences in taxonomic concepts. The causes of particularly large error bars were individually checked and doubtful cases eliminated. Often these were due to exceptionally wide sample spacing or low sedimentation rates. Finally, a global mean age (first appearance datum (FAD) or last appearance datum (LAD)) and a standard deviation from all local mean ages was calculated for each event; the latter is an indication of the chronologic quality of an event, that is of how much variation exists in the calibrated ages for an event.

Potential and Actual Resolution and Precision of Current Neogene Plankton Biochronology

One hundred and twenty-four Neogene plankton events could be calibrated paleomagnetically in at least four holes (Table 1). The data indicate some general comments and interpretations about the quality of Neogene plankton biochronology, which we summarize first. In subsequent sections we will analyze in more detail possible biases and causes for the observed trends in and differences among the various plankton groups.

It is interesting to compare the theoretical (expected) distribution of the events in our data set through time with the actual resolution observed. To quantify the age resolution, we hypothesize an homogenous distribution and calculate the age interval covered by each event by dividing the time interval by the number of events. The average age resolution obtainable with the currently described and commonly used approximately 400 plankton events for the Neogene (0-24 Ma) ought to be $(24:400 =) 0.06$ m.y. If restricted to the 124 paleomagnetically calibrated events, the average resolution obtainable is 0.194 m.y. Brief inspection and analysis of the data in Table 1 reveal, however, that the plankton events are rather unevenly distributed with respect to time and plankton group. The number of biostratigraphic events per million years available in our compilation decreases with increasing age (Figure 3). For the past 5 million years there are an average of 16 events per million years available allowing an average resolution of 0.063 m.y. A maximum average biochronologic resolution of 0.043 m.y. is currently possible in the early Pliocene (3-4 Ma, 23 events). For the Miocene (5-24 Ma), there are only an average of 2.3 events

per million years, allowing for an average resolution of 0.43 m.y. The reason for this decrease is not a significantly lesser number of plankton events available in the Miocene (i.e., lower evolutionary rates), but rather the decreasing number of sections with magnetostratigraphic control drilled so far (Figure 4).

As a measure of actual reproducibility (precision) of plankton biochronology, we can use the standard deviations computed for each event from its varying relative position with respect to the neighboring magnetic reversals in each section (i.e., offset from the correlation line in the respective age/depth plots). The standard deviations in Table 1 range from a minimum of 0.04 m.y. for the nannofossil FAD *E. huxleyi* to a maximum of 5.41 m.y. for the diatom LAD *A. ingens*. The mean standard deviation for all Neogene plankton events is 0.598 m.y., that is, 3 times larger than the 0.194 m.y. average resolution possible. The general increase of biochronologic resolution and precision expressed as the mean standard deviation of bioevents per million year interval through the Neogene is shown in Figure 5. For most of the Neogene the biochronologic uncertainties are far greater than the theoretically obtainable resolution, either because of true time-transgressiveness of first and last occurrences or because of insufficiently detailed information. Thus application of biochronologic methods for age determinations of deep-sea sediments is currently limited mostly by precision (apparent diachrony) in the late Neogene and by resolution (insufficient numbers of well-calibrated sections) in the Miocene. Potential causes for the varying quality of biochronologic events are differential preservation, uncertain taxonomy and true diachrony (i.e., immigration and emigration).

There are notable differences in the chronological sequence of events based on the mean age estimates from the age/depth plots and the sequence obtained from the probabilistic stratigraphy analysis (Table 1, column 8). The sequential offsets in the probabilistic succession are usually associated with events that are documented in only a few holes and show a comparatively high standard deviation of the age calibrations, i.e. have taxonomic or preservation problems, show frequent reworking or are truly diachronous. We concur with *Agterberg and Gradstein* [1988], who also believed that probabilistic stratigraphy alone has only a limited usefulness. This is because probabilistic analyses do not allow the identification of outlier entries, potentially caused by dissolution, reworking, hiatuses, etc., which may strongly affect the results. Such outliers, however, can be easily identified and subsequently analyzed on an age/depth plot.

For readers wishing to perform their own analyses, the whole set of data, including the holes where each event was reported, their depth, age interval and all subsequent calculations, is available as an electronic supplement¹.

¹An electronic supplement of this material may be obtained on a diskette or Anonymous FTP from KOSMOS.AGU.ORG. (LOGIN to AGU's FTP account using ANONYMOUS as the username and GUEST as the password. Go to the right directory by typing CD APEND. Type LS to see what files are available. Type GET and the name of the file to get it. Finally, type EXIT to leave the system.) (Paper 94PA01456, How synchronous are Neogene marine plankton events?, by C. Spencer-Cervato, H. R. Thierstein, D. B. Lazarus, and J-P Beckmann). Diskette may be ordered from American Geophysical Union, 2000 Florida Avenue, N.W., Washington, DC 20009; \$15.00. Payment must accompany order.

Table 1. List of the Studied Biostratigraphic Events and Their Age Calibrations

Group	Event Name	Plot Code	Mean Age	Number of Events	Mean Standard Deviation	Low-Latitude Age	Probabilistic Stratigraphy Position	Earliest FAD/Latest LAD
N	A E. huxleyi	A Ehu	0.14	9	0.08	0.085	1	
N	B E. huxleyi	B Ehu	0.30	13	0.04	0.28	2	0.37
R	B Collosphaera tuberosa	BCOTU	0.36	4	0.06	0.68	5	0.44
R	T Stylatractus universus	TSYUN	0.40	8	0.12	0.42	3	0.16
N	T P. lacunosa	T Pla	0.44	20	0.10	0.47	4	0.28
D	T N.fossilis	tNf	0.71	9	0.15	0.85	7	0.51
M	Brunhes	B1N1	0.73			0.73	8	
M	Jaramillo	T1N2	0.91			0.91	9	
M	Jaramillo	B1N2	0.98			0.98	11	
F	T G.tosaensis	Ttos	1.03	5	0.55	0.6	10	0.38
R	B Lamprocyrtis nigrinae (haysi)	BLMNI	1.04	7	0.37	1.2	12	1.59
R	T Theocorythium vetulum	TTHTV	1.05	4	0.27	1.2		0.65
N	T H. sellii	T Hse	1.14	15	0.38	1.37	13	0.00
R	B Pterocorys hertwigii	BPCHE	1.17	5	0.46	0.8	14	1.64
N	T C. macintyreii	T Cma	1.40	21	0.40	1.45	21	0.48
D	T N.reinholdii	tNr	1.40	14	1.34	0.65	6	0.34
N	B G. oceanica	B Goc	1.43	17	0.42	1.68	15	1.92
D	T R.praebergonii v. robusta	tRpr	1.57	4	0.17	1.55	17	1.38
N	B G. caribbeanica	B Gca	1.58	12	0.36	1.74	22	1.90
M	Olduvai	T2N1	1.66			1.66	23	
F	B G.truncatulinoidea	Btrc	1.68	16	0.72	1.9	20	2.68
R	T Pterocanium prismatium	TPTPS	1.70	5	0.20	1.6	19	1.45
D	T R.praebergonii	tRp	1.78	5	0.15	1.85	24	1.55
R	B Theocorythium trachelium	BTHTR	1.83	7	0.67	1.5	16	2.83
N	B G. aperta	B Gap	1.85	5	0.69	2.2	34	2.29
M	Olduvai	B2N1	1.88			1.88	25	
F	T G.fistulosus	Tfst	1.90	4	0.43	1.6	30	1.49
N	T D. brouweri	T Dbr	1.92	22	0.22	1.9	28	1.49
R	B Anthocyrtdium angulare	BACAN	1.94	4	0.47	1.7	18	2.61
N	T D. triradiatus	T Dtr	1.94	14	0.31	1.9	29	1.52
D	B P.doliolus	bPd	1.97	11	0.18	1.8	26	2.35
F	T G.miocenica	Tmio	2.17	4	0.13	2.2	32	1.99
N	T D. pentaradiatus	T Dpe	2.31	19	0.14	2.4	35	2.08
D	T T.convexa	tTc	2.34	5	0.26	2.1	37	1.92
N	T D. surculus	T Dsu	2.43	18	0.19	2.4	42	2.08
M	Gauss	T2AN1	2.47			2.47	38	
F	T G.obliquus extremus	Tobe	2.47	7	1.06	1.8	31	1.42
N	T D. asymmetricus	T Das	2.49	13	0.44	2.2	40	1.66
F	T G.multicamerata	Tmtc	2.51	6	0.48	2.9	41	1.95
D	T N.jouseae	tNj	2.57	11	0.31	2.6	43	1.72
F	T G.pertenuis	Tprt	2.67	4	0.46	2.5	39	2.26
N	T D. tamalis	T Dta	2.72	19	0.18	2.6	44	2.29
D	B R.praebergonii	bRp	2.73	7	0.48	3	45	1.92
F	BT G.inflata	Bifl	2.74	11	1.04	3	36	3.97
R	B Cycladophora davisiana	BCYDA	2.82	5	0.30	2.43	46	3.30

Table 1. (continued)

Group	Event Name	Plot Code	Mean Age	Number of Events	Mean Standard Deviation	Low-Latitude Age	Probabilistic Stratigraphy Position	Earliest FAD/Latest LAD
R	T <i>Stichocorys peregrina</i>	TSCPE	2.88	9	0.41	2.6	61	2.53
F	BT <i>G.tosaensis</i>	Btos	2.91	7	0.58	3.1	33	3.39
M	Gauss	B2AN1	2.92			2.92	47	
R	T <i>Phormostichoartus fistula</i>	TPHFI	2.95	6	0.44	3.3	53	2.33
M	Gauss (^kaena)	T2AN2	2.99			2.99	49	
F	T <i>Gq.altispira</i>	Talp	3.00	11	0.29	2.9	48	2.58
F	B <i>G.fistulosus</i>	Bfst	3.01	4	0.36	2.9	50	3.46
F	T <i>P.primalis</i>	TPpr	3.02	5	0.87	3.5	58	1.49
F	T <i>Spherinoidellopsis</i> spp	TSdp	3.06	6	0.18	3	57	2.76
D	T <i>Actinocyclus ingens</i>	tAi	3.06	4	5.41	11.5	117	0.12
R	T <i>Phormostichoartus doliolum</i>	TPHDO	3.06	4	0.50	3.5	62	2.33
M	Gauss	B2AN2	3.08			3.08	55	
N	T <i>D. variabilis</i>	T Dva	3.17	17	0.57	2.9	54	2.49
M	Gauss (^mammoth)	T2AN3	3.18			3.18	56	
F	B <i>G.miocenica</i>	Bmio	3.31	5	0.41	3.4	67	3.97
M	Gauss	B2AN3	3.4			3.4	59	
R	T <i>Lychnodictyum audax</i>	TLDAU	3.43	4	0.23	3.4	68	3.21
F	B <i>G.crassula</i>	Bcr1	3.44	5	0.46	3.1	60	3.97
N	T <i>R. pseudoumbilicus</i>	T Rps	3.47	25	0.15	3.5	63	2.83
F	B <i>Spheroinidella dehiscens</i> s.s.	BSdd	3.49	7	0.29	5.1	70	3.89
N	B <i>P. lacunosa</i>	B Pla	3.54	17	0.38	3.4	51	4.11
N	T <i>S. neoabies</i> or <i>abies</i>	T Sna	3.54	18	0.31	3.47	64	3.02
D	B <i>T.convexa v.convexa</i>	bTcc	3.59	4	0.10	3.6		3.66
N	B <i>D. tamalis</i>	B Dta	3.61	16	0.28	3.8	69	4.05
F	T <i>G.margaritae</i>	Tmgt	3.69	13	0.36	3.4	65	3.06
R	B <i>Spongaster tetras</i>	BSPTTE	3.75	4	0.11	3.7	75	3.87
F	B <i>G.pertenuis</i>	Bprt	3.76	5	0.31	3.3	66	4.16
N	T <i>A. delicatus</i>	T Ade	3.83	14	0.40	3.7	76	3.31
F	B <i>G.crassaformis</i> s.s.	Bcrs	3.88	12	0.98	4.1	74	4.73
M	Gilbert-cochiti	T3N1	3.88			3.88	71	
R	T <i>Prunopyle titan</i>	TPRTI	3.91	4	0.53	3.32	52	3.18
N	T <i>A. primus</i>	T Apr	3.93	13	0.33	4.4	77	3.46
N	T <i>A. tricorniculatus</i>	T Atr	3.93	11	0.23	3.7	79	3.76
M	Gilbert-cochiti	B3N1	3.97			3.97	72	
F	T <i>G.nepentes</i>	Tnep	4.01	9	0.46	3.9	82	3.54
M	Gilbert-nunivak	T3N2	4.1			4.1	73	
R	T <i>Spongaster berminghami</i>	TSPBE	4.14	4	0.35	4.2	91	3.74
M	Gilbert-nunivak	B3N2	4.24			4.24	83	
F	T <i>G.cibaoensis</i>	Tcbn	4.32	5	0.50	4.4	96	3.82
F	B <i>G.puncticulata</i>	Bptc	4.33	8	0.40	4.4	81	4.94
M	Gilbert-sidufjall	T3N3	4.4			4.4	84	
D	T <i>N.cylindrica</i>	tNc	4.42	5	0.21	4.3	80	4.25
F	B <i>G.tumida</i>	Btum	4.44	7	1.77	5.2	99	5.73
M	Gilbert-sidufjall	B3N3	4.47			4.47	86	

