

STEPWISE MASS EXTINCTIONS AND IMPACT EVENTS: LATE EOCENE TO EARLY OLIGOCENE

GERTA KELLER

Department of Geological and Geophysical Sciences, Princeton University, Princeton, NJ 08544 (U.S.A.)

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Abstract

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Species ranges and relative abundances of dominant planktonic foraminifers of eight late Eocene to early Oligocene deep-sea sections are discussed to determine the nature and magnitude of extinctions and to investigate a possible cause–effect relationship between impact events and mass extinctions.

Late Eocene extinctions are neither catastrophic nor mass extinctions, but occur stepwise over a period of about 1–2 million years. Four stepwise extinctions are identified at the middle/late Eocene boundary, the upper *Globigerapsis semiinvoluta* zone, the *G. semiinvoluta*/*Globorotalia cerroazulensis* zone boundary and at the Eocene/Oligocene boundary. Each stepwise extinction event represents a time of accelerated faunal turnover characterized by generally less than 15% species extinct and in itself is not a significant extinction event. Relative species abundance changes at each stepwise extinction event, however, indicate a turnover involving > 60% of the population implying major environmental changes.

Three microtektite horizons are present in late Eocene sediments; one in the upper *G. semiinvoluta* zone (38.2 Ma) and two closely spaced layers only a few thousand years apart in the lower part of the *Globorotalia cerroazulensis* zone (37.2 Ma). Each of the three impact events appears to have had some effect on microplankton communities. However, the overriding factor that led to the stepwise mass extinctions may have been the result of multiple causes as there is no evidence of impacts associated with the step preceding, or the step following the deposition of the presently known microtektite horizons.

Introduction

From a paleontological point of view the Eocene/Oligocene boundary is perhaps the most complex boundary event of the Cenozoic. Significant events surrounding this boundary include a series of rapid stepwise extinctions (Keller, 1983a, b), a permanent drop in bottom water temperatures by about 3–5°C (Douglas and Savin, 1978; Shackleton and Kennett, 1975; Keigwin, 1980), three microtektite horizons indicating multiple impacts possibly from a comet shower (Keller et al., 1983; Hut et al., in press), a global deepening of the carbonate compensation

depth (CCD) by over 2000 m (Berger, 1972; Van Andel et al., 1975) lowering of sea level (Vail and Hardenbol, 1979), and widespread hiatuses (Rona, 1973; Van Andel et al., 1975; Kennett, 1977; McGowran, 1978; Moore et al., 1978; Thiede et al., 1981; Keller et al., 1985; Miller et al., 1985) suggesting profound changes and intensification in bottom water circulation.

Many of these events appear to be directly related to long-term climatic trends. The stable isotope record indicates major cooling episodes beginning in the late middle Eocene and continuing through the late Eocene with generally cool fluctuating conditions cul-

minating in a permanent drop in bottom water temperatures at the Eocene Oligocene boundary (Keigwin, 1980; Keller, 1983a, b; Corliss et al., 1984; Miller and Thomas, 1985; Keigwin and Corliss, 1986). Cool fluctuating temperatures prevailed through the early Oligocene reaching a maximum low by 29 Ma suggesting that a significant volume of continental ice existed at this time (Keigwin and Keller, 1984; Miller and Thomas, 1985).

These climatic changes appear to be associated with the development of the circum-Antarctic current circulation made possible by the northward movement of Tasmania and Australia by middle Eocene time (Weissel and Hayes, 1972; McGowran, 1973). Subsequent cooling of Antarctica followed by production of cold Antarctic bottom water presumably led to the drop in bottom water temperatures by Eocene-Oligocene boundary time (Shackleton and Kennett, 1975). A series of widespread hiatuses document the development of this change in the Antarctic current circulation patterns (Rona, 1973; Kennett et al., 1975; McGowran, 1978; Thiede et al., 1981).

Faunal changes generally parallel the climatic trends. Middle Eocene to Oligocene warm water planktonic foraminiferal faunas are successively replaced by cooler water faunas during short stratigraphic intervals which are marked by major species extinctions and originations (Keller, 1983a, b). This cooling trend has also been observed in calcareous nannoplankton and ostracod faunas (Haq and Lohmann, 1976; Steineck et al., 1984). The Eocene-Oligocene bottom water temperature drop, however, did not have a profound effect on either benthonic (Corliss, 1981) or planktonic foraminifera in middle to low latitudes; the latter indicate cooling by an increase in relative abundance of cool water species (Keller, 1983a). Hence, planktonic and benthonic faunas indicate that the Eocene-Oligocene boundary event is part of a continued cooling trend which began during the middle Eocene.

The recent discovery of at least three microtektite layers in deep-sea sediments by Keller et al. (1983) as well as anomalously high iridium concentrations by Ganapathy (1982), Alvarez et al. (1982) and Keller et al. (in press) has again raised the spectre of catastrophic events near this boundary. The closely spaced microtektite horizons suggest that the earth was in the path of a comet shower lasting about 1-2 million years (Hut et al., in press).

What effect did these impacts have on planktonic marine faunas? Is there a cause-effect relationship between impact events and species extinctions and abundance changes? Are climatic changes triggered by impact events? Late Eocene sediments provide the unique opportunity to answer some of these questions. To help provide answers to these questions this paper investigates the stratigraphic relationship of the microtektite layers and examines the nature of the Eocene-Oligocene extinction record based on species extinctions and relative abundance changes of species as a measure of the percent fauna affected.

Methods

Sediments were soaked in calgon solution mixed from 40 g sodium hexa-metaphosphate, 20 l of deionized water and buffered with ammonia hydroxide (58% solution) to bring the pH to 7. Disaggregated samples were washed over a 63 μm screen with tap water and the residue oven dried at 50°C. Dried samples were sieved through a 150 μm fraction screen and an aliquot of 300-500 specimens of the >150 μm fraction was split with an Otto microsplitter and used for biostratigraphic and quantitative faunal analysis.

Each sample aliquot of 300-500 specimens of planktonic foraminifers was picked and species identified and mounted on microslides as permanent record. The remaining sample was examined for rare species. Relative species abundances were recorded as percent of total population.

The sample residue $>100\ \mu\text{m}$ was examined for microtektites. Microtektites were picked and mounted on microslides as permanent record and for geochemical analysis and $^{40}\text{Ar}/^{39}\text{Ar}$ dating. The precise core position of microtektite layers was determined from archive cores using a binocular microscope.

Multiple microtektites horizons

Multiple microtektite horizons as observed in Late Eocene sediments are not unique in geologic history and have also been reported from the Pleistocene known as Australasian and Indochinese tektites (Glass et al., 1979) with $^{40}\text{Ar}/^{39}\text{Ar}$ ages of 0.88 and 0.69 Ma respectively (Storzer et al., 1984). More microtektite horizons will undoubtedly be discovered as more research is directed towards their analysis in deep-sea sediments.

Microtektites are commonly found in Late Eocene sediments. They are believed to be the residue of comet or meteorite impacts, although some workers consider them the product of lunar volcanism (O'Keefe, 1976, 1980, 1986). These glassy objects are predominantly spherical-, teardrop-, or dumbbell-shaped and range from transparent colorless, yellow and bottle green to translucent black. They generally have smooth surfaces, but may be pitted or grooved due to solution (Fig. 1). Microtektites are most commonly present in the 100–150 μm size fraction. They are most highly concentrated in a narrow band of 2–5 cm (>1000 per cm^3) and few to rare can be found within a 25 cm interval as a result of dispersal due to bioturbation.

