

The latest Paleocene crisis in the deep sea: Ostracode succession at Maud Rise, Southern Ocean

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ABSTRACT

During the late Paleocene thermal maximum (ca. 55.50 Ma) mid-bathyal ostracodes at Maud Rise in the Southern Ocean (Ocean Drilling Program Site 689) underwent a sudden, dramatic turnover synchronous with a global extinction in deep-sea benthic foraminifers and with large-scale, short-lived negative excursions in the stable isotope record of foraminiferal calcite. A previously stable and long-lived ostracode assemblage, dominated by heavily calcified, chiefly epifaunal taxa, was replaced within ~10 k.y. by a taxonomically novel association of small, thin-walled opportunistic and generalist forms that persisted for ~25–40 k.y. Thereafter, ostracode faunas recovered and common bathyal forms returned, although species were smaller and/or less-heavily calcified than before the turnover. The complex fabric of change in ostracode shell morphology and assemblage composition and structure reflects both long-term and sudden perturbations in seawater chemistry at this site. Ostracode data are in agreement with the hypothesis that the latest Paleocene extinctions in the deep sea were caused by a change in the dominant source area of intermediate water mass from high altitudes to the subtropics. These data also suggest that warm saline waters persisted at Maud Rise for the next 100 k.y.

INTRODUCTION

A rapid negative excursion in oxygen isotope values of benthic and planktonic foraminifera at high latitudes and benthic foraminifera worldwide demonstrates that one of the most dramatic, short-lived warming events of the geologic record occurred ca. 55.5 Ma, just before the Paleocene-Eocene boundary (Rea et al., 1990; Kennett and Stott, 1991; Thomas and Shackleton, 1996). This warming event, the late Paleocene thermal maximum (Zachos et al., 1993), was associated with a global mass extinction of deep-sea benthic foraminifera, in which up to 50% of species became extinct, and a major upheaval in the global carbon cycle as indicated by a sharp, short-lived decline in carbon isotope values of benthic and planktonic foraminifera worldwide (Kennett and Stott, 1991; Thomas, 1990b, 1996; Thomas and Shackleton, 1996), as well as in continental records (Koch et al., 1995).

Prior to the late Paleocene thermal maximum, deep-sea benthic foraminiferal faunas were cosmopolitan, highly diverse and dominated by large, robustly calcified species that probably inhabited epifaunal microhabitats (e.g., Kaiho, 1994). Postextinction faunas vary geographically, but generally have low diversity and are dominated by small, thin-walled species with infaunal morphologies. At some locations, the common to abundant occurrence of usually rare species such as *Tappanina selmensis* and

Aragonia aragonensis may indicate a high flux of organic matter to the sediments, and/or low-oxygen conditions in the water column or at the sediment-water interface (Thomas, 1996).

Several investigators have argued that the benthic foraminiferal extinction was triggered by the sudden switch in dominant sites of deep-water formation from high to subtropical latitudes (Thomas, 1990a; Pak and Miller, 1992; Kaiho, 1994; Thomas and Shackleton, 1996). The extinction may have been caused by the increased temperature and concomitant decreased oxygen content of the newly formed water masses and aggravated by the rapidity of change. Locally, new patterns of upwelling, thus of productivity and of “aging” of deep waters may have contributed to the severity of the crisis and to the fabric of recovery in its aftermath.

In this paper we describe the uppermost Paleocene ostracode succession at Ocean Drilling Program Site 689 (Fig. 1). Our data demonstrate that these complex deep-water metazoans underwent catastrophic turnover coincident with the crisis in the much simpler protistan benthic foraminifera (Thomas, 1990b). The ostracode turnover is notable for its magnitude, species selectivity, and novel sequelae, and provides additional evidence for latest Paleocene water-mass developments in the Weddell Sea.