Table 1. (continued)

Group	Event Name	Plot Code	Mean Age	Number of Events	Mean Standard Deviation	Low-Latitude Age	Probabilistic Stratigraphy Position	Earliest FAD/Latest LAD
N	B D. asymmetricus	B Das	4.47	17	0.68	4.1	87	6.04
N	B C. rugosus	B Cru	4.53	17	0.30	4.5	88	5.30
N	T C. acutus	T Cac	4.55	12	0.18	4.57	85	4.24
D	B N.jouseae	bNj	4.57	8	0.38	4.5	90	5.19
M	Gilbert-thvera	T3N4	4.57			4.57	89	
F	T G.conomiozea	Tcmz	4.76	5	0.36	3	94	4.34
M	Gilbert-thvera	B3N4	4.77			4.77	92	
N	B C. acutus	B Cac	4.84	14	0.18	5	93	5.12
D	B T.oestrupii	bTo	4.87	9	0.83	5.1	95	6.10
F	B P.primalis	BPpr	4.96	4	0.65	5.8	102	5.59
D	T T.miocenica	tTm	5.14	5	0.21	5.1	107	4.89
N	B A. tricorniculatus	B Atr	5.15	7	0.78	6	101	6.42
D	T A.acutiloba	tAa	5.25	4	0.20	5.35	108	5.02
N	T D. quinquerramus	T Dqu	5.26	17	0.40	5.6	98	4.83
F	B G.margaritae	Bmgt	5.33	6	1.20	5.6	103	5.94
M	3A/chron 5	T3AN1	5.35			5.35	109	
D	T N. miocenica	tNm	5.40	6	0.50	5.55	119	4.44
F	B G.conglobatus	Bcgb	5.48	7	0.60	5.3	116	6.14
F	T G.seiglei	Tsgl	5.51	4	0.92	4.3	97	4.73
M	3A/chron 5	B3AN1	5.53			5.53	110	
F	B N.humerosa	Bhum	5.54	8	1.55	7.5	104	8.72
N	T A. amplificus	T Aam	5.60	5	0.19	5.6	100	5.37
N	T D. berggreni	T Dbe	5.66	5	0.39	5.6	105	5.00
M	3A/chron 5	T3AN2	5.68			5.68	111	
D	B N. reinholdii	bNr	5.73	6	1.50	7.3	133	7.21
D	T T.praeconveza	tTp	5.73	4	0.11	5.8	112	5.58
N	T T. rugosus	T Tru	5.81	11	0.85	5	106	4.63
M	3A/chron 5	B3AN2	5.89			5.89	113	
F	B G.conomiozea	Bcmz	5.93	5	0.75	6.1	123	6.76
N	B A. amplificus	B Aam	6.02	6	0.29	5.9	114	6.42
N	B A. delicatus	B Ade	6.17	9	0.46	6.5	122	6.81
R	Be Stichocorys peregrina	ESCPE	6.18	4	0.13	6.3	120	6.36
N	B A. primus	B Apr	6.35	16	0.60	6.5	127	7.44
M	3B/chron 6	T3BN1	6.37			6.37	121	
D	T N.porteri	tNp	6.44	6	0.28	6.7	126	5.96
M	3B/chron 6	B3BN1	6.5			6.5	125	
R	B Solenosphaera omnitubus	BSOOM	6.69	4	0.12	6.5	128	6.85
M	4/chron 7	T4N1	6.7			6.7	129	
F	B G.cibaoensis	Bcbn	6.75	10	1.60	5.3	140	9.33
M	4/chron 7	B4N1	6.78			6.78	130	
M	4/chron 7	T4N2	6.85			6.85	131	
R	T Diartus hughesi	TDIHU	7.11	4	0.07	7	135	7.03
M	4/chron 7	B4N2	7.28			7.28	132	
F	T G.dehiscens	TGqd	7.31	8	1.86	5.3	124	4.98

Table 1. (continued)

Group	Event Name	Plot Code	Mean Age	Number of Events	Mean Standard Deviation	Low-Latitude Age	Probabilistic Stratigraphy Position	Earliest FAD/Latest LAD
M	4/chron 7	T4N3	7.35			7.35	134	
M	4/chron 7	B4N3	7.41			7.41	137	
M	4A/chron 9	T4AN1	7.9			7.9	139	
N	B D. quinqueringus	B Dqu	8.01	8	0.56	8.2	141	8.65
M	4A/chron 9	B4AN1	8.21			8.21	142	
M	4A/chron 9	T4AN2	8.41			8.41	143	
M	4A/chron 9	B4AN2	8.5			8.5	144	
F	B N.acostaensis	Bac	8.51	4	2.08	10.2	155	10.41
M	4A/chron 10	T4AN3	8.71			8.71	150	
M	4A/chron 10	B4AN3	8.8			8.8	151	
N	T D. hamatus	T Dha	8.81	9	0.29	8.85	148	8.54
M	5/chron 11	T5N1	8.92			8.92	152	
N	T D. exilis	T Dex	9.12	7	0.65	8.8	154	8.47
N	B D. hamatus	B Dha	9.96	7	0.41	10	156	10.61
F	B G.nepenthes	Bnep	10.14	4	2.31	11.3	166	11.65
M	5/chron 11	B5N1	10.42			10.42	158	
M	C5	T5N2	10.54			10.54	160	
M	C5	B5N2	10.59			10.59	161	
N	B C. coalitus	B Cco	10.67	5	0.57	10.8	162	11.67
M	C5	T5N3	11.03			11.03	163	
M	C5	B5N3	11.09			11.09	164	
M	C5A	T5AN1	11.55			11.55	168	
M	C5A	B5AN1	11.73			11.73	169	
M	C5A	T5AN2	11.86			11.86	170	
M	C5A	B5AN2	12.12			12.12	171	
N	B D. kugleri	B Dku	12.33	6	0.67	13.1	172	12.99
M	C5A	T5AN3	12.46			12.46	175	
N	T C. floridanus	T Cfl	12.48	8	0.98	11.6	174	11.41
M	C5A	B5AN3	12.49			12.49	176	
M	C5A	T5AN4	12.58			12.58	177	
M	C5A	B5AN4	12.62			12.62	178	
F	T G.peripheroronda	Tpr	12.82	5	2.08	14.6	190	9.20
M	C5AA	T5AAN1	12.83			12.83	181	
D	T S.jouseana	tSj	13.00	4	2.10	10.4	165	10.11
M	C5AA	B5AAN1	13.01			13.01	182	
M	C5AB	T5ABN1	13.2			13.2	183	
M	C5AB	B5ABN1	13.46			13.46	184	
D	T C.lewisianus	tCl	13.53	5	1.30	12.7	180	12.10
M	C5AC	T5ACN1	13.69			13.69	185	
N	T S. heteromorphus	T She	13.85	7	1.05	14.4	189	12.43
N	B T. rugosus	B Tru	13.87	6	0.71	14	186	14.73
M	C5AC	B5ACN1	14.08			14.08	187	
M	C5AD	T5ADN1	14.2			14.2	188	
M	C5AD	B5ADN1	14.66			14.66	191	

Table 1. (continued)

Group	Event Name	Plot Code	Mean Age	Number of Events	Mean Standard Deviation	Low-Latitude Age	Probabilistic Stratigraphy Position	Earliest FAD/Latest LAD
F	B <i>O.suturalis</i>	BOst	14.86	4	0.68	15.2	195	15.31
M	C5B	T5BN1	14.87			14.87	192	
M	C5B	B5BN1	14.96			14.96	193	
M	C5B	T5BN2	15.13			15.13	194	
M	C5B	B5BN2	15.27			15.27	196	
M	C5C	T5CN1	16.22			16.22	197	
M	C5C	B5CN1	16.52			16.52	198	
M	C5C	T5CN2	16.56			16.56	199	
M	C5C	B5CN2	16.73			16.73	200	
M	C5C	T5CN3	16.8			16.8	203	
M	C5C	B5CN3	16.98			16.98	204	
F	B <i>G.miozea</i>	Bmza	17.29	4	0.51	16.8	201	17.94
M	C5D	T5DN1	17.57			17.57	205	
N	T <i>S. belemnos</i>	T Sbe	17.84	5	0.98	17.4	207	17.10
N	B <i>S. heteromorphus</i>	B She	17.86	5	0.70	17.1	206	18.60
M	C5D	B5DN1	17.9			17.9	209	
M	C5D	T5DN2	18.12			18.12	210	
M	C5D	B5DN2	18.14			18.14	211	
M	C5E	T5EN1	18.56			18.56	212	
M	C5E	B5EN1	19.09			19.09	213	
M	C6	T6N1	19.35			19.35	214	
M	C6	B6N1	20.45			20.45	215	
M	C6A	T6AN1	20.88			20.88	217	
N	B <i>D. druggii</i>	B Ddr	21.15	4	2.24	23.2	227	23.14
M	C6A	B6AN1	21.16			21.16	218	
M	C6A	T6AN2	21.38			21.38	219	
M	C6A	B6AN2	21.71			21.71	220	
M	C6AA	T6AAN1	21.9			21.9	221	
M	C6AA	B6AAN1	22.06			22.06	222	
M	C6AA	T6AAN2	22.25			22.25	223	
M	C6AA	B6AAN2	22.35			22.35	224	
M	C6B	T6BN1	22.57			22.57	225	
M	C6B	B6BN1	22.97			22.97	226	
M	C6C	T6CN1	23.27			23.27	228	
F	B <i>Gq.dehiscens</i>	BGqd	23.33	4	0.25	23.2	229	23.70
M	C6C	B6CN1	23.44			23.44	231	

The first column indicates either the plankton group (D, diatom; F, foraminifera; N, nannofossil; R, radiolarian) or a magnetostratigraphic event (M). The second column is the full name of the biostratigraphic event (A, abundant; B, first appearance datum FAD; T, last appearance datum LAD) or geomagnetic boundary. Column 3 lists the plot codes, column 4 the mean age in Ma, and column 6 the standard deviation (in m.y.) as result of this work. The number of holes in which the event has been calibrated is given in column 5. A low-latitude calibration (*Berggren et al.* [1985] for planktonic foraminifera and calcareous nannofossils; *Barron* [1985] modified in the work by *Mikkelsen* [1990] for diatoms; *Johnson and Nigrini* [1985] for radiolarians) is given in column 7. The succession of plankton events from the probabilistic stratigraphy analysis is in column 8. In column 9 is given the earliest age for FADs or the latest age for LADs.

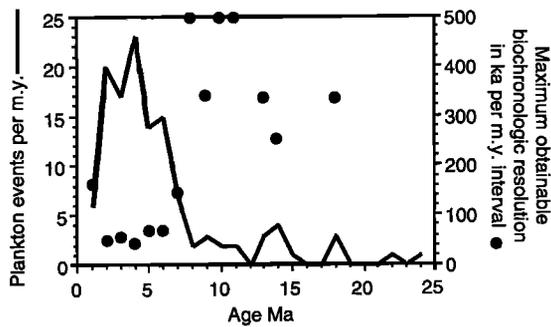


Figure 3. Number of oceanic plankton events per million years which have been calibrated in at least four magnetostratigraphically dated deep sea sections throughout the Neogene (solid line). Average theoretical time resolution (in thousand years) to be expected for one million year intervals from the frequency distribution of events (dots). See text for discussion.

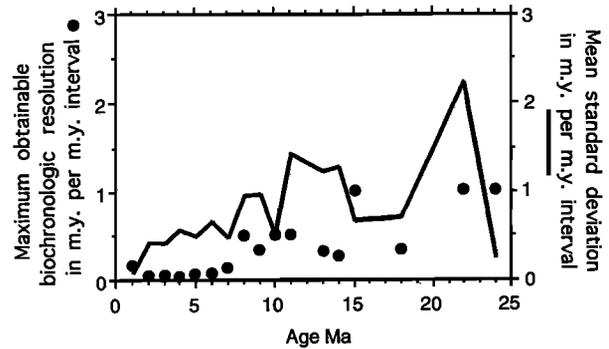


Figure 5. Age distribution of average theoretical time resolution per million year interval (dots, see also Figure 3) and mean standard deviations of all plankton event age calibrations per million year interval throughout the Neogene (solid line). Differences show potential for further refinement of biochronologic dating.