Based on stratigraphic evidence Keller et al. (1983; in press) observed at least three microtektite layers in late Eocene sediments; one in the upper part of foraminiferal Zone P15 (*Globigerapsis semiinvoluta*) and two closely spaced layers in Zone P16 (*Globorotalia cerroazulensis*) near the radiolarian Subzone *Calocyclus bandyca/Cryptopora ornata* boundary of *Thyrsocyrtis bromia* Zone (Glass et al., 1982; Saunders et al., 1984;

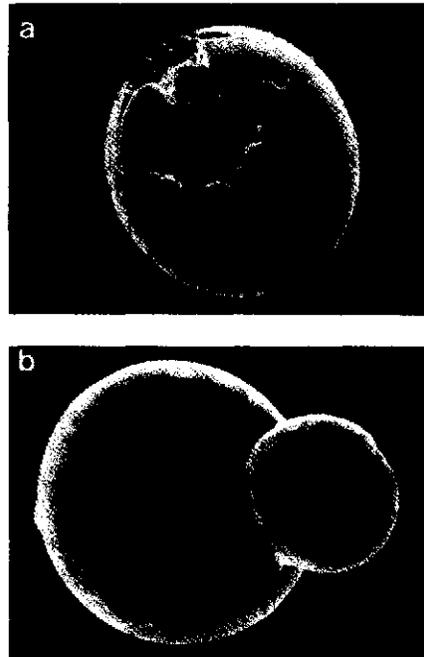


Fig. 1. a. Microtektite with solution pits from Caribbean piston core RC9-58 (240–243 cm). b. Microtektite consisting of two fused spheres from DSDP Site 292 Core 38-2 (35 cm) (1 mm in diameter).

Sanfilippo et al., 1985). Evidence of three impact events was disputed by Glass et al. (1985) who originally believed that only one late Eocene microtektite layer, the North American layer, was present (Glass et al., 1979, 1982), but now agree that a second layer characterized by clinopyroxene (cpx)-bearing spherules is also present (Glass et al., 1985). These two layers are closely spaced in marine sediments, separated by about 25 cm of sediment, representing impacts only a few thousand years apart (Keller et al., in press). These layers correspond to the upper two microtektite layers of Keller et al. (1983). The uppermost Zone P15 (*G. semiinvoluta*) layer Glass and co-workers (1985) believe to be either reworked microtektites, or the same as the cpx-spherule layer of Zone P16. They have reached this conclusion based on major element composition of microtektites, but ignoring completely the stratigraphy.

A report by D'Hondt et al. (in press)

shows that major element compositional analysis of microtektites alone is an insufficient criterion for distinguishing between different microtektite layers. Major element compositional overlap was observed even between the late Eocene and the Pleistocene Australasian and Ivory Coast microtektites, as would be expected if the impacted target rocks were similar. However, their report also shows that multivariate statistical analysis of microtektites permits identification of three distinct although somewhat overlapping late Eocene impact glass horizons. Their report stresses the need for stratigraphic control in establishing the relationship of microtektites to a particular impact glass horizon or strewn field.

Of thirty-seven late Eocene to Oligocene sections examined, 18 contain microtektite layers (Fig. 2, Table I). The youngest microtektite layer has been found primarily in the Caribbean, Gulf of Mexico and recently also off the Coast of New Jersey (Site 612; Thein, 1986) and is known as the North American strewn field (Glass et al., 1979, 1982). The second layer, the cpx-spherule layer, is also found in the Caribbean, Gulf of Mexico and in the equatorial Pacific. The disputed third

microtektite layer in the uppermost part of Zone P15 has been found in the West equatorial Pacific (Site 292), the Indian Ocean (Site 216) and most recently also in southern Spain (Keller et al., in press). Based on sedimentation rates, this layer is about 1 m.y. older and stratigraphically occurs about 15–20 m below the two closely spaced Zone P16 microtektite layers. The following section explores the relationship between these impact glass horizons and stepwise extinctions and illustrates the stratigraphic position of the microtektite layers.

Datum events

A high resolution biostratigraphic key for upper Eocene to lower Oligocene marine sediment has been developed based on datum events, species abundance changes, microtektite horizons and hiatuses of eleven low latitude sections.

Calculated ages of 44 datum events extrapolated from sediment accumulation rate curves of 11 low latitude deep-sea sites are listed in Table II. Planktonic foraminiferal analyses were done by Keller (1983a, 1985a, this report), nannoplankton and radiolarian

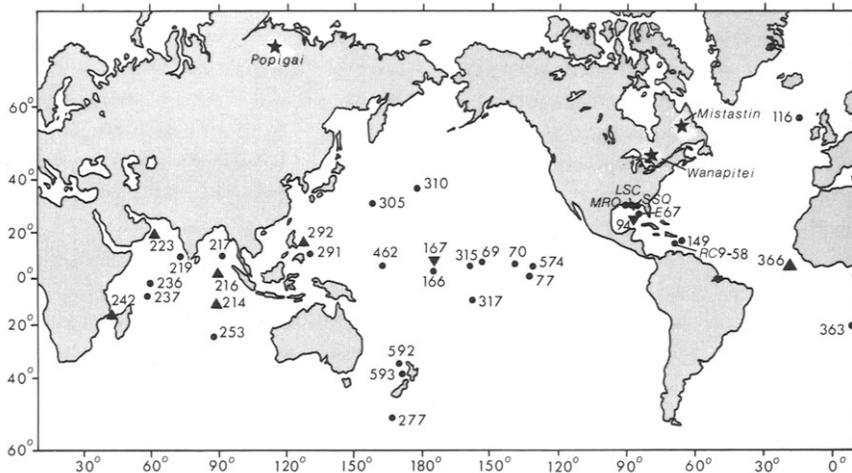


Fig. 2. Location map of late Eocene to Oligocene DSDP sites studied for this report (triangles) and reported elsewhere (circles) (Keller, 1983a, b; 1985a). Stars mark locations of impact craters of late Eocene age, Popigai 39 ± 4 Ma, and Wanapitei 37 ± 3 Ma (Grieve, 1982).

TABLE I

Upper Eocene to lower Oligocene sections studied quantitatively for planktonic foraminifers where preservation allowed and microtektite horizons. Location of microtektite horizons noted in either foraminiferal or radiolarian zones; radiolarian zone 16a, b, c refers to subzones *C. azyx*, *C. bandyca* and *C. ornata* of *T. bromia* zone

Site	Depth (m)	Longitude	Latitude	Quant. foram.	Type sediment	Microtektites	Comments	Refs. ^a
<i>Pacific Ocean</i>								
69A	4978	6°00.00'N	152°51.93'W		silic.	yes, 16b, c	CaCO ₃ dissolution	2, unpub.
70A	5059	6°20.08'N	140°21.72'W		silic.	yes, 16c	CaCO ₃ dissolution	2, unpub.
77B	4291	0°28.90'N	133°13.70'W	yes	carb.	no	poor pres. E/O	4, 9
166	4950	3°45.70'N	175°04.80'W		silic.	yes, 16b, c	CaCO ₃ dissolution	unpub.
167	3166	7°0.410'N	176°49.50'W	yes	carb.	yes, P16	poor recovery	2, 6
277	1214	52°13.43'S	166°11.48'E	yes	carb.	no	good, high lat.	4, 11
291	5217	12°48.43'N	127°49.85'E		silic.	yes, 16, CP15	CaCO ₃ dissolution	unpub.
292	2943	15°49.11'N	124°39.05'E	yes	carb.	yes, P16 and P15	good	1, 4, 6, 8
305	2903	32°00.13'N	157°51.00'E		carb.	cosmic spherule P15	poor preserv.	unpub.
315	4152	4°10.26'N	158°31.54'E		silic.	yes, NP21/20	poor preserv.	8
317B	2598	11°00.09'S	162°15.78'W	yes	carb.	no	good	unpub.
462	5181	7°14.25'N	165°01.88'E	poor	carb./sil.	yes, P15	poor pres. rework.	8
574	4561	4°12.52'N	133°19.81'W	no	carb.	no	poor pres. E/O	12
592	1098	36°28.40'S	165°26.53'E	no	carb.	no	good	10, 11
593	1068	40°30.47'S	167°40.47'E	no	carb.	no	volcanic breccia	10, 11
<i>Indian Ocean</i>								
214	1671	11°20.21'S	88°43.08'E	yes	carb.	no	CaCO ₃ dissolution	6
216	2262	1°27.73'S	90°12.48'E	yes	carb.	yes, P16/P15	poor core recov.	6
217	3030	8°55.57'N	90°32.33'E	yes	carb.	yes, P16/P15	CaCO ₃ dissolution	unpub.
219	1764	9°01.75'N	72°52.67'E	yes	carb.	no	good	1, 4
223	3633	18°44.98'N	60°07.78'E	yes	carb.	no	coring gap	6
236	4487	1°40.62'S	57°38.85'E	poor	carb.	no	poor core recov.	unpub.
237	1632	7°0.499'S	58°07.48'E	poor	carb.	no	poor core recov.	unpub.
242	2275	15°50.65'S	41°49.23'E	yes	carb.	?	poor core recov.	6
253	1962	24°52.65'S	87°21.97'E	yes	carb.	no	hiatus	4
<i>Atlantic—Caribbean</i>								
94	1793	24°31.64'N	88°28.16'W	yes	carb.	yes, P16, 16c	good	5, 6
116	1151	57°29.76'N	15°55.48'W		carb.	P15 microspherules	poor preserv.	unpub.
149	3972	15°06.25'N	69°21.86'W		silic.	yes, 16b, c	dissol. reworking	2, 7
363	2248	19°38.75'S	09°02.80'E	yes	carb.	no	poor core recov.	1, 4
366	2853	05°40.70'N	19°51.10'W	yes	carb.	no	good	6
612	1404	38°49.21'N	72°46.43'W	yes	carb.	yes, P16	hiatus P16/P12	8
RC9-58		14°33.4'N	70°48.6'W		silic.	yes, 16b, c	CaCO ₃ dissolution	3, 7, 8
E67-128	1494	28°14'N	86°56'W	yes	carb.	yes, P16, P15	some reworking	5, unpub.
St. Stephens Quarry, Alabama				yes	carb.	? P21	good, reworking?	5, 7
Little Stave Creek, Alabama				yes	carb.	no	good	5
Miss Lite Quarry, Mississippi				yes	carb.	yes, P16	no E/O boundary	5
Molino de Cobo, Spain				yes	carb.	yes, P15	good	8