MATERIALS AND METHODS

Ocean Drilling Program Site 689 (64°31.009'S, 03°05.996'E, present water depth 2080 m, paleodepth 1100 m) was drilled on the northeastern side of Maud

Rise (Fig. 1), an aseismic seamount about 750 km north of the Antarctic continent. Uppermost Paleocene sediments occur in an unconformity-bounded section deposited within an ~1 m.y. period (Thomas et al., 1990; Thomas and Shackleton, 1996; Aubry et al., 1996). We analyzed ostracode assemblages (>150 µm) in 12 samples (Table 1). We examined the stratigraphic range and relative frequency of numerically significant genera, and the patterns in carapace design and degree of calcification. For the sake of brevity, genera with covarying ranges and abundances have been placed into operational taxonomic groups (see Appendix).

FAUNAL ANALYSIS

Samples 12 to 6 (56.37–55.50 Ma) are characterized by a uniform taxonomic composition and gradual changes in relative frequencies and for important genera (Fig. 2). *Krithe* and OTG 6 jointly account for 45%–85% of the sample populations. A steep decline in abundance of *Krithe* and the disappearance of OTG 6 define a major, severely negative turnover between samples 6 and 5 (55.50–55.49 Ma), synchronous with the benthic foraminiferal extinction and the beginning of the negative carbon and oxygen isotope anomalies (Fig. 2).

Samples 5 and 4 (55.49–55.48 Ma), from the interval with very low carbon isotope values, contain a taxonomically novel assemblage composed of indigenous taxa that

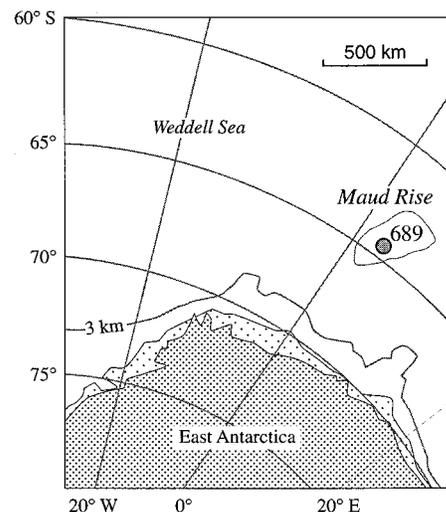


Figure 1. Location of Site 689 in eastern Weddell Sea. Submarine contour outlining Maud Rise is drawn at 3 km.

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TABLE 1. SAMPLE DATA AND OSTRACODE ASSEMBLAGE PARAMETERS

Sample number	Core/section	Interval (cm)	m bsf	Size (cm ³)	Age (Ma)*	Infaunal specimens (%)	Generic ⁺ diversity	Ostracode [§] abundance
1	22-4	108-116	203.08	50	55.401	18.2	29	24.8
2	22-5	40-42	203.91	15	55.427	18.6	27	29.6
3	22-5	113-118	204.63	50	55.450	28.0	26	25.6
4	22cc		205.43	62	55.475	7.0	47	30.6
5	23-1	40-42	207.61	15	55.490	8.0	14	13.3
6	23-1	113-119	208.38	50	55.501	7.0	18	24.1
7	23-2	119-125	209.91	50	55.665	8.1	20	25.7
8	23-3	111-118	211.36	50	55.820	8.8	21	18.5
9	23-4	89-95	212.62	50	55.955	3.7	21	17.2
10	23cc		212.85	50	55.980	10.5	18	16.3
11	24-1	110-119	217.90	50	56.275	5.0	21	16.4
12	24cc		219.58	50	56.373	8.8	26	10.9

* Age model after Thomas et al. (1990), as adapted by Thomas and Shackleton (1996) to the stratigraphic interpretation of Aubry et al. (1996).

⁺ Number of genera represented by more than one specimen.

[§] Number of specimens per cubic centimetre.

were rare in older samples (e.g., *Cytheropteron* s.l.), and a host of immigrants including "*Propontocypris*" and OTG 2 and 3. This association lacks any close analogue in previously described deep-sea faunas. A second, less-severe turnover occurs between samples 4 and 3 (55.48–55.45 Ma), at the level where the large isotopic anomalies end, typical bathyal taxa reappear (OTG 4 and 5), and forms common in the no-analogue fauna disappear (OTG 2) or decline precipitously ("*Propontocypris*") (Fig. 2).