Biases in Current Data Base

Author Biases

As stated in the introductory part, this analysis was based on data published in the DSDP and ODP reports. Since the data were collected by different authors over a two-decade period of rapid development of stratigraphic methods, we emphasize the potential bias that this may have brought to our data set. Although impossible to quantify, we believe that the age variability shown by some events is due to this effect. This shows the importance of recent studies, such as those by *Johnson and Nigrini* [1985], *Wei* [1993], and *Miller et al.* [1994], where plankton events are identified and calibrated in several holes. The aim of our analysis is to survey and critically analyze the data as currently available from DSDP and ODP reports in globally distributed holes.

Differences in Documentation Among Major Plankton Groups

There are some significant differences among the four major plankton groups with respect to their biochronologic applicability (Table 2). The majority of the 124 biochronologic events in our database belong to the calcareous plankton: nannofossils: 46

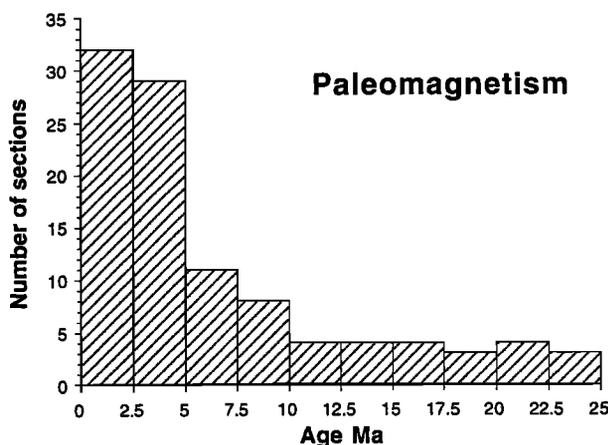


Figure 4. Age distribution (per 2.5 m.y. interval) of paleomagnetically dated sections available for our analysis. Note pronounced skew.

events, foraminifera: 38; only about one third belong to siliceous microfossils: diatoms: 21 and radiolarians: 19 events. The number of holes in which events have been recorded is variable also. Calcareous nannofossil events are the most frequently reported: each event occurs on average in 13.5 holes. Foraminifera and diatoms are documented on average in about 6.5 holes, whereas radiolarians only in about 5. The most frequently reported event is the LAD of the nannofossil *Reticulofenestra pseudoumbilicus*, which is known from 28 magnetostratigraphically calibrated holes.

Obvious and expected biases in our data base which may be responsible for differences among the plankton groups are the number of specialists available for collecting data for each of the plankton groups and the differential development histories for the taxonomy and biostratigraphy of the four groups. Complete Neogene zonation using planktonic foraminifera had been established prior to the start of the Deep-Sea Drilling Project 25 years ago [e.g., *Bolli*, 1966; *Blow*, 1969] and were followed by zonation for the calcareous nannofossils [e.g., *Hay et al.*, 1967; *Martini*, 1971], and subsequently for the radiolarians and diatoms [e.g., *Riedel and Sanfilippo*, 1970; *Burckle*, 1972; *Schrader*, 1973; *Koizumi*, 1973], which were developed largely in DSDP sections. There are several other biases that could possibly affect the results and it is necessary to evaluate their potential effect on our conclusions.

Skewed Age Distribution

From the distribution of FADs and LADs through time (Figure 6), we can see that most of the events analyzed occur in the Plio-Pleistocene, more exactly in the last 6 million years; relatively few Miocene events are included in this study, mostly FADs. The distribution of siliceous microfossil events is even more extremely concentrated in the Plio-Pleistocene: only three diatom and three radiolarian events are older than 6 Ma. The dearth of Miocene siliceous microfossil data, despite the known global abundance of siliceous sediments in the Miocene, is an artefact of the selected dataset due to the age distribution of the sections studied (Figure 4). Only a few holes have an established magnetostratigraphy for the Miocene, and the fact that we selected events that have been reported in at least four magnetostratigraphically dated holes, reduces drastically the number of Miocene events. Moreover, the

Table 2. Number of Events by Group, Average Number of Holes in Which One Event is Recorded, Number of FADs and LADs in One Group, and Average Standard Deviation of FADs and LADs by Group

Plankton Group	Number of Events	Average Occurrence in Holes	Number of FADs	Number of LADs	Average Standard Deviation of FADs	Average Standard Deviation of LADs
Calcareous nannofossils	46	13.5	21	25	0.57	0.60
Diatoms	21	6.5	7	14	0.57	0.85
Planktic foraminifera	38	6.5	22	16	0.88	0.68
Radiolarians	19	5.0	9	10	0.30	0.31

The results of the χ^2 test [Davis, 1973] with the assumption of an equal distribution of FADs and LADs is a Pearson χ^2 of 3.40 (degrees of freedom DF=3), which gives a probability that the assumption is valid of 0.334. The disequilibrium exists for diatoms and foraminifera.

Miocene sediments in the selected holes are dominantly calcareous, as they are located in the tropical and subtropical southern Pacific Ocean (holes 588 to 594), in the North Atlantic (hole 608) and in the equatorial Indian Ocean (sites 709 and 710). Since the publication of the Initial Reports, additional information with much higher resolution has become available [Miller *et al.*, 1985], which, upon initial examination, strengthen our conclusions.

Speciations, Extinctions and Reworking

Events included in our database are both first and last occurrences (Table 2). LADs are widely used in industrial drill-hole applications, because of the presence in the drill mud of all microfossils encountered in formations already penetrated, whereas FADs are often preferred in scientific work, because they are not plagued by the problems of reworking by bioturbation, erosion and bottom currents. For these reasons, one might expect the FADs to show a somewhat higher reproducibility than LADs. Comparisons of the standard deviations of our age estimates, however, do not indicate such differences (Table 2) and thus do not confirm the evidence of Johnson and Nigrini [1985], who found in their study of Pacific radiolarian events diachrony to be more frequent in first appearances than in last appearances. There are no significant differences between the number of FADs and LADs available in the various groups with the exception of the diatoms, which have twice as many well-calibrated extinctions as appearances (Table 2).

Although we tried to eliminate data of reworked microfossils, the summary of the ages obtained for an event in the latitude versus age plots sometimes showed us anomalous values: these were individually checked for a second time in the distribution charts. If we had no reasons to doubt the validity of those points, that is, if an occurrence was the highest in a continuous sequence of samples, it was considered a true last appearance. In some cases we identified reworked specimens (i.e., rare, discontinuous) and corrected the entered depth for that event. As already mentioned before, occurrences in proximity of a hiatus were eliminated from the database as soon as the age model was constructed.

The most striking feature of our compilation are the small standard deviations of radiolarian events, which are about half of those of the other groups. There are several conceivable reasons why this might be so, but the possible preferential use of FADs

over LADs resulting in lesser reworking, can be ruled out. Other causes will have to be considered in the following.

Geographic Distribution of Records

The geographic distribution of the well-calibrated sections currently available does not appear to be strongly biased with respect to age. The geographic distribution of the selected sections divided into two age intervals is shown in the maps of Figure 7. Even though there are much fewer sections from the Miocene (5 to 25 Ma) than from the Plio-Pleistocene (0-5 Ma), the former cover all the major biogeographic regions that are represented in the late Neogene data set. However, there is a hemispheric bias: the early and middle Miocene interval is better represented in the southern than in the northern hemisphere (Table 3).

The biogeographic extent of the various plankton groups and their differential preservation should influence their biochronological applicability. A comparison of the frequency of events versus their total latitudinal range among plankton groups in this compilation demonstrates some major differences (Figure 8). While most calcareous nannofossil events cover a rather broad latitudinal range, most of the radiolarian events are latitudinally restricted. In contrast, the diatoms and foraminifera show a more even distribution of endemic and cosmopolitan taxa. As we shall discuss below, these patterns strongly influence the "quality" of the global age calibration.

The events that show a very limited latitudinal range in Figure 8, might be a result of scarce documentation in our data set. Additional analysis on these events have shown that some of these, although not as restricted as shown in Figure 8, are indeed endemic (i.e., the foraminifera *Globigerinoides seigliei*, *Pulleniatina primalis* and *Globorotalia miozea* and the diatoms *Rhizosolenia praebergonii* var. *robusta*, *Thalassiosira convexa* var. *convexa* and *Thalassiosira porteri*), while others are artefacts of our data set (i.e., the nannofossils *Gephyrocapsa aperta* and *Catinaster coalitus* or the diatoms *Nitzschia cylindrica* and *Nitzschia reinholdii*). Because of this limitation, we decided to use the terms endemic and cosmopolitan not as a general statement about the real geographic distribution of a species but simply to indicate how widespread an event is in our data set. Although it has been common practice to use low- and high-latitude zonations for siliceous microfossils, a similar approach has only recently been taken for calcareous plankton [e.g., Wei and Wise, 1992]. Our analysis has a global focus because we

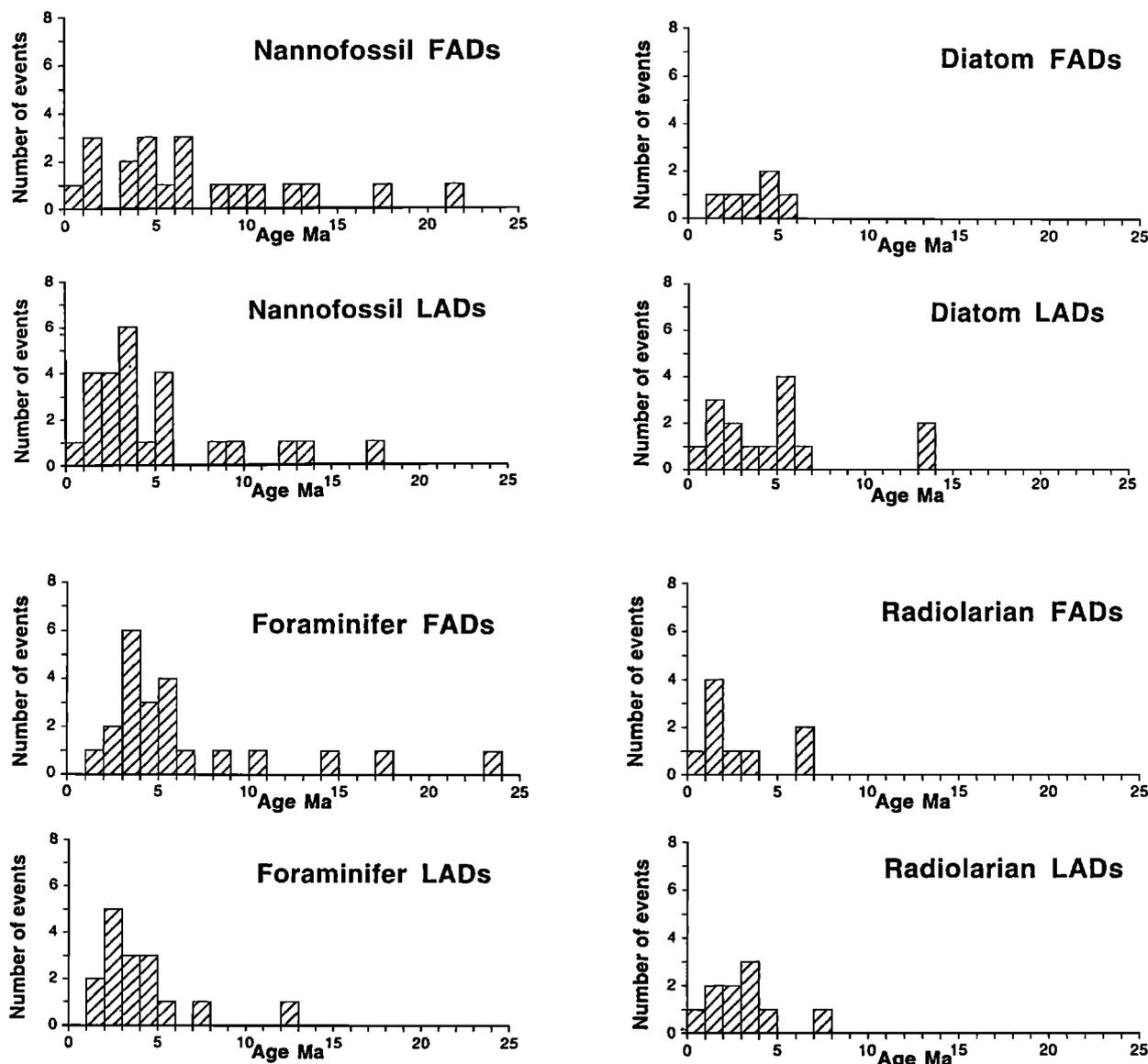


Figure 6. Age distribution of first (FADs) and last (LADs) appearance datums of the 124 studied plankton events.

suspect that diachrony has great potential for a better understanding of evolutionary and ecological processes.