^aReferences: 1. Corliss et al., 1984; 2. Glass and Crosbie, 1982; 3. Glass et al., 1982; 4. Keller, 1983a, b; 5. Keller, 1985a; 6. Keller, this paper; 7. Keller et al., 1983; 8. Keller et al., in press; 9. Keigwin and Keller, 1984; 10. Kennett et al., 1985; 11. Murphy and Kennett, 1985; 12. Miller and Thomas, 1985.

data were taken from the Initial Reports of the Deep Sea Drilling Project. Datum events represent first and last appearances as well

as final decline in the abundance of specific species. Ranges of species which are easily identifiable and solution resistant are gen-

*	<i>Gr. mex. howei</i>	38.3	rare	37.7	37.8	38.3	37.7	38.3*	
LAD	<i>Gr. semivoluta</i>	37.7	37.7	37.7	37.7	37.8	37.7	37.7	
*	<i>Gr. semivoluta</i>	38.3	rare	38.3	38.3	38.3	few	38.3*	
LAD	<i>T. rohri</i>		40.1		40.4	40.1	40.1	40.1	
*	<i>T. rohri</i>					40.5	40.5	40.5*	
LAD	<i>T. collactea</i>			40.0	40.4	40.1		40.1?	
LAD	<i>Gl. carcossellensis</i>			38.2-40.0	38.3	38.3	37.5-38.7	38.3?	
FAD	<i>Gl. gemma</i>				36.8		35.6	?	
<i>Radiolaria and nannoplankton^a</i>									
FAD	<i>T. bromia</i>			39.4	39.7			39.4-39.7?	
LAD	<i>T. bromia</i>	37.3		37.7	37.3			37.3	
LAD	<i>T. rhizodon</i>			37.7	37.3			37.3	
LAD	<i>T. tetracantha</i>			37.7	37.3			37.3	
LAD	<i>T. mongolfieri</i>	36.6		36.5	36.8			36.6-36.8	
LAD	<i>T. armadillo</i>	36.0-36.6		36.5	36.8			36.5-36.8	
LAD	<i>L. jacchia</i>	36.5		37.7	36.8			36.8?	
LAD	<i>C. azyx</i>			37.9				?	
LAD	<i>C. formosa</i>	36.6			34.8		36.8	unreliable	
LAD	<i>D. tani</i>	36.6			42.6		34.5	unreliable	
LAD	<i>D. saipanensis</i>	36.6		36.8	36.8	36.8	36.8	36.8	
LAD	<i>D. barbadoensis</i>	36.6		36.8	36.8	36.8	36.8	36.8	
LAD	<i>H. reticulata</i>	36.0					35.6	?	
LAD	<i>R. umbilica</i>			34.4			34.5	unreliable	
FAD	<i>S. distentus</i>	33.1		34.1			34.5	unreliable	
FAD	<i>S. predistentus</i>				35.6		34.7	unreliable	

^aAbbreviations used: *Gl.* = *Globorotalia*; *G.* = *Globigerina*; *H.* = *Hantkenina*; *P.* = *Pleurohastigerina*; *Ch.* = *Chiloguembelina*; *Gq.* = *Globoquadrina*; *C.* = *Corporanistrum*; *Gr.* = *Globigerapsis*; *T.* = *Truncorotaloides*; *D.* = *Discoaster*; *R.* = *Reticulo*; *S.* = *Sphenolithus*.

erally found to be isochronous, whereas species which are more difficult to identify are more often found to be diachronous. A number of species which are too rare in the sections studied are either not included or marked as questionable (?) datum events which need further study. Ages are based on the paleomagnetic time scale of Berggren et al. (1985) and extrapolation from sediment accumulation rates.

A total of 29 planktonic foraminiferal datum events are found to be reliable stratigraphic indicators for upper Eocene to lower Oligocene sediments (Table II). Eight radiolarian events (three questionable) are also found to be useful stratigraphic markers. Coccolith datum events proved to be highly variable with the exception of the last appearances of *Discoaster saipanensis* and *D. barbadoensis*. This variability may be due to difficulties in identifying first or last appearances of transitional species.

Reliable datum events are listed in Fig. 3 along with microfossil zonations and the paleomagnetic time scale of Berggren et al. (1985). The list of datum events differs somewhat from that previously published in Keller (1983a); the difference is the result of a larger number of sites studied (11 as compared to 4). A change is suggested in the age of the middle/late Eocene boundary of *Truncorotaloides rohri*/*Globigeropsis semiinvoluta* zone boundary of Berggren et al. (1985) who place this boundary at 41.3 Ma based on the last appearance of *T. rohri* and first appearance of *G. semiinvoluta*. During examination of over 20 deep-sea sites (Table I) it has been noted that this boundary coincides with the CP14/CP15 and NP17/NP18 nannoplankton zone boundaries and falls within the radiolarian *Corpocanistrum azyx* subzone of the *Thyrsocyrtis bromia* zone. Therefore, the age of the *T. rohri*/*Gr. semiinvoluta* zone boundary should be at 40.0 Ma.

It is noteworthy that most of the datum events, 17 out of 26, cluster between the Eocene—Oligocene boundary and 38.4 Ma, a

period of 1.8 million years. This reflects the rapid species turnover during a time of accelerated stepwise extinctions as discussed below.

Stepwise mass extinctions

Paleontological research has made it increasingly clear that both faunal and climatic changes are characterized by long periods of stability separated by brief episodes of rapid faunal turnover and climatic fluctuations. During middle Eocene to early Oligocene each faunal turnover is characterized by replacement of tropical marine faunas and floras by cooler subtropical and temperate elements as observed by Haq and Lohmann (1976), Haq et al. (1977), Kennett (1977, 1978), Berggren (1978), McGowran (1978), Keller (1983a, b) and Corliss and Keigwin (1986). Recently, Berger et al. (1981) discussed major faunal turnovers at the Cretaceous—Tertiary and Eocene—Oligocene boundaries and the late Miocene in terms of major steps in Cenozoic evolution. Keller (1983a, b) studied one of these "steps" at the Eocene—Oligocene boundary and observed that faunal changes occurred in a series of yet smaller steps related to successively cooler climatic conditions. Such stepwise faunal changes were also observed by Kauffman (1984a, b) in late Cretaceous invertebrate faunas and he redefined the late Cretaceous mass extinctions as "stepwise mass extinctions" occurring over a period of 1–3 million years (Kauffman, 1984a). The term stepwise extinctions best characterizes the late Eocene to early Oligocene faunal turnover.