The composition and generic proportions

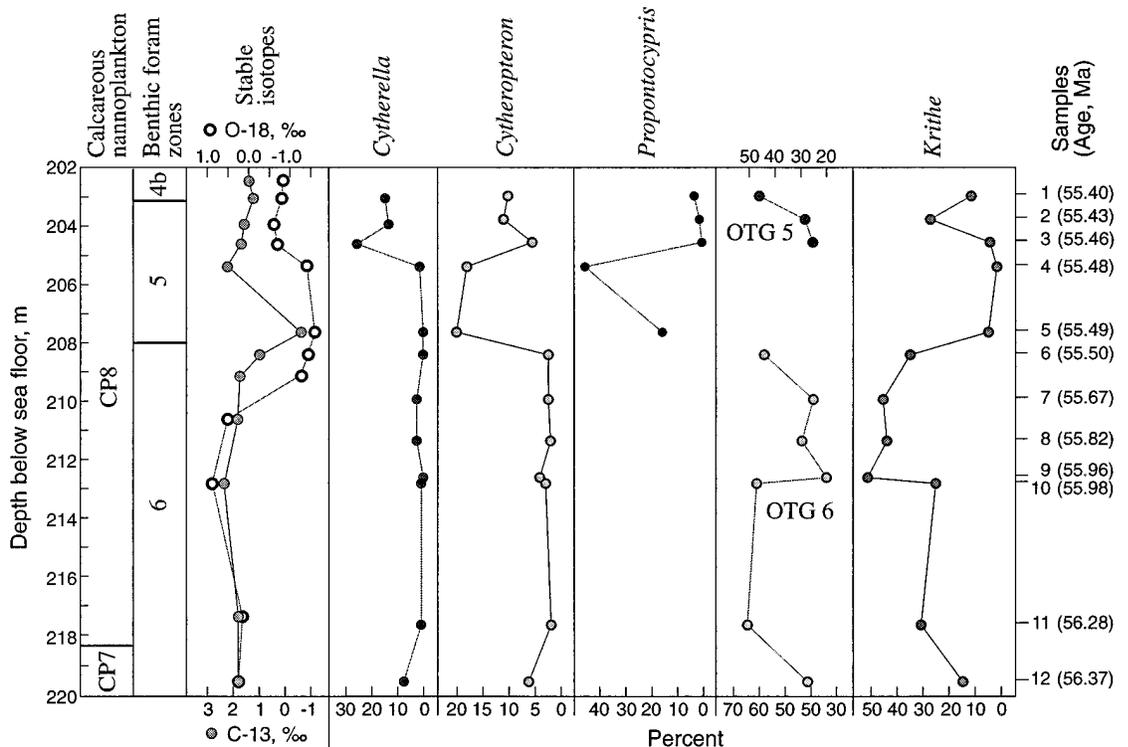
of the no-analogue fauna are entirely unexpected for samples of this age and paleobathymetry. Taxa normally of paramount importance are either absent or rare. Of the common taxa in these samples, only *Argilloecia* and *Cytheropteron* s.l. are ubiquitous in the deep sea. The remainder are either undescribed ("*Propontocypris*") or widespread but rare and sporadic components of deep-sea assemblages. The high relative frequencies (47%) of a new genus of the *Propontocypris* genus group accentuate the paradoxical nature of this short-lived asso-

ciation. *Propontocypris* and its relatives are most common in sublittoral, coralline, and phytal substrates, where they feed on a soft diet (Maddocks, 1969, 1991). Prior to 1987 this group was thought to be absent from deep-water settings, and the few records in the literature were interpreted as post-mortem contamination. Recent studies, however, have identified abundant living propontocyprids in wood-based and hydrothermal vent communities at bathyal and abyssal depths (Maddocks and Steineck, 1987; Van Harten, 1992). In these localized and transient, but food-rich environments, propontocyprids form an important part of an endemic fauna from which normal deep-sea ostracodes are absent (Steineck et al., 1990).

MORPHOTYPE ANALYSIS

The chemistry of seawater strongly affects carbonate metabolism rates, which influence the design and degree of