Biochronologic Quality Differences Among Plankton Groups

The biochronologic value of a particular plankton event is dependent on its demonstrated synchrony over a given geographic range. As a measure for synchrony we use the standard deviations calculated for each event (Table 1). Small standard deviations represent synchronous events and usually also show a general agreement with the published age calibration of an event. A comparison among plankton groups revealed some surprising differences: the mean standard deviation of all radiolarian events is 0.30 m.y., for calcareous nannofossil events 0.47 m.y., for diatom events 0.77 m.y., and for foraminifer events it is 0.80 m.y. (Table 2). Further analysis reveals that these differences are strongly influenced by a small but variable number of

significantly diachronous events. For the majority of events in all groups, however, there is a cluster of standard deviations with a near-Gaussian distribution over a few hundred thousand years (Figure 9). Nannofossils have standard deviations lower than 1.1 m.y., with the exception of one occurrence of 2.2 m.y. standard deviation (FAD of *Discoaster druggii*). The majority of diatom events (15 out of 21) have standard deviations less than 0.6 m.y., the others are larger, with an uniquely large standard deviation of 5.4 m.y. for the diatom event LAD of *Actinocyclus ingens* (Figure 10). This event shows almost an 11 m.y. age difference between the low-latitude calibration (hole 574) and the southern high-latitude ages (holes 514 and 690B in the Atlantic Ocean; hole 594 in the Pacific Ocean). The standard deviations calculated for planktonic foraminifer events show a continuous range of values up to 2.4 m.y., whereas all radiolarian events have values lower than 0.7 m.y.

There is a general trend towards larger standard deviations with increasing age, although there are some notable differences

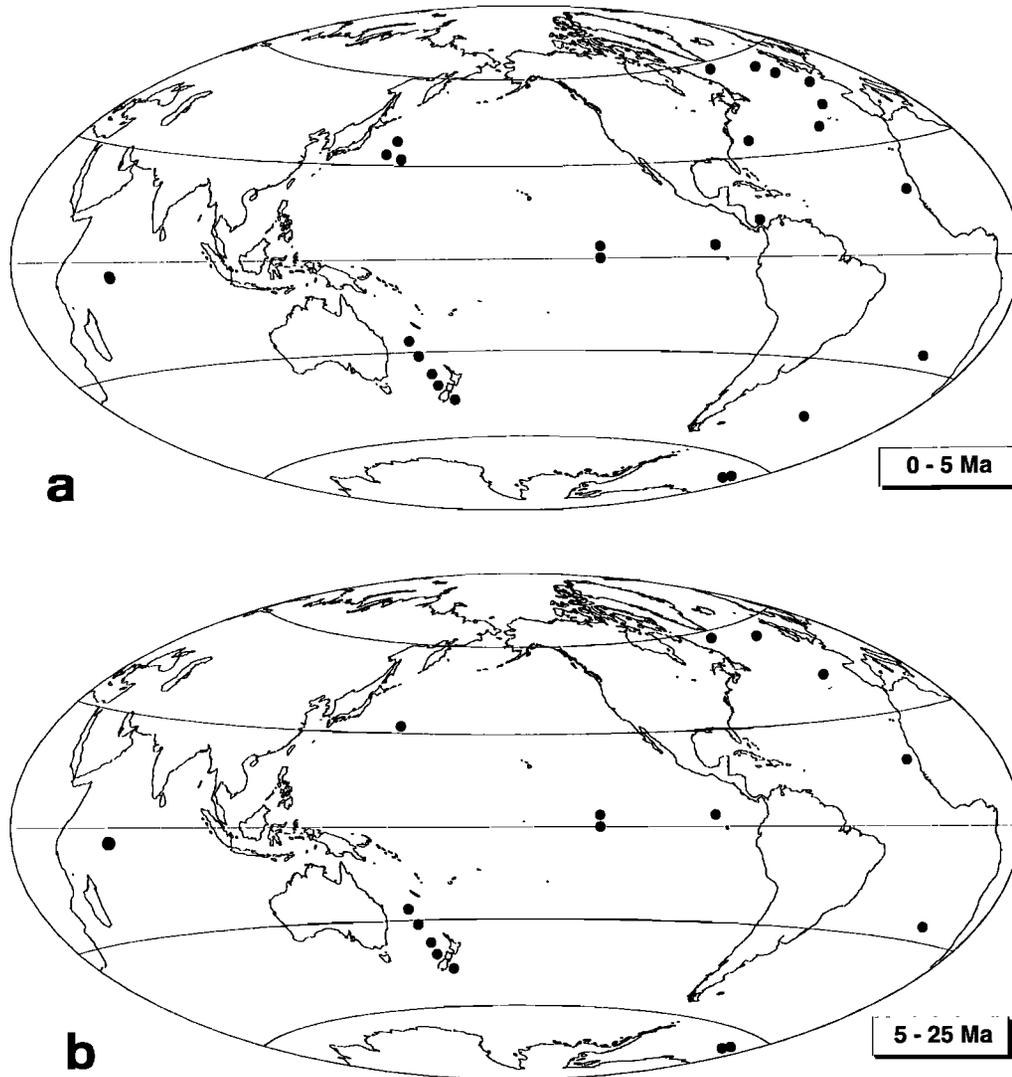


Figure 7. Geographic distribution of holes covering the time intervals (a) 0 to 5 Ma and (b) 5 to 25 Ma.

among the plankton groups (Figures 11a-11d). For nannofossils there is a gradual but continuous increase in standard deviations with increasing age of the events (Figure 11a). Diatom events tend to show a similar trend, although there is much more scatter. A rapid increase in standard deviations with age is observed for planktonic foraminiferal events, particularly up to 10 Ma (Figure 11b). Three older events (FAD of *Orbulina suturalis*, FAD of *Globorotalia miozea*, and FAD of *Globoquadrina dehiscens*), however, show a much lower standard deviation of less than 0.7

m.y. A likely cause for their significantly lower diachrony is their endemism in tropical waters (see following paragraph and Figure 12c). Radiolarian events are concentrated in a narrow range of age (all younger than 7 Ma) and are characterised by low standard deviations.

One major cause for the observed differences in the standard deviations of the local age calibrations becomes apparent when they are plotted relative to the latitudinal range of the sites where they have been recorded (Figures 12a-12d). Events of

Table 3. Latitudinal Distribution of the DSDP and ODP Sections Considered

Age Interval, Ma	Northern Hemisphere	Equator	Southern Hemisphere
0 to 5	11	13	10
5 to 10	4	8	8
10 to 25	1	2	7

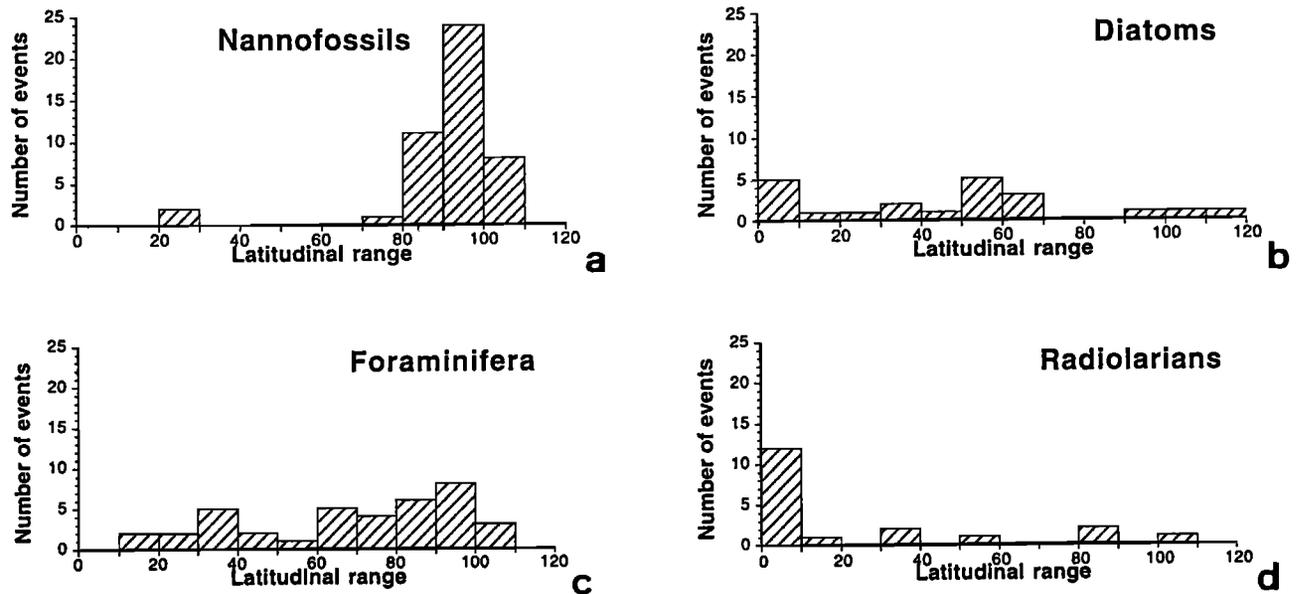


Figure 8. Latitudinal range (complete latitudinal distribution of an event in the northern and southern hemispheres) over which the 124 plankton events analyzed are documented, by plankton group. Note differences between more cosmopolitan nannofossils and more endemic radiolarians.

cosmopolitan species tend to have larger standard deviations than those of endemic species, and endemism seems much more prevalent among the selected radiolarian than nannofossil events. The three early Miocene foraminiferal events with low standard deviations mentioned in the preceding paragraph are endemic (squares in Figure 12d).

Synchronous Events

Many of the events that we have included in this work can be considered synchronous, within the resolution of our method. To keep our interpretation conservative, we consider the resolution of our method to be equal to twice the average sample spacing in our

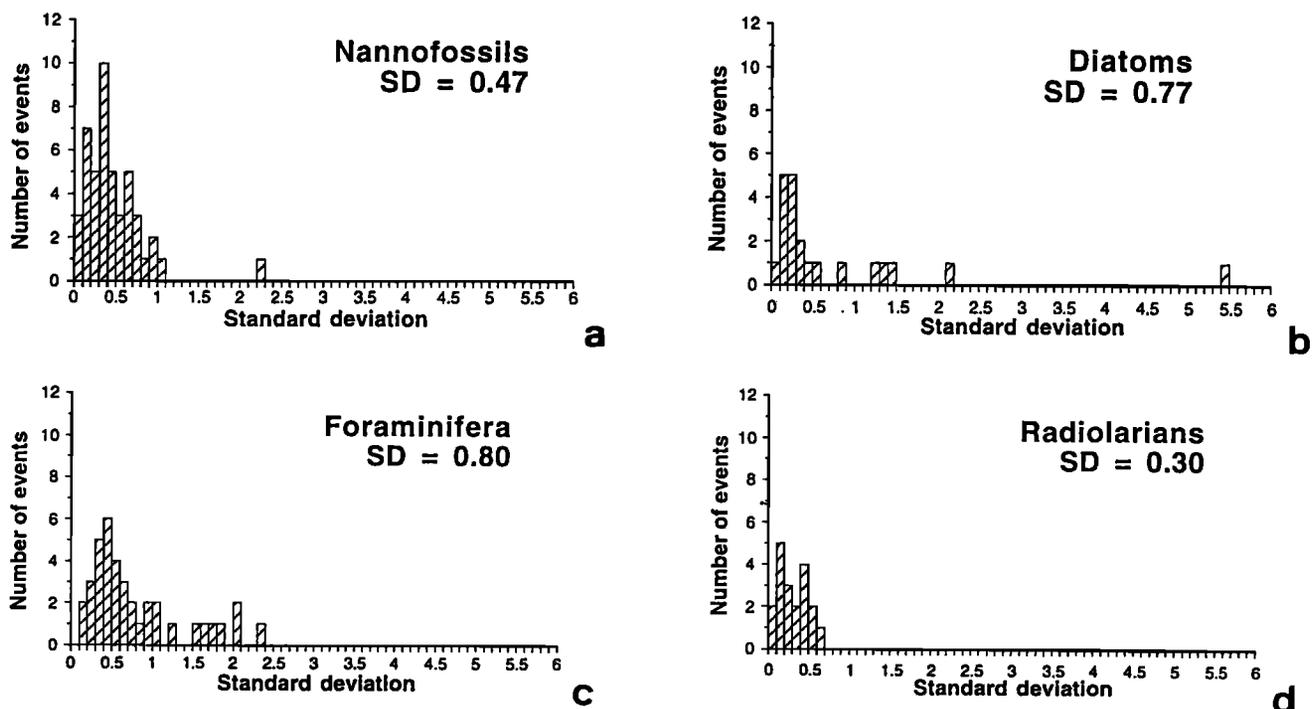


Figure 9. Frequency distribution of standard deviations (in m.y.) of the studied plankton events. SD, mean standard deviation for group.