Contrary to repeated claims of mass extinctions at the Eocene—Oligocene boundary, this faunal turnover occurs over a period of 2–3 million years beginning in the late Eocene and culminating in the early Oligocene. Corliss et al. (1984) have shown that during this time an average 2–4 (6–12%) species became extinct per million years and

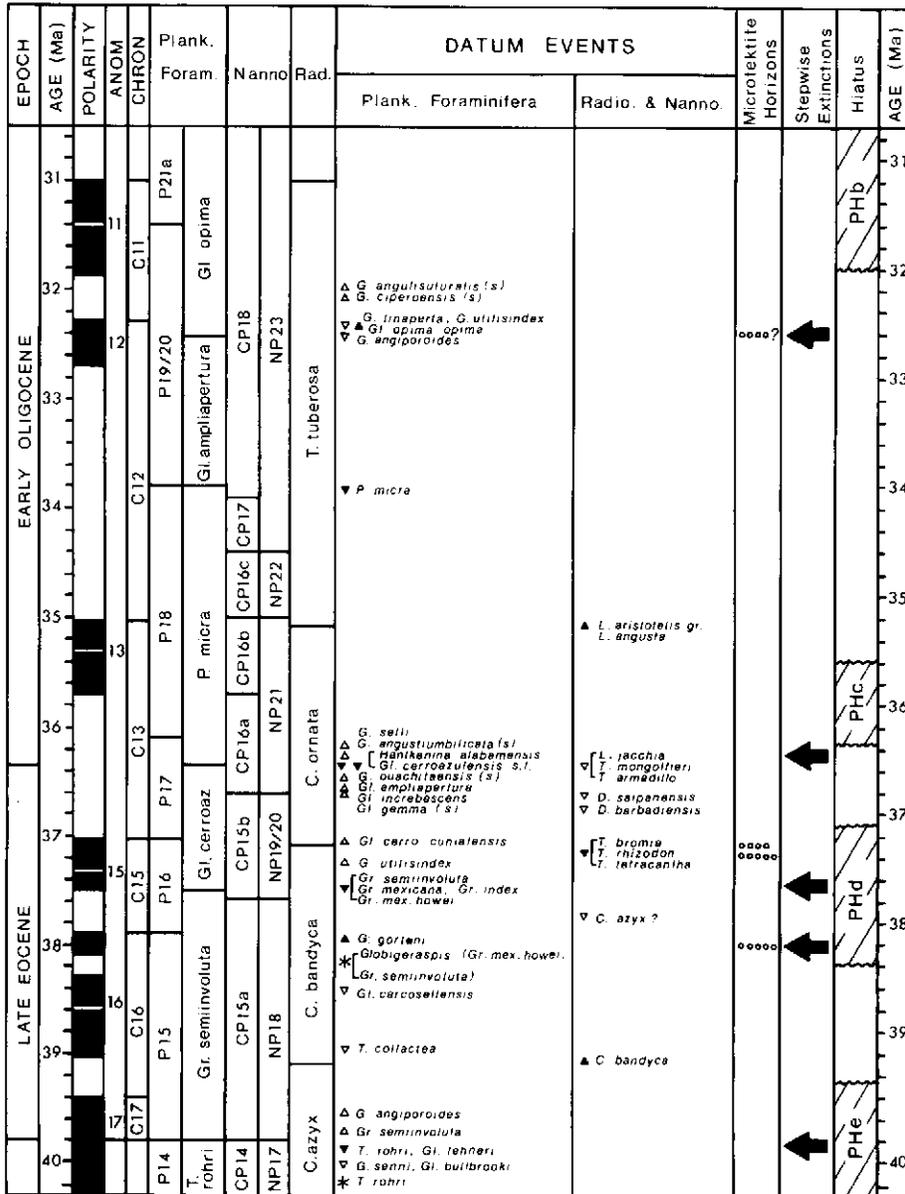


Fig. 3. Late Eocene to early Oligocene datum events, microtektite horizons, stepwise extinctions and widespread hiatuses. Hiatuses are labeled PH for Paleogene Hiatus b, c, d and e; PHa is present at the uppermost Oligocene. Paleomagnetic time scale and microfossil zonation after Berggren et al. (1985). Radiolarian zonation after Reidel and Sanfilippo in Saunders et al. (1985). Open triangles mark first (Δ) and last (∇) appearances of species; black triangles indicate zone and subzone marker species; asterisk marks last abundance peak. Planktonic foraminiferal zonation after Bolli (1957) and Stainforth et al. (1975).

an equal number of species originated among three microfossil groups (benthic and planktonic foraminifers, calcareous nannoplankton). An equally low number of species ex-

tinctions and originations was observed in the radiolarians (Saunders et al., 1984; Sanfilippo et al., 1985). This represents a maximum of 6–12% species extinct in any

one fossil group at a given 1-m.y. interval and can hardly be construed as a mass extinction, but it does represent a stepwise sequence of extinction events as discussed below.

To demonstrate the nature of late Eocene extinctions and their relationship to impact events faunal analysis are presented from Atlantic Sites 94 and 366, Pacific Sites 167 and 292, and Indian Ocean Sites 214, 216, 223 and 242 (Figs. 4–11). Selected species ranges are illustrated along with species abundance distributions of the dominant faunal elements. In sections where microtektites are present their location in the core is marked to show the relationship to faunal changes. Intervals of carbonate dissolution are also marked to show dissolution induced changes in species abundances. Solution effects are easily recognizable as they increase the relative abundance of dissolution resistant species such as *Catapsydrax* and *Globorotaloides suteri*. Where available from the Initial Reports of the Deep Sea Drilling Project, radiolarian and nannoplankton zonations are provided for each site. As noted earlier nannoplankton zonations frequently are not in stratigraphic agreement with other microfossil zonations perhaps due to difficulties in identifying zonal marker species. The radiolarian *Thyrsocyrtis bromia* zone has been subdivided into three subzones (*Copocanistrum azyx*, *Calocyclus bandyca*, *Cryptopora ornata*) following Reidel and Sanfilippo (in Saunders et al., 1984).

Close examination of the species record indicates that successive extinctions occur abruptly during short stratigraphic intervals creating a stepwise extinction effect (Figs. 4, 6, 7 and 9). In some instances, however, this stepwise extinction pattern is exaggerated due to incomplete sediment recovery during the drilling process. Nonetheless, the same species extinction pattern is generally preserved. Steps are separated by relatively stable or quiescent periods (see also Site 219, Keller, 1983a). Each step is marked by the extinction of 2–5 species usually associated with one to several originations

of species over a few tens to a few 100,000 years and represent an accelerated faunal turnover. Such accelerated stepwise extinctions occur near several zonal boundaries; *T. rohri*/*Gr. semiinvoluta* zone boundary at 40.0 Ma, *Gr. semiinvoluta*/*Globorotalia cerroazulensis* zone boundary at 37.7 Ma, *Globorotalia cerroazulensis*/*Pseudohastigerina micra* zone boundary at 36.6 Ma (E/O boundary) and the *Globorotalia ampliapertura*/*Globorotalia opima* zone boundary at 32.6 Ma (Fig. 3). In addition, a stepwise extinction occurs in the late *Gr. semiinvoluta* zone between 38.2–38.3 (Fig. 3). The late Eocene stepwise extinctions estimated as occurring between 40.0–40.4 Ma, 38.3–38.1, 37.7–37.2, and 36.5–36.8 Ma, altogether represent a time of highly accelerated faunal turnover followed by a quiescent period to 32.6 Ma.

The number of species extinct at each stepwise extinction event represents generally less than 15% of the species population and hence cannot be considered a mass extinction. But the sum total of the late Eocene stepwise extinctions over a 3.4 million year interval (40.0–36.6 Ma) results in a near complete faunal turnover with only about 20% of the species surviving into the Oligocene where they become extinct in the early *Globorotalia opima* Zone (Fig. 3). When populations in terms of relative numbers of individuals per species are considered, the faunal changes at each stepwise extinction event appear more drastic for the late Eocene, but are relatively minor at the Eocene–Oligocene boundary.

Population dynamics

Abundance fluctuations, which are a measure of relative success of species within the total foraminiferal population, are sensitive paleoclimatic and paleoceanographic indicators responding to changing paleotemperature, density, salinity and nutrient conditions. Their precise relationship, however, is unclear except for temperature which

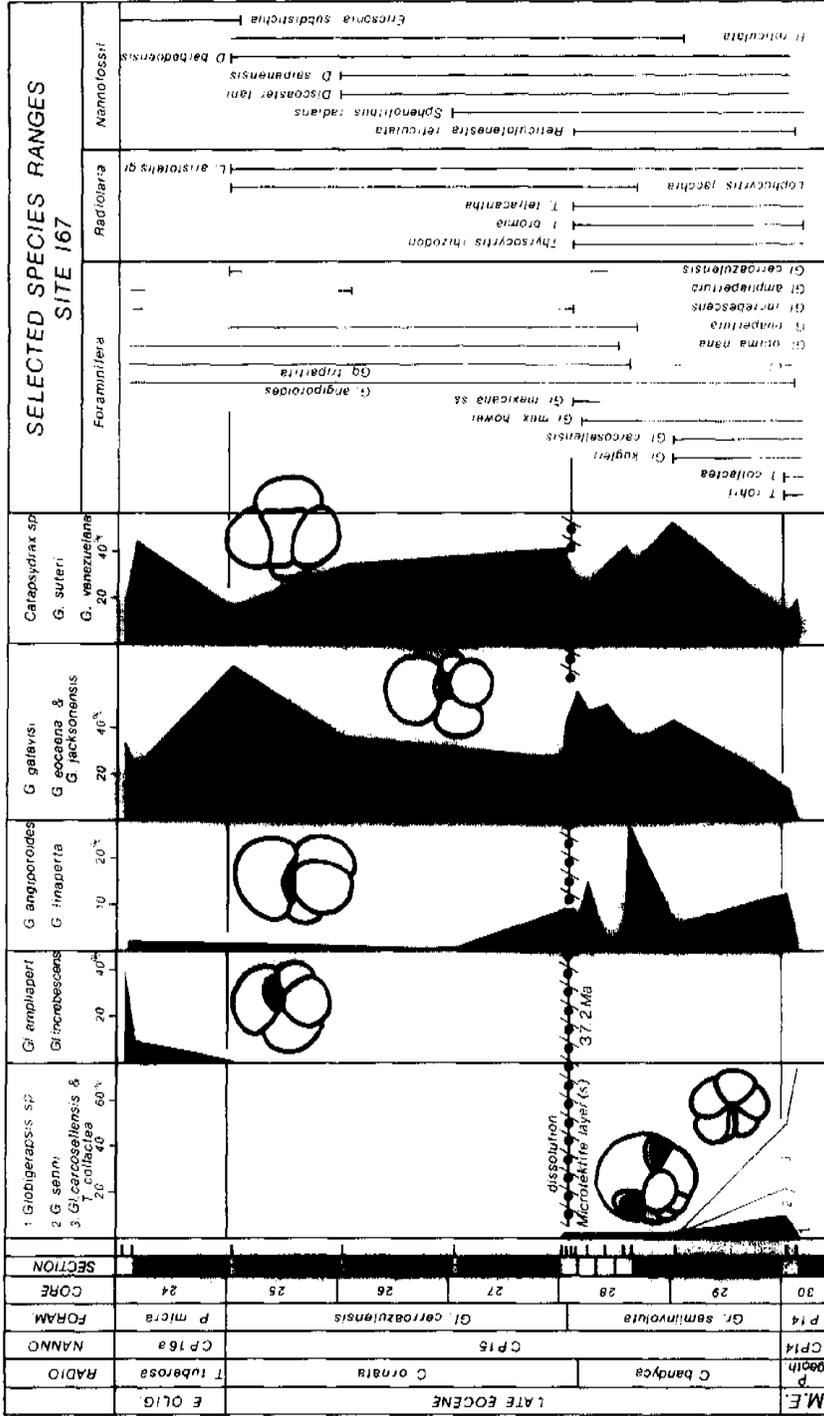


Fig. 5. Relative abundances of dominant species and selected species ranges of planktonic foraminifers, radiolaria (Moore, 1973) and nannoplankton (Roth, 1973) from site 167. Note microtektite horizon near extinction of *Globigerina seminivoluta* correlating to Site 292 core 36-4. See Fig. 4 for complete explanation.

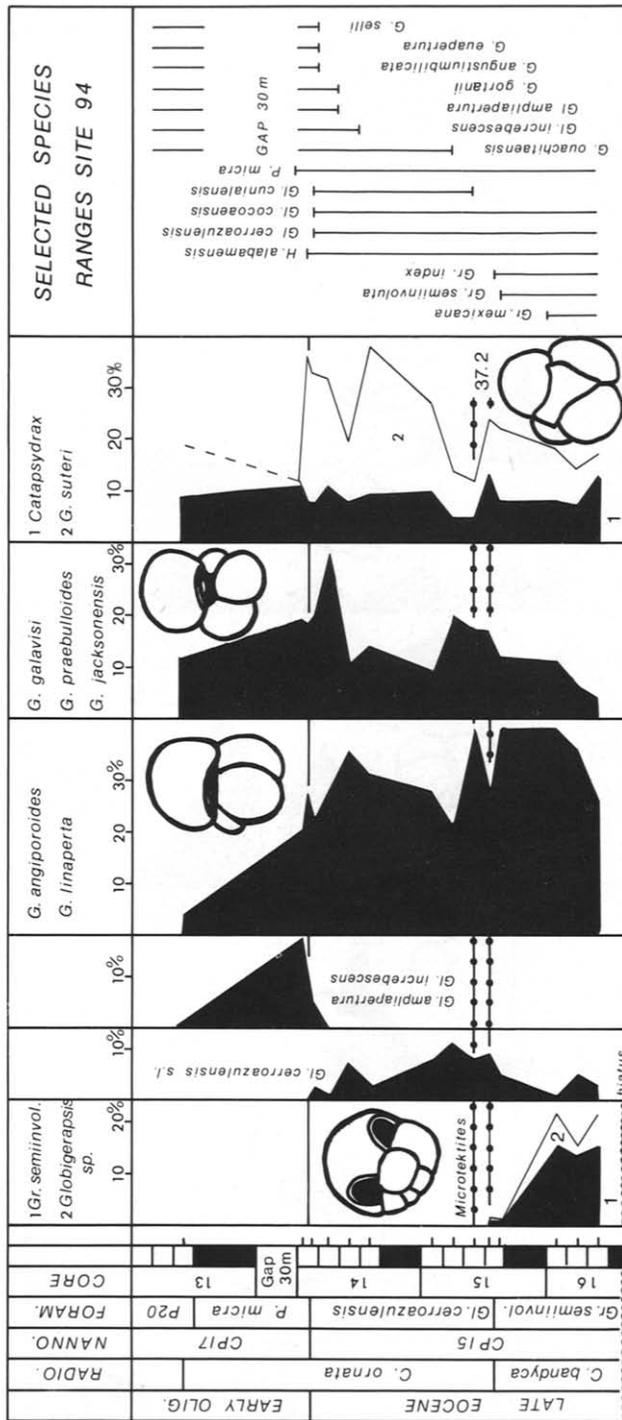


Fig. 6. Relative abundances of dominant species, selected species ranges and microtektite occurrences in Site 94.