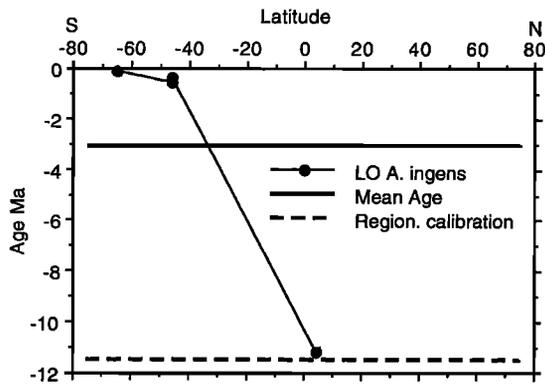


Figure 10. Latitude versus age (in Ma) plot of the LAD of *A. ingens* (diatom). Each point (LO) is plotted with its standard deviation (vertical bar), that is smaller than the symbol. The global mean age (LAD) is represented by the continuous horizontal line, the low-latitude calibration by the dotted horizontal line. Northern latitudes are expressed as positive numbers, southern latitudes as negative numbers. This event is reported, from north to south, in holes 574, 594, 514, and 690B.

database. The mean sample spacing is 0.185 m.y., therefore the precision of our method is 0.37 m.y.

For a growing number of these events, synchrony is being established by correlation with the late Neogene oxygen isotope stratigraphy, often at a resolution of better than 10 k.y., that is, far better than it is possible with the database as used here. Among

the nannofossils, FAD of *Emiliania huxleyi* has been shown to occur globally in oxygen isotope stage 8 (Figure 13a), LAD of *Pseudoemiliania lacunosa* in stage 12 (Figure 13b); the radiolarian LAD of *Stylatractus universus* is calibrated between stage 12 and 11 (Figure 13c) [Hays and Shackleton, 1976; Thierstein et al., 1977].

Our current analyses also indicate that the nannofossil events LAD of *Discoaster brouweri* (Figure 14a), LAD of *Discoaster pentaradiatus* (Figure 14b), LAD of *Discoaster surculus* (Figure 14c), LAD of *Discoaster tamalis* (Figure 14d), LAD of *Amaurolithus tricorniculatus* (Figure 14e), LAD of *R. pseudoumbilicus* (Figure 14f), and FAD of *Ceratolithus acutus* (Fig. 14g) are widely reported events that are reasonably synchronous (for age estimates see Table 1). The first four of these events were calibrated with oxygen isotope stratigraphy by Wei [1993]. There is a general agreement between our results and Wei's [1993] with a maximum difference of 0.1 m.y.

Over half of the diatom events (12 out of 21) are synchronous. Nine of these are recorded only around the equator and our mean age determinations are within ± 0.5 m.y. of the ages given by Barron [1985a] and Mikkelsen [1990] in low latitudes (see Table 1). The only 2 non equatorial synchronous diatom events are: the LAD of *Nitzschia fossilis* (Figure 15a) and FAD of *Pseudoenotia doliolus* (Figure 15b).

Considering the noise in the foraminifera data and the rather low precision of our method, only one quarter of the events in our compilation (9 out of 38) can be surely considered synchronous within the latitude range where they are reported: LAD of *Globorotalia miocenica*, LAD of *Globoquadrina altispira*, FAD

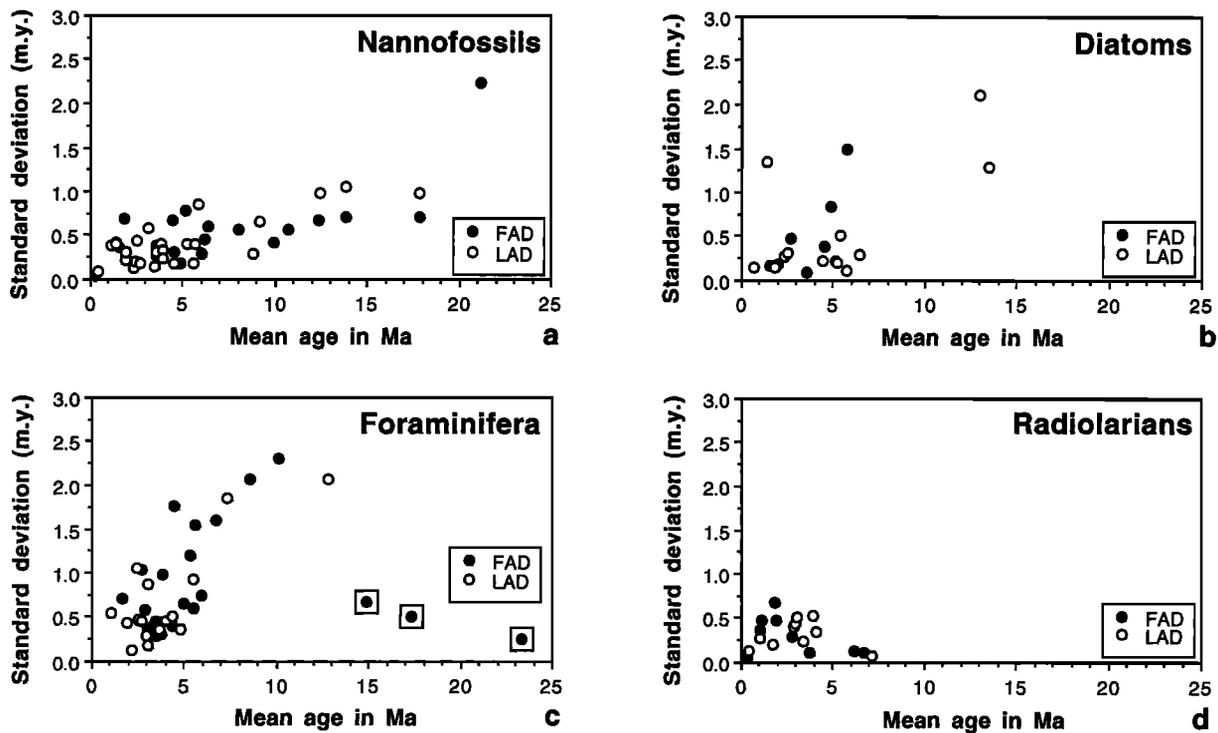


Figure 11. Mean age (in Ma) versus standard deviation (in m.y.) plots for the four plankton groups. In the foraminifera plot (c) the three points inscribed into a square are mentioned in the text and are identified also in Figure 12c. The LAD of *A. ingens* diatom event, is not included in these and the following plots.

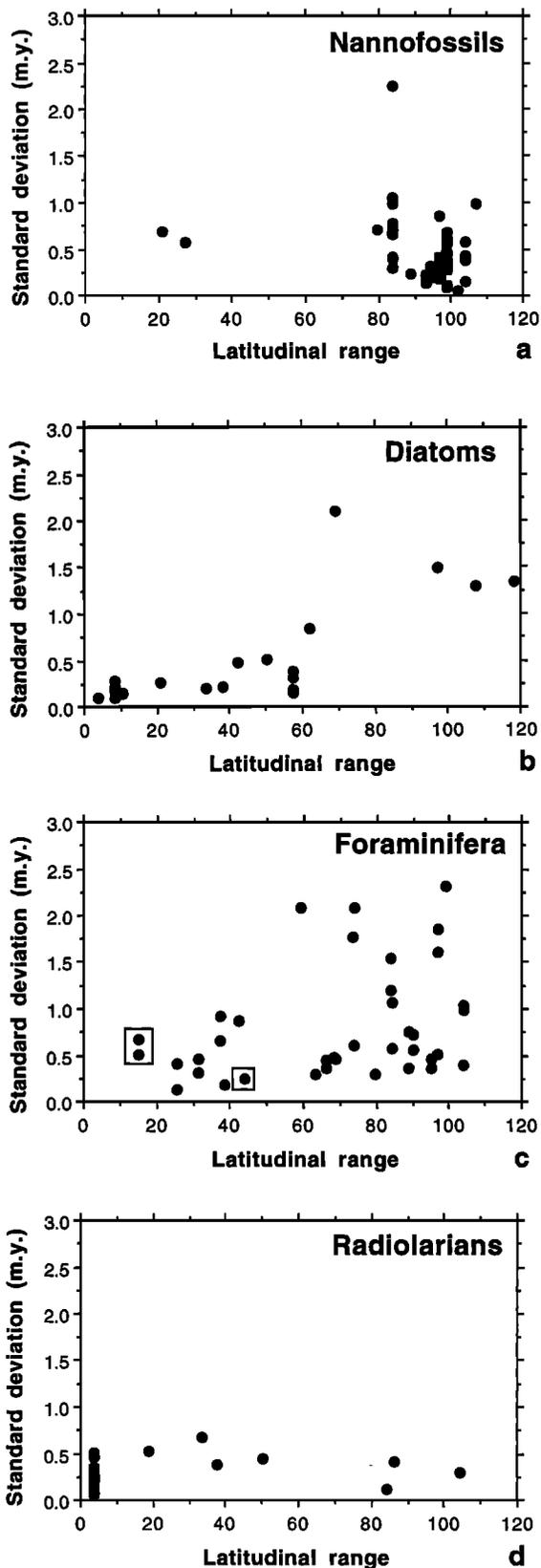


Figure 12. Latitudinal range versus standard deviation (in m.y.) plots for the four plankton groups. In the foraminifera plot (c) the three points inscribed into a square are discussed in the text and are identified also in Figure 11c.

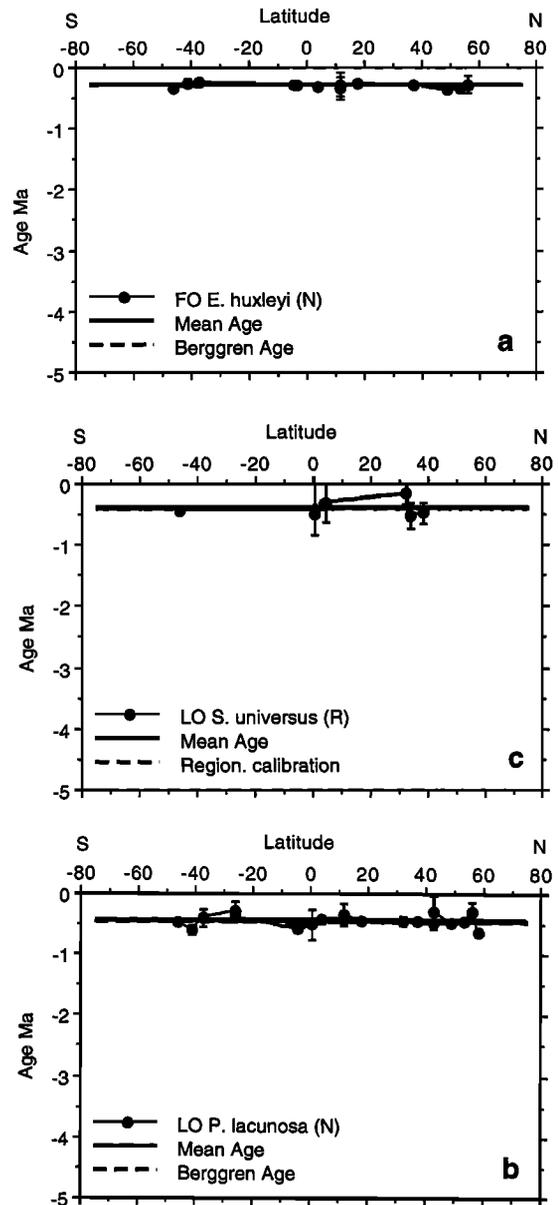


Figure 13. Examples of plankton events whose global synchrony has been demonstrated by correlations with oxygen isotope stratigraphy: (a) FAD *E. huxleyi* (reported from north to south in holes 552A, 610A, 548, 606, 659A, 502A, 502B, 503A, 709A, 710B, 592, 593, 594), (b) LAD *P. lacunosa* (holes 646B, 552A, 610A, 548, 608, 608A, 606, 577, 659A, 502A, 502B, 503A, 573, 709A, 710B, 522, 588, 592, 593, 594), (c) LAD *S. universus* (holes 579A, 578, 577, 574, 503B, 573, 573A, 594).

of *Globigerinoides fistulosus*, LAD of *Sphaeroidinellopsis* spp. (Figure 15c; recorded in the northern latitudes from 0°N to 40°N, with an age of 3.0 Ma, that agrees with *Berggren et al.* [1985] age), FAD of *Sphaeroidinella dehiscens s.s.*, LAD of *Globorotalia margaritae*, FAD of *Globorotalia pertenuis*, and LAD of *Globorotalia conomiozea*.