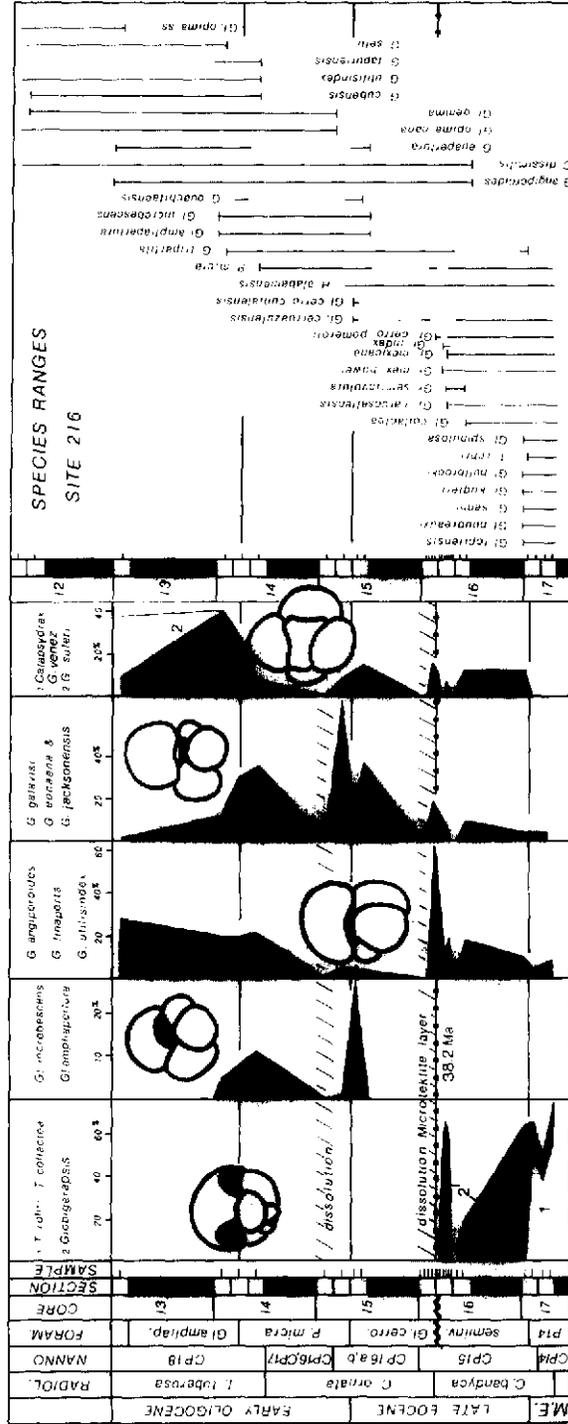


Fig. 9. Relative abundance of dominant species and selected species ranges from Site 216. Note microtektite layer between sections 1 and 2 of core 16. A short hiatus appears to be present at this interval (wavy line).

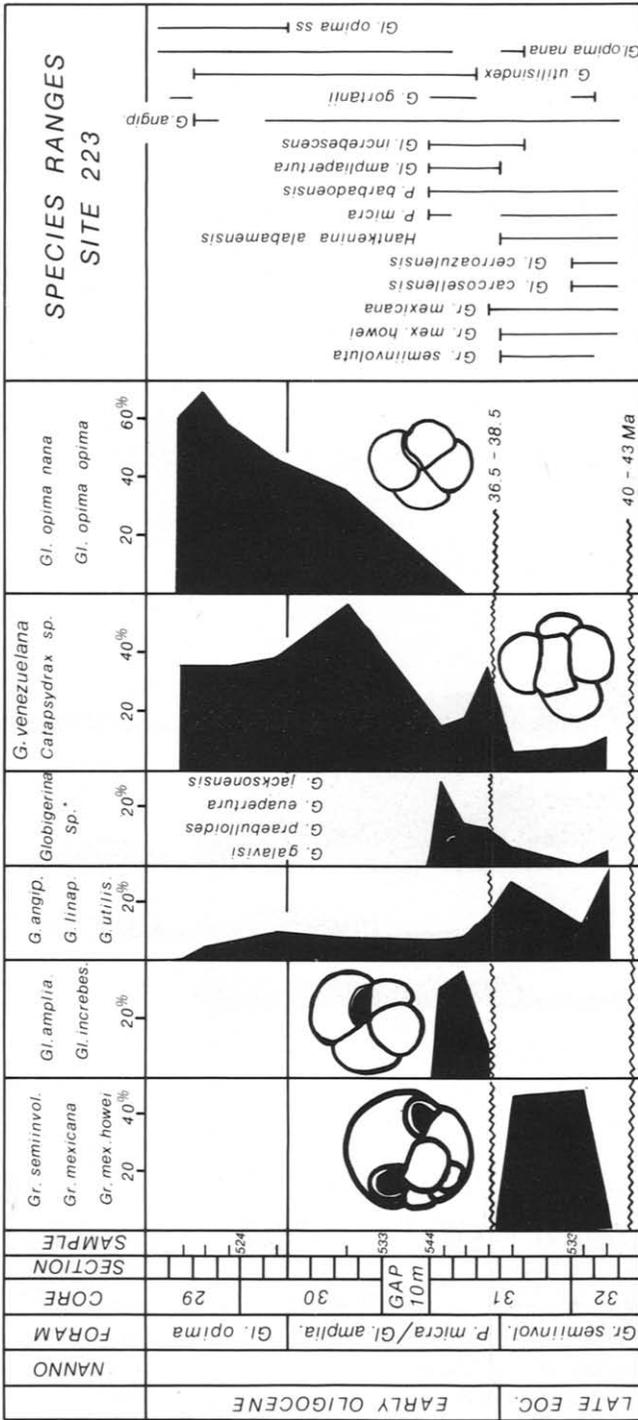


Fig. 10. Relative abundance of dominant species and selected species ranges from Site 223. Note hiatuses present (wavy lines).

appears to directly influence foraminiferal distributions (Keller, 1985b; Kennett et al., 1985). Stable isotope analysis of individual planktonic foraminiferal species reveals a depth stratification related to temperature and density conditions in the upper water column (Boersma and Shackleton, 1978; Fairbanks et al., 1980, 1982; Keller, 1983b, 1985b; Poore and Matthews, 1984; Savin et al., 1985). Abundance fluctuations are therefore indicators of paleoclimatic oscillations and the degree of water mass stratification.

Planktonic foraminiferal populations are usually dominated by about 6–7 species, or about 20% of the species present in the population (Figs. 4–11). Yet they comprise about 80–90% of the individual members of the population. Hence, 80% of the species make up only 10–20% of the individuals of the total population. Extinction of several of these species will have a minor impact on the total population as their combined species abundances are not likely to exceed 2–10%. Extinction of one or more of the dominant species, however, will have a major impact as they may comprise 50% or more of the total population.

Nonetheless, extinction data of species may not be the best indicators of environmental changes for the following reasons. Quantitative analysis has shown that the population of a species is generally very low (1–2%) at the time of evolution and at the time of extinction and reaches its apex in between (Keller, 1983c). This implies that species become extinct when they are most vulnerable and minor environmental perturbations may cause their demise. Hence, species extinctions alone may not be good indicators for major environmental changes. A more sensitive measure is the final decline of a species from its apex which signals the change in environmental conditions that ultimately led to its demise. For instance, *Globorotalia kugleri* declined in the early Miocene at 21.4 Ma from 50% to 10–20% within about 100,000 years and became

extinct at 20.1 Ma (Keller, 1981, 1983c). The permanent decline in the species abundance signals a major oceanographic change whereas its extinction represents a secondary event. The faunal parameters of species extinctions and species abundance changes are discussed below for each stepwise extinction event.

Middle/late Eocene boundary event: 40.0–40.4 Ma

The middle/late Eocene boundary represents the last of a series of stepwise extinction levels that led to the demise of the spinose species that dominated the early and middle Eocene. Most of the non-spinose survivors of this group became extinct during the late Eocene stepwise extinction events. At least four species (~12%) became extinct near the *Truncorotaloides rohri*/*Globigerapsis semiinvoluta* zone boundary following the decline in the ultimate abundance peak of *T. rohri* at 40.4 Ma (Table II). The *T. rohri* group (including *T. collectea*) comprises 40–60% of the foraminiferal population prior to this abundance decline.

Global cooling accompanied by intensification of current circulation is indicated in the stable isotope record (Keigwin and Corliss, 1986) and in the presence of a widespread hiatus (Paleogene Hiatus PHe, Fig. 3) at the middle/late Eocene boundary (Keller, 1983a, b). Thus, global cooling and changing water mass stratification may account for the demise of the spinose species at this time. An increase in the water mass stratification is implied in the increased abundance of intermediate water dwelling species (*P. micra*, *G. galavisi*, *G. eocaena*, *G. linaperta*) and deep water species (*Catapsydrax*, *G. venezuelana*) (Keller, 1983a, b). No evidence of an impact event has been found at this extinction event.

Late Eocene: 38.3–38.1 Ma event

The second late Eocene stepwise extinction event is marked by the final abundance decline of *Globigerapsis semiinvoluta* and

Globigerapsis species (*Gr. mexicana*, *Gr. mexicana howei*). This decline appears isochronous at about 38.3–38.2 Ma in middle to low latitude regions as shown in Sites 292, 94, 214, and 216 (Figs. 4, 6, 8, 9 and Table II). *Globigerapsis* species were generally rare after this abundance decline until their demise at about 37.7 Ma. Prior to the abundance decline, the *Globigerapsis* group comprised about 40–60% of the planktonic foraminiferal population (primarily *Gr. semiinvoluta* and *Gr. mexicana howei* in low latitudes) and rapidly declined to a few percent over 50,000–100,000 years time also. *Globorotalia carcosellensis* became extinct at this time. In high latitudes, *Globigerapsis index* dominated during the late Eocene, but also appears to have declined at this time and became extinct near the Eocene Oligocene boundary (Keller, 1983a; Murphy and Kennett, 1985).

The ecologic niche lost by the *Globigerapsis* group in low latitudes appears to have been occupied by the cooler water *Globigerina galavisi*–*G. eoacena* group which shows a population expansion at this time (Figs. 4, 6, 7, 9). The *Globigerina linaperta*–*G. angiporoides* group increases or remains stable in Site 292 (Fig. 4), but rapidly declines in the early part of the *Globorotalia cerroazulensis* Zone in all sections examined except Site 94 (Fig. 6).

A microtektite horizon at 38.2 Ma indicates an impact occurred near or at the time of the *Globigerapsis* decline. At Site 292 a microtektite layer is present in core 38-2 with a maximum concentration of microtektites between 75–80 cm and dispersal of microtektites due to bioturbation between 10–90 cm of Core 38-2. The last abundance peak of *Gr. semiinvoluta*, *G. mexicana*, and *Gr. mexicana howei* occurs in core 38-2 (110–114 cm) and CaCO₃ dissolution affected foraminifers above this interval to Core 38-1.

Recently, a microtektite layer was also discovered in the uppermost part of *Gr. semiinvoluta* (P15) Zone in a section in southern

Spain (Keller et al., in press). The faunal abundance changes are similar to those in Site 292 except that *Gr. index* is more abundant than *Gr. semiinvoluta*, as would be expected at this cooler middle latitude location. However, similar to Site 292, the *Globigerapsis* group abruptly declined at the microtektite layer. The presence of a microtektite layer coincident with the decline in the *Globigerapsis* group strongly suggests a cause–effect relationship between this impact event and the demise of the *Globigerapsis* group.

In many deep-sea sites the Zone P15/P16 boundary interval is associated with a widespread hiatus (Paleogene Hiatus PHd, Fig. 3) as also present in Sites 223, 214, and 216 (Figs. 8–10). The hiatus in Site 216 removes about a 1 m.y. interval and hence the microtektite layer could be either one or both of the microtektite layers of Zone P16 at 37.20 and 37.21 Ma, or of *G. semiinvoluta* Zone (P15) at 38.2 Ma. Major element composition of microtektites suggest that it is the Zone P15 event (Keller et al., in press). Longer hiatuses are present in Site 214 (37.0–38.3 Ma) and Site 223 (36.5–38.5 Ma). Poor core recovery in Sites 94, 167, 242 and 366 (Figs. 5, 6, 7, 11) may account for the absence of the 38.2 Ma microtektite horizon at these locations.

Late Eocene: 37.2 Ma events

The third late Eocene faunal turnover involved major species frequency changes and was marked by two closely spaced microtektite layers only a few thousand years apart. No planktonic foraminiferal species extinctions were associated with these impact events, but 0.5 m.y. prior to the impact the *Globigerapsis* group (*Gr. semiinvoluta*, *Gr. mexicana*, *Gr. mexicana howei*, *Gr. index*) which began its decline at the Zone P15 impact event (38.2–38.3 Ma) became extinct in low latitudes. In high latitudes *Gr. index* ranged to the Eocene–Oligocene boundary (Jenkins, 1974; Keller, 1983a; Kennett et al., 1985). At the time

of the extinction of the *Globigerapsis* group the relative abundance of these species was only about 1–2%, and hence their demise was hardly catastrophic.

The major faunal turnover associated with the two Zone P16 impact events involved the decline in the *Globigerina linaperta*–*G. angiporoides* group, the rise in the *G. galavisi*–*G. eocaena* group and the evolution and rapid rise to dominance in the *Globorotalia ampliapertura*–*Globorotalia increbescens* group (Figs. 4–9). *Pleudohastigerina micra* (>150 μm) also exhibited highest frequencies after this event (Fig. 4). Among radiolaria four species became extinct coincident with the lower of the two impact glass horizons (cpx-layer) (Sanfilippo et al., 1985). Even though no major species extinctions occurred, the major assemblage turnover suggests profound environmental perturbations at this time.

The two closely spaced Zone P16 or *C. ornata*/*C. bandyca* boundary impact glass horizons have been found in over 16 sections and form an easily recognizable datum plane. The stratigraphic position of the microtektite layers in relation to species frequency changes is indicated in Figs. 4, 5, 6 and 9. Table III lists sites and core-depth intervals where microtektites have been found. Because of the close spacing of these layers (~20–25 cm) in deep-sea sediments, it is not always possible to identify both layers. In addition, the lower or cpx-layer is more solution prone due to higher FeO and MgO.

Eocene/Oligocene boundary event: 36.6 Ma

The fourth stepwise extinction event marks the E/O boundary and is marked by the extinction of the *Globorotalia cerroazulensis* group (*Globorotalia cerroazulensis*, *Globorotalia cunialensis*, *Globorotalia cocoaensis*) and *Hantkenina* group (*H. alabamensis*, *H. longispina*, Figs. 4–11). At the time of extinction the relative abundance of these species was less than 2% of the foraminiferal assemblage (Figs. 4, 6). As at the previous extinction events, the demise of these species did

not have a significant impact on the foraminiferal assemblage.

Frequency changes in dominant species are less extensive at the Eocene–Oligocene boundary than at earlier stepwise extinction events. Significant species abundance changes include the decline of *P. micra* > 150 μm , although this species remains common in the smaller size fraction (Fig. 4); a decline in *Globorotalia increbescens*–*Globorotalia ampliapertura* and *Globigerina linaperta*–*G. angiporoides* groups and an increase in the *Globigerina* group (*G. galavisi*, *G. eocaena*, *G. jacksonensis*, *G. praebulloides*; Figs. 4–11). Thus, the Eocene–Oligocene boundary extinction event in low to middle latitudes represents primarily a redistribution in the abundance of dominant species. Temperature affinities of these species indicate a gradual replacement of warm water species by cooler water species.

Early Oligocene

Foraminiferal assemblages of the early Oligocene are relatively stable and no significant extinctions occur between 36.6 and 32.5 Ma with the exception of one species (*P. micra*) extinct at 34.0 Ma (Table III). Frequency fluctuations in dominant species are partly due to climatic oscillations and partly a result of carbonate solution cycles. Increased carbonate solution is recognized in the frequency peaks of solution resistant species (*Catapsydrax*, *Globorotaloides suteri*, *Globoquadrina venezuelana*, Figs. 6, 7, 8, 11).

The first major Oligocene faunal turnover occurs in the lower part of *Globorotalia opima* zone (31.5–32.5 Ma) when most of the remaining Eocene survivors became extinct (*Globigerina linaperta*, *G. angiporoides*, *G. utilisindex*, *G. ampliapertura*) and several new species evolved (*Globigerina angulisuturalis*, *G. ciperoensis*, *Globorotalia opima opima*). Population changes in terms of species abundance fluctuations are also significant and indicate a trend towards warmer surface water conditions (*Globigerina angus-*

TABLE III

Core locations of microtektite layers and dispersal of microtektites due to bioturbation in deep sea drilling sites and piston cores. Sedimentation rates are based on the paleomagnetic time scale of Berggren et al. (1986)