Almost all of the radiolarian events are more or less synchronous, but two-thirds of them are recorded only around the equator (see Table 1). This explains the low average standard

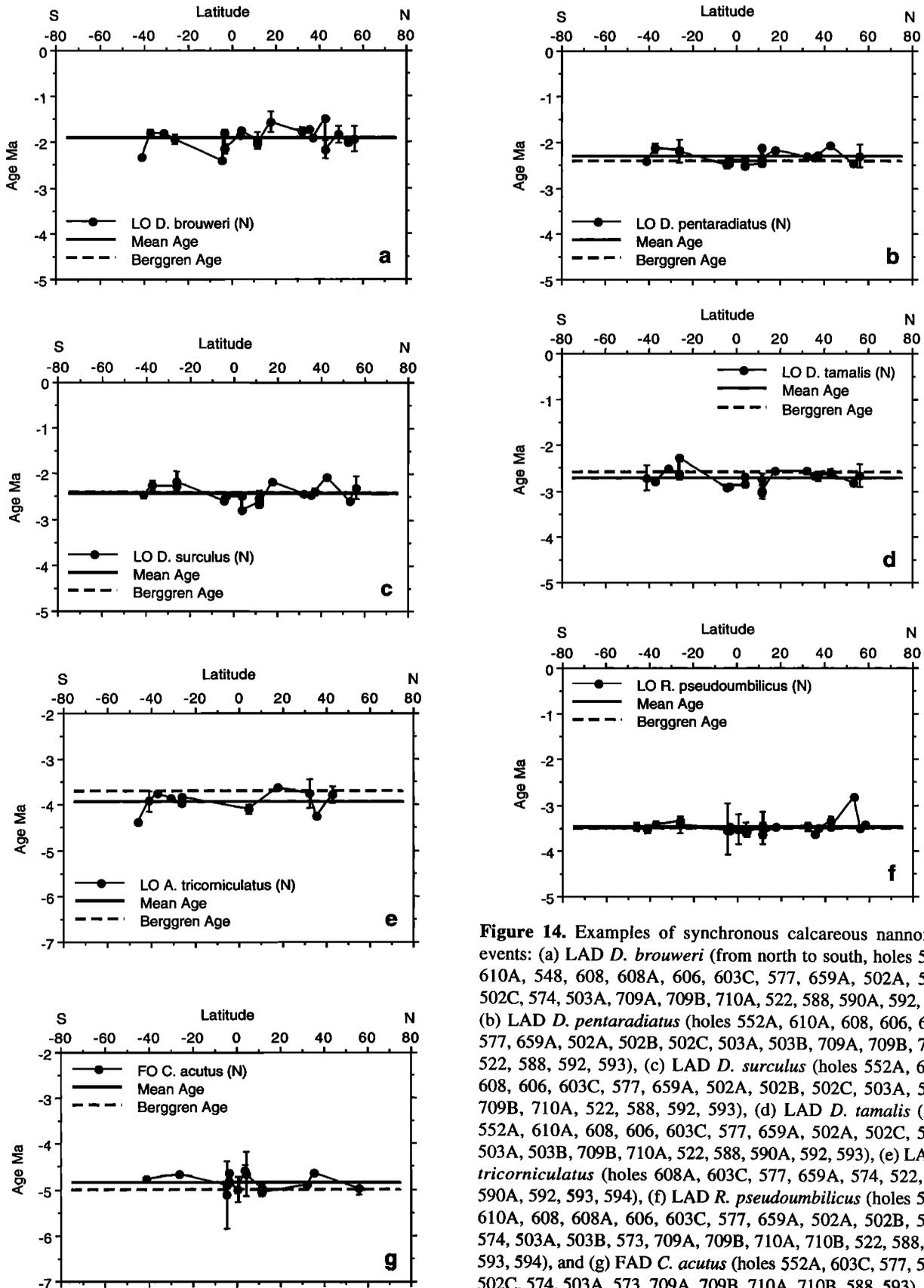


Figure 14. Examples of synchronous calcareous nannofossil events: (a) LAD *D. brouweri* (from north to south, holes 552A, 610A, 548, 608, 608A, 606, 603C, 577, 659A, 502A, 502B, 502C, 574, 503A, 709A, 709B, 710A, 522, 588, 590A, 592, 593), (b) LAD *D. pentaradiatus* (holes 552A, 610A, 608, 606, 603C, 577, 659A, 502A, 502B, 502C, 503A, 503B, 709A, 709B, 710A, 522, 588, 592, 593), (c) LAD *D. surculus* (holes 552A, 610A, 608, 606, 603C, 577, 659A, 502A, 502B, 502C, 503A, 503B, 709B, 710A, 522, 588, 592, 593), (d) LAD *D. tamalis* (holes 552A, 610A, 608, 606, 603C, 577, 659A, 502A, 502C, 502C, 503A, 503B, 709B, 710A, 522, 588, 590A, 592, 593), (e) LAD *A. tricomiculatus* (holes 608A, 603C, 577, 659A, 574, 522, 588, 590A, 592, 593, 594), (f) LAD *R. pseudoumbilicus* (holes 552A, 610A, 608, 608A, 606, 603C, 577, 659A, 502A, 502B, 502C, 574, 503A, 503B, 573, 709A, 709B, 710A, 710B, 522, 588, 592, 593, 594), and (g) FAD *C. acutus* (holes 552A, 603C, 577, 502A, 502C, 574, 503A, 573, 709A, 709B, 710A, 710B, 588, 593).

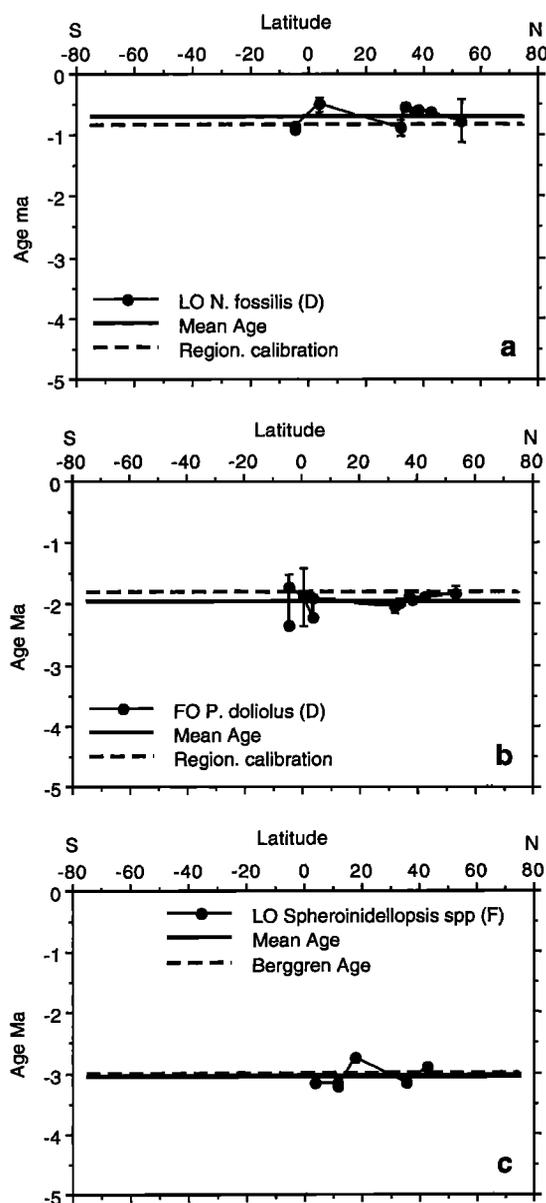


Figure 15. Other examples of synchronous events: (a) LAD *N. fossilis* (from north to south, holes 610A, 608, 579A, 606, 578, 577, 503A, 710A, 710B), (b) FAD *P. doliolus* (holes 610A, 608, 579A, 606, 578, 577, 503A, 503B, 573A, 710A, 710B), (c) LAD *Spheroidinellops* spp. (holes 608, 603C, 659A, 502A, 502C, 503B).

deviation of the radiolarians. However, several diachronous tropical radiolarian events have been reviewed by *Johnson and Nigrini* [1985].

Diachrony: Possible Causes and Applications

Within the stated limitations of the database we attempt to document and further analyze events that are not demonstrably synchronous and discuss their implications for the causes of biostratigraphic uncertainty, possible cures, but also new opportunities to better understand processes of plankton

evolution. Such analyses, however, require definition of the criteria used to separate diachronous from synchronous events, that is, when a derived local age estimate for an event is likely beyond the variability expected from sample spacing, incomplete recovery, sedimentation rate changes, etc. The age uncertainties caused by these processes had already been computed in our age/depth plots (vertical bars in Figure 2). The mean value of all these uncertainties (0.185 m.y.) is about one third of the mean standard deviation (0.6 m.y.) of all plankton events. By these criteria there remains the surprising number of 71 traditionally used plankton events which are apparently diachronous, out of a total of 124 bioevents investigated in this study.

We can think of at least four hypotheses for the causes of such diachrony: change in environmental gradients through time, evolutionary adaptation of populations, migration due to water mass changes, and investigator biases. In the following discussion we will attempt to demonstrate evidence for three of these, using plots of local bioevent age estimates versus latitude. This approach is feasible and appropriate, since modern plankton distributions vary primarily with latitude, and it allows us to make maximum use of the rather limited number of data points for many of the events.

Hypothesis 1: Change of Environmental Gradients Through Time

An increase in latitudinal gradients through time is expected from our knowledge of Tertiary cooling of polar areas [Kennett, 1982]. An expected response by the planktonic biota would be the replacement of cosmopolitan by endemic taxa. As demonstrated above, diachrony tends to be higher in cosmopolitan taxa than in endemic ones (Figure 12); thus a general decrease of diachrony through the Neogene would be expected. Such trends are indeed observed, at least in some plankton groups, such as the nannofossils, diatoms, and foraminifera (Figure 11). However, a statistical test for correlation of age of events versus their latitudinal range has shown a very small correlation coefficient ($R^2 < 0.1$). Therefore other causes for the observed decrease in diachrony through time are more likely.

Hypothesis 2: Evolutionary Adaptation

Evolutionary adaptation of plankton populations would be an obvious mechanism leading to diachrony of events. For FADs we should expect a progressively younger age starting from a location of evolutionary first appearance to other areas as the species gradually expands its geographic range through adaptive immigration. In a similar way, certain adaptive capabilities of populations may be eliminated through geologic time, leading to diachrony of extinctions. We have found several examples for such a mechanism for both FADs and LADs, especially among diatoms. Among first occurrences we find the following: the FAD of *Rhizosolenia praebergonii* is recorded in seven holes and its age decreases from about 3 Ma in equatorial areas to about 2 Ma at northern high-latitude sites (Figure 16a); the FAD of *Thalassiosira oestrupii* is recorded in eight holes and shows a time-transgressiveness from about 6 Ma in the southern high latitudes to 3.5 Ma in the northern high latitudes (Fig. 16b). One radiolarian event, FAD of *Theocorythium trachelium* has an age of 2.5 to 3.0 Ma in two holes from the northern midlatitudes and of only 1-1.5 Ma in four holes around the equator (Figure 16c).

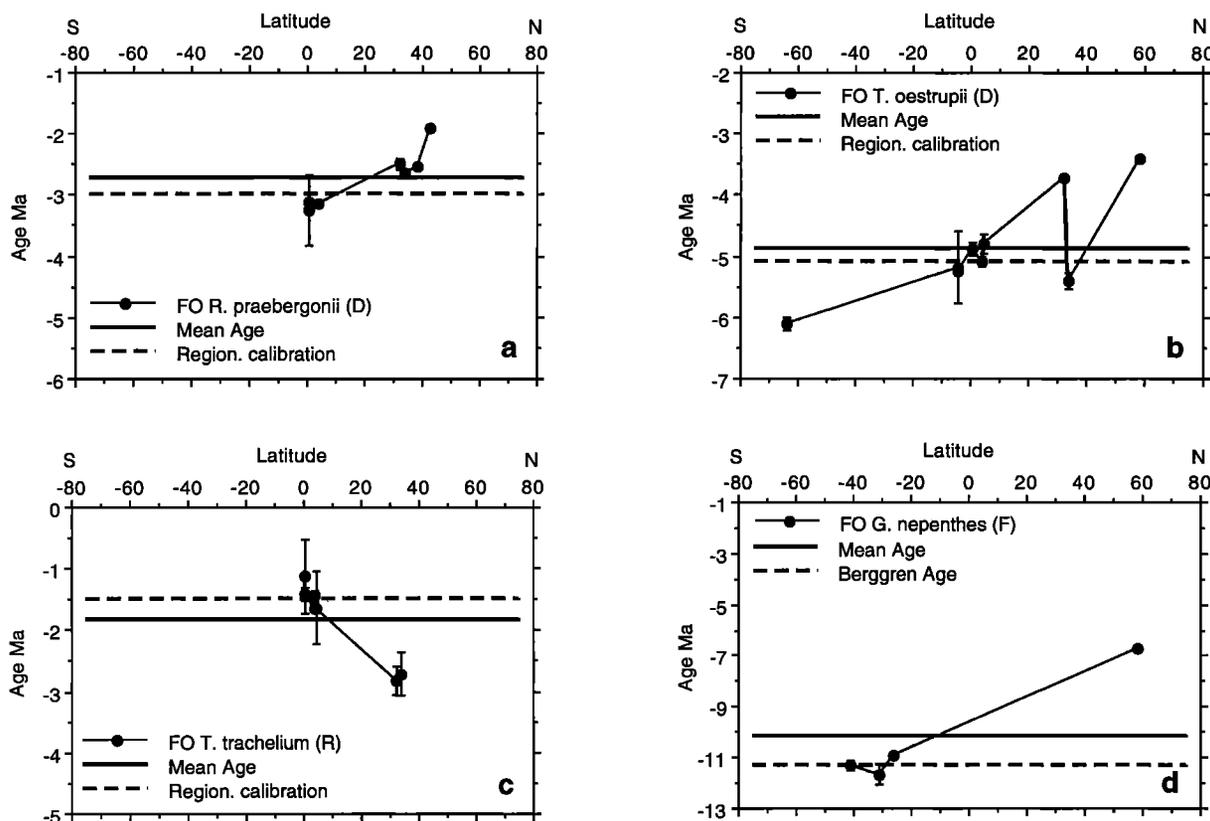


Figure 16. Examples of hemispherical diachrony of local first occurrence levels (FADs): (a) *R. praebergonii* (from north to south, holes 608, 579A, 578, 577, 503A, 573, 573A), (b) *T. oestrupii* (holes 646B, 578, 577, 574, 503A, 573, 710A, 710B, 689B), (c) *T. trachelium* (holes 578, 577, 574, 503A, 503B, 573, 573A), (d) *G. nepenthes* (holes 646B, 588A, 590B, 593).

The diachrony of this event has been previously studied by *Baker and Johnson* [1982]. Among the calcareous plankton, the FAD of *Globigerina nepenthes* (Figure 16d), calibrated at four sites, ranges from about 11 to 12 Ma in the subtropical southern latitudes to 7 Ma in one hole in the northern high latitudes.

Extinction events showing a latitudinal diachrony include several diatom events: the previously discussed LAD of *Actinocyclus ingens* (Figure 10), which became extinct at 11.5 Ma in low latitudes and only at 0.5 Ma in the southern high latitudes; the LAD of *Nitzschia reinholdii*, recorded in 13 holes, which shows a remarkably "hemispherical" diachrony pattern: it is calibrated at about 4.5 Ma in the Southern Ocean and is as young as 0.5 Ma in the northern high latitudes (Figure 17a); the LAD of *Synedra jouseana*, recorded in 5 holes, which has a difference of 4.5 Ma between the southern high-latitude calibration at about 14.5 Ma and the low-latitude calibration at about 10 Ma (Figure 17b); for the nannoplankton a significant example is the LAD of *Cyclicargolithus floridanus* (Figure 17c). This event was calibrated in the southern high latitudes by *Wei and Wise* [1992] at 12.2 Ma. However, based on our age models, we obtain for this event the oldest age in the southern high latitudes (hole 689B) around 14.5 Ma. This disagreement is due to the fact that *Wei and Wise* [1992] consider the species *Reticulofenestra hesslandii* as a possible synonym of *C. floridanus* and call it *C. floridanus s.l.*, whereas in the range chart published by *Wei and Wise* [1990] the two species were reported separately. We have restricted our

analysis to *C. floridanus*, which disappears in hole 689B around 2 m.y. before *R. hesslandii*. The pattern of this event shows that it becomes progressively younger toward the north, with the youngest ages recorded at the southern midlatitudes in the Pacific and northern high latitudes in the Atlantic; an intermediate age calibration of 12.7 Ma from the Indian Ocean does not fit the latitudinal trend and may be due to ocean basin bioprovincialism previously demonstrated by *Johnson and Nigrini* [1985] for radiolarians. The examples presented here support this hypothesis as a possible reason of diachrony.

Hypothesis 3: Migration Due to Water Mass Changes

Climatic and ocean current variability can restrict or enlarge the area where suitable living conditions for planktonic organisms exist. Considering the dominantly temperature-correlated latitudinal biogeographies of most living plankton species, diachrony of plankton events is to be expected because of the overall late Cenozoic cooling of polar areas [e.g., *Haq and Lohmann*, 1976; *Haq*, 1980; *Kennett*, 1982, p. 65]. During a cooling phase cosmopolitan taxa may first disappear in high latitudes and only later in low-latitudes, whereas high-latitude taxa may immigrate after speciation into cooling lower latitudes. Because of the generally observed decrease of species richness in plankton with increasing latitude, the first process may dominate. During a warming phase, on the other hand, low-latitude taxa may

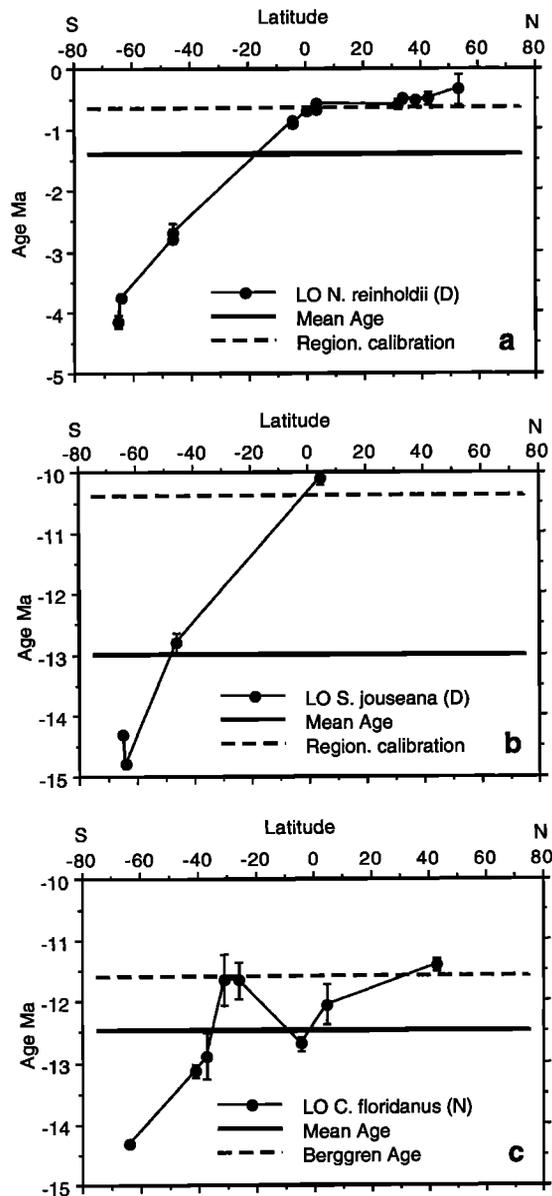


Figure 17. Examples of hemispherical diachrony of local extinction levels (LADs), suggesting survival refugia in equatorial areas and the northern hemisphere for the diatoms (a) *N. reinholdii* (from north to south, holes 610A, 608, 579A, 578, 577, 503A, 503B, 573A, 710A, 710B, 594, 514, 689B, 690B) and (b) *S. jouseana* (holes 574, 594, 689B, 690B), and the nannofossil (c) *C. floridanus* (holes 608, 574, 710A, 588A, 590B, 592, 593, 689B).

migrate toward higher latitudes (dominant effect because of higher species richness in low latitudes) and high-latitude taxa may disappear earlier at lower latitudes.

In our data set, diachronous survival in low latitudes can be documented for nine calcareous plankton events, two of which are nannofossils: the LAD of *Sphenolithus heteromorphus* (Figure 18a) is time-transgressive from 15.2 Ma at 40°S to 12.5 Ma at the equator; the time-transgressive first appearances of midlatitude to high-latitude species is less frequent, but does occur: the nannofossil *Triquetrorhabdulus rugosus* (Figure 18b) appeared 17 Ma at 40°N and immigrated in subtropical areas only at 13 Ma.

Among the foraminifera, the time-transgressiveness of LAD of *Globoquadrina dehiscens* (Figure 18c) is particularly well documented and ranges from 9.5 Ma at 40°S to 5 Ma at the equator; that of LAD of *Globorotalia peripheroronda* ranges from 9 to 14 Ma (Figure 18d) and of LAD of *Pulleniatina primalis* from 1.5 to 3.5 Ma (Figure 18e).

The first appearance of several radiolarian taxa in the north Pacific and their subsequent migration towards the equatorial area during the late Neogene has recently been documented by Spencer-Cervato *et al.* [1993]. Diachrony patterns expected during warming periods are also observed: the FAD of *Nitzschia reinholdii* (Figure 18f) is dated at 7 Ma at the equator at only 4–4.5 Ma at 30°N and 65°S, and the LAD of *Nitzschia miocenica* is 6 Ma at low latitudes and 4.5 Ma at high southern latitudes. Both cover the time of earliest Pliocene warming. The pattern shown by the FAD of the foraminifera *Globorotalia tumida* is due to an isolated, very young age in northern mid-high latitudes (0.5 Ma), whereas the ages recorded between 20°N and 30°S are between 4.1 and 5.7 Ma.

Some of these diachronies may be related to ecological factors that differentiate siliceous and calcareous plankton, and also phytoplankton and zooplankton: calcareous plankton is highly diverse in warmer waters, whereas siliceous microfossils are widespread also in cooler water masses. We interpret the fact that we see a pattern of latitudinal restriction mostly in foraminifera, as an indication of their higher sensitivity to temperature changes. There are several lines of evidence that suggest that CaCO₃-secreting organisms tend to be limited by cold water temperatures [e.g., Clarke, 1990]. In addition, Wei and Kennett [1986] described the changes of diversification rates for planktonic foraminifera during the Neogene. They distinguished between an early Miocene period of increasing diversification, a middle to late Miocene period of equilibrium and a Plio-Pleistocene period of declining diversification. A similar diversification trend has also been observed in Neogene calcareous nannofossil [Lohmann and Carlson, 1981]. Wei and Kennett [1986] related these periods to oceanographic and climatic variations during the Neogene.

Hypothesis 4: Taxonomic Bias

An additional potential cause for diachrony to be considered is the effort made to verify presence and absence of taxa in certain samples and the ease of identifying them properly at the species level. The data interpreted here were collected by numerous authors over a time span of more than two decades, during which taxonomic concepts may have evolved. An expected characteristic of diachrony caused by differential taxonomic concepts of various authors would be the absence of a biogeographically coherent pattern. A likely example for such a cause is the FAD of the nannofossil *Discoaster asymmetricus* (Figure 19a): it is recorded in 16 holes with ages between 6 and 3 Ma. The close morphological similarities with *Discoaster pentaradiatus*, which differs from *D. asymmetricus* only by a more regular spacing of the 5 arms, are likely responsible for inconsistent identifications and thus for the observed age variability. We suspect that some of the *Discoaster* events (17 in our data set) and several events of *Gephyrocapsa* species also show some disagreement in the age calibrations due to the uncertain and variable species concepts. We illustrate specifically the LAD of *Discoaster variabilis* (Figure 19b) and the LAD of *T. rugosus* (Figure 19c), both of which show an irregular geographic pattern of age calibrations.