Site	Ir		Microtektites layer	bioturbation	Sed. rate (m/my)	Strewn field ^a	Zone
	(ppt)						
69A	190	9-4(145)-9-5(20)		9-4(140)-9-5(25)	2.6	cpx	<i>T. bromia</i> , b/c
69A	210	9-5(40-42)		9-5(25-20)	2.6	cpx	<i>T. bromia</i> , b/c
70A		27-3(28-30)		27-3(20-37)		cpx	<i>T. bromia</i> , b/c
94	30	15-3(97-112)		15-3(78-120)	10.0	N. Am.	<i>T. bromia</i> , b/c, P16
94	400	15-4(40-42)		15-4(0-90)	10.0	cpx?	<i>T. bromia</i> , b/c, P16
149	480	31-1(0-10)		31-1(0-51)	2.8	cpx	<i>T. bromia</i> , b/c
166	360	12-6(65-72)		12-6(41-93)		cpx	<i>T. bromia</i> , b/c
167		*28-1(36-38)		28-1(5-62)	24	cpx	<i>T. bromia</i> , b/c, P16
167		few		28-3(99-101)	24	cpx	<i>T. bromia</i> , b/c, P16
216	200	16-1(145)-16-2(5)		16-1(140)-16-2(15)	10	P15/cpx	<i>T. bromia</i> , b/c, P16/15
217		few		*9-6(90-93)	7	P15?	P15/16
291		few		*4-2(40-120)		P15?	<i>T. bromia</i>
292	22	few		36-2(70-130)	16	cpx	<i>T. bromia</i> , c, P16
292	29	few		36-4	16	cpx	<i>T. bromia</i> , b/c, P16
292	51	38-2(75-80)		38-2(35-90)	16	P15	<i>T. bromia</i> , b, P15
315A	250	10-6(43-47)		10-5(27)-10-6(50)	2-4	cpx	<i>T. bromia</i> , NP20/21
462	330	36-1(145)-36-2(7)		36-1(134)-36-2(108)	23-30	cpx	<i>T. bromia</i> , P16/P15
612		21-5(115-117)		None	42	N. Am.	<i>T. bromia</i> , b/c, P16
E67-128		few		5198 ft	4	cpx/N. Am.	P15/P16
E67-128		few		5209-5213 ft	4	cpx/N. Am.	P15
RC9-58	40	254 cm			2.5	N. Am.	<i>T. bromia</i>
RC9-58	400	280 cm			2.5	cpx	<i>T. bromia</i>
Miss Lite Q		few			16	N. Am?	P16
Bath Cliff	103	0-8 cm				N. Am.	<i>T. bromia</i> , b/c, P16
Bath Cliff	290	rare MT, Ir peak 25 cm below MT layer			56	cpx	<i>T. bromia</i> , b/c, P16
Molino de Cobo		MC-4 21 MT			18.7	P15	P15

*: MT layer not observed in archive cores.

a cpx = clinopyroxene spherules; N. Am. = North American; P15 = uppermost *Globigeropsis seminvoluta* Zone horizon.

tiumbilicata, *G. ciproensis*, *G. angulisuturalis*) (see Keller, 1983a for details). Rare microtektites have been found at several deep-sea sites at this interval, including Site 292, but no detailed study has been carried out.

Discussion and conclusions

Late Eocene to early Oligocene extinctions are neither catastrophic nor mass extinctions, but occur in a series of steps marked by increased faunal turnovers and are therefore appropriately termed stepwise mass extinctions. Each of these species extinction events affects generally less than 15% of the assemblage. Thus, each is a significant extinction event, but not a catastrophe, as shown by Corliss et al. (1984). The sum total of these late Eocene—early Oligocene stepwise extinctions, however, results in replacement of two-third of the species and must be considered a major though stepwise mass extinction.

The number of species extinctions is not always the best indicator of the biotic response to environmental changes. A more accurate indicator of ecologic success is population size as measured by the relative number of specimens in a given sample which belong to individual species. When viewed in this context, each of the stepwise faunal turnovers involved 50–80% of the population.

Is there a relationship between impact events and stepwise species extinctions or stepwise faunal turnovers? Four stepwise extinctions extended from the middle/late Eocene boundary to the Eocene—Oligocene boundary and spanned the interval in which three microtektite layers were deposited.

The most significant of these extinction steps occurred near the middle/late Eocene Zone P14/P15 boundary. At this time the warm-water spinose middle Eocene planktonic foraminiferal species became extinct and were subsequently replaced primarily by temperate-water species along with an increasing number of cooler-water species. These extinctions are interpreted to be the

result of rapid, short-term global climatic cooling as supported by isotopic data (Keller, 1983a; Keigwin and Corliss, 1986). No evidence for major impacts at the time of these extinctions has been found so far.

The second species extinction step followed shortly after deposition of the earliest microtektite layer in the uppermost Zone P15 (*G. semiinvoluta*) and involved the extinction of the *Globigerapsis* group (4 species) and *Globorotalia carcosellensis*. Because these species were rare at the time of their extinction (< 1%), their demise did not appreciably affect the remaining population. However, a major faunal turnover is associated with the microtektite layer. At this time the *Globigerapsis* group declined from about 50% of the total population prior to the impact to 1% or less at the microtektite horizon (Site 292, Fig. 4). A similar dramatic and permanent reduction of this group was observed at the microtektite horizon in the Molino de Cobo section of Spain (Keller et al., in press), and occurred globally in middle and low latitude sections at this time. At about the same time *Globorotalia carcosellensis* also decreases from about 30% to 1% in sites 167 and 366 (Figs. 5, 7), no microtektites have been found in these sections. The ecologic niche vacated by the decline of these species was occupied by expanding populations of cooler water species.

Coccolith species abundances are not routinely studied and their global population changes are less well known. Perch-Nielsen et al. (1986) and Molina et al. (in press) reported major species abundance changes which occurred in the upper *Gr. semiinvoluta* Zone P15 microtektite layer in two sections of southern Spain, (Molino de Cobo, and Fuente Caldera). In these sections two species, *Discoaster barbadiensis* and *D. saipanensis*, decreased from about 50% of the total population below the *Gr. semiinvoluta* Zone (P15) microtektite layer to near extinction at the microtektite layer. In the Molino de Cobo section, *Reticulo fenestra umbilica* terminally declined in Zone P16 (Molina et al., in press).

Further quantitative studies will be necessary to examine the nature of relationships between these coccolith abundance changes and microtektite layers.

Foraminiferal response to the impact event that produced the clinopyroxene-bearing spherules of the second layer (Zone P16) and strong iridium anomaly in the *Globorotalia cerroazulensis* zone is unclear because of severe carbonate dissolution in all sections studied. However, there was an abrupt extinction of five species of radiolarian coincident with the Ir anomaly in two sections in Barbados (Sanfilippo et al., 1985). These five species constitute one-fourth of the extant radiolarian taxa.

No species extinctions occurred among radiolaria or planktonic foraminifers at the time of the third impact event which produced the North American microtektite strewn field, but there was a major effect on planktonic foraminiferal populations. At Site 612 off New Jersey, the impact event was accompanied by mass mortality among the plankton, as indicated by abundant pyrite that probably was the result of a major influx of organic matter. Moreover, the indigenous cool water fauna exhibits the effects of stress at this time in the form of small dwarfed specimens of *Globigerina linaperta* and *G. angiporoides* (Keller et al., in press).

The fourth species extinction step marks the Eocene—Oligocene boundary. About five species of the *Globorotalia cerroazulensis* and *Hantkenina* groups became extinct at this time; their combined abundance was less than 5% of the individuals of the population. Thus, this stepwise extinction was less dramatic in terms of faunal turnover than the preceding extinctions events.

The Late Eocene impact events did not cause instantaneous species extinctions among the foraminifers, but at least two of these events may have caused changes in the environment that ultimately led to the demise of the ecologically most sensitive and generally warmer water or surface dwelling species.

The stepwise mass extinctions, however, may be the result of multiple causes, as there is no evidence of impacts associated with the step preceding or the step that followed the deposition of the presently known microtektite layers. Perhaps the ultimate cause of the late Eocene stepwise mass extinctions must be looked for in the long range paleoclimatic, paleoceanographic and tectonic changes of the middle Eocene to early Oligocene. These changes are most closely related to the development of the circum-Antarctic circulation, subsequent cooling of Antarctica followed by production of Antarctic bottom water which ultimately led to the permanent bottom water temperature drop at the Eocene/Oligocene boundary.

Stepwise extinctions are not unique to the Late Eocene. Preliminary quantitative analysis of late Cretaceous to Paleocene planktonic foraminifers indicates that the Cretaceous/Tertiary boundary mass extinction may also have occurred as a sequence of stepwise extinctions spread over several million years culminating in the K/T boundary event (D'Hondt and Keller, 1985).

Kauffman (1984a, b) found that the Cenomanian/Turonian boundary mass extinction also occurred as stepwise extinctions over several million years. Thus, it is possible that the periodicity in mass extinctions discussed by Raup and Sepkoski (1984) represents periods of accelerated faunal turnovers influenced by a wide range of climatic and environmental conditions, rather than single catastrophic events. Further detailed studies at these and other mass extinction boundaries are necessary before any conclusions can be reached as to whether impacts from comet showers over a 1–3 million year interval may act as triggering mechanisms to climate changes and stepwise extinctions.

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