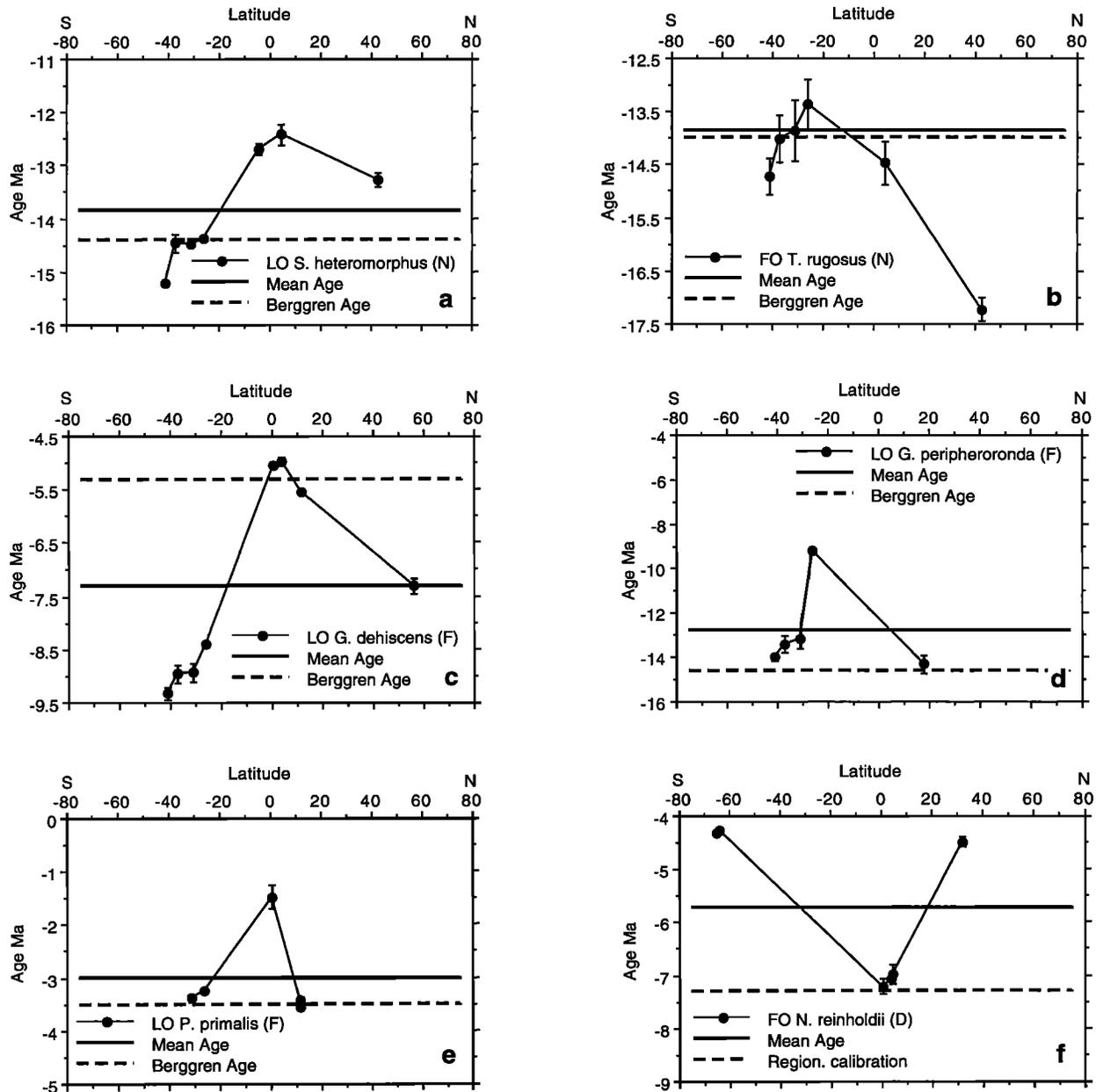


Figure 18. Examples of diachronous events related to climatic changes: (a) LAD *S. heteromorphus* (from north to south, holes 608, 574, 710A, 588A, 590B, 592, 593), (b) FAD *T. rugosus* (holes 608, 574, 588A, 590B, 592, 593), (c) LAD *G. dehiscens* (holes 552A, 502A, 503A, 573, 588, 590B, 592, 593), (d) LAD *G. peripheroronda* (holes 659A, 588, 590B, 592, 593), (e) LAD *P. primalis* (holes 502A, 502C, 573, 588, 590A), (f) FAD *N. reinholdii* (holes 577, 574, 503A, 573, 689B, 690B).

Latitudinal Diachrony - Evidence for Speciation Centers and Survival Refugia?

Knowledge of the geographic location of the oldest FAD and of the youngest LAD of species would allow us to identify regions of the ocean that have acted either as centers of evolution, or as evolutionary refugia - ideas which have been much debated [e.g., Berggren, 1969; Haq, 1980; Emiliani, 1982; Wei and Kennett, 1983, 1986]. Wei and Kennett [1986] showed that average evolutionary rates of planktonic foraminifera are geographically randomly distributed, although the number of

extinctions and speciations is higher in the tropical assemblages because of their generally higher diversity.

In Table 4 we summarise the geography of diachronous FADs and LADs for the whole set of data and for the single plankton groups. We have separated equatorial areas from northern and southern midlatitude to high-latitude areas at 15° latitude. Speciations (FADs) of oceanic plankton in general seem to be randomly distributed, whereas survival refugia (LADs) appear to be slightly more abundant in the northern hemisphere and the equatorial region. With respect to the individual plankton groups there is no evidence for a general nonrandomness with the

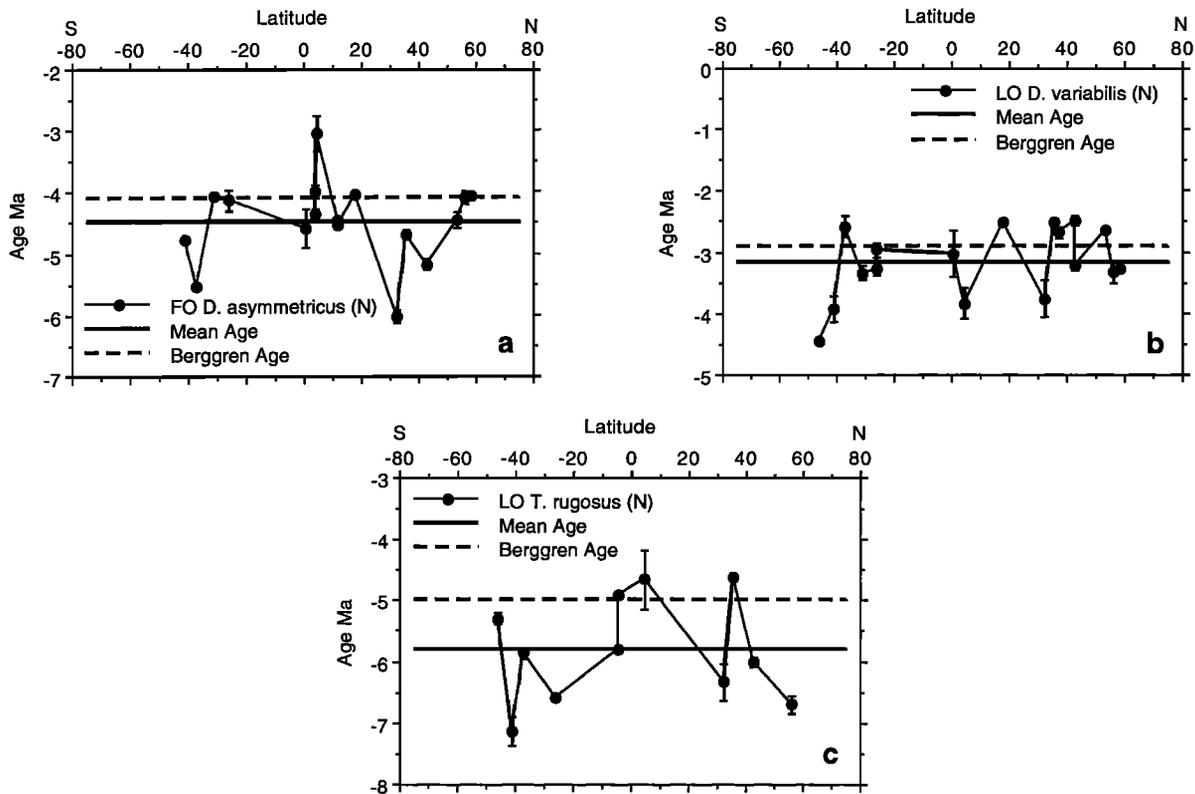


Figure 19. Examples of diachrony of calcareous nannofossils likely due to taxonomic problems: (a) FAD *D. asymmetricus* (from north to south, holes 646B, 552A, 610A, 608, 603C, 577, 659A, 502A, 502C, 574, 503A, 503B, 573, 522, 590A, 592, 593), (b) LAD *D. variabilis* (holes 646B, 552A, 610A, 608, 608A, 606, 603C, 577, 659A, 574, 573, 522, 588, 590A, 592, 593, 594), (c) LAD *T. rugosus* (holes 552A, 608, 603C, 577, 574, 710A, 710B, 588, 592, 593, 594).

exception of the nannofossils, which show a higher frequency of youngest LADs in the northern hemisphere (Table 4). The apparent tendency of diatom and radiolarian FADs and LADs to be concentrated near the equator is not statistically significant because of the small number of cases. Thus, while we see no evidence for any one region of the ocean acting as a predominant

centre for the evolution of new taxa, there is some evidence (mostly from nannofossils) that taxa tend to become locally extinct in the southern hemisphere prior to their final extinction in equatorial or northern hemisphere waters. Specific examples of taxa showing this pattern include the nannofossil LADs of *C. floridanus* (Figure 17c) and *Sphenolithus heteromorphus* (Figure

Table 4. Latitudinal Distribution of Oldest FADs and Youngest LADs for the Groups and in Total

	Diatom Oldest FADs	Diatom Young- est LADs	Nanno- fossil Oldest FADs	Nanno- fossil Young- est LADs	Radio- larian Oldest FADs	Radio- larian Young- est LADs	Foram- inifera Oldest FADs	Foram- inifera Young- est LADs	Oldest FADs (Total)	Young- est LADs (Total)
Northern hemisphere	0	3	9	16	1	1	6	6	16	26
Equator	6	9	8	4	7	8	6	6	27	27
Southern hemisphere	1	2	4	5	1	1	10	4	16	12
Chi square			2	11.1			1.56	0.6	4.05	6.39
Percent			20-30%	0%			~20%	~50%	~10%	<5%

The equatorial area is considered between 15°N and 15°S.

Table 5. Summary of Synchrony and Diachrony of Studied Events

Group	Unclassifiable	Synchronous	Hemispherical Diachrony	Latitudinal Diachrony	Incoherent Diachrony	Total
Nannofossils	5	20	2	2	17	46
Diatoms	1	12	6	2	0	21
Foraminifera	6	9	6	8	9	38
Radiolarians	3	12	2	0	2	19
Total	15	53	16	12	28	124

18a), and the diatom LADs of *Nitzschia reinholdii* (Figure 17a) and *Synedra jouseana* (Figure 17b). In these cases the northern hemisphere oceans may thus have acted as survival refugia.

Summary and Conclusions

By the criteria used a surprisingly small proportion (42%) of 124 commonly used Neogene biostratigraphic plankton events are actually recorded at synchronous levels in magnetostratigraphically calibrated sections (Table 5). A considerable number show coherent latitudinal gradients in their diachrony, holding the promise to further elucidate paleoceanographic and evolutionary processes. Some 70% of the studied bioevents (FADs and LADs) are from latitudinally widespread species and show more frequently diachrony than latitudinally restricted taxa. Diachrony also seems to increase with increasing age of the event. Four likely causes for these diachrony patterns have been considered: decrease of global environmental gradients through time, evolutionary adaptation, migration due to climatic changes, and uncertainties in the taxonomic concepts. The last three hypotheses have been illustrated by specific examples. However, many of the events examined during this study are more or less synchronous, and their age calibrations generally coincide with the published low-latitude calibrations.

From the results obtained it is possible to make some suggestions on how to improve the general quality of the biostratigraphy of the Neogene. The highest possibility to significantly improve the biochronologic resolution appears to lie in a recalibration of numerous events of species with uncertain or variable taxonomic definitions. We estimate this potential to be particularly high for calcareous plankton events (see Table 5, column 6). Moreover, a tighter sample spacing could provide additional resolution beyond the average current sample spacing (0.185 m.y.). Great potential exists in pre-Pliocene intervals, where only a small number of paleomagnetically calibrated sections are available. To conclude, we think that the reality of common diachrony should be accepted by biostratigraphic workers. This implies that regional rather than global age calibrations should be made and more frequently used.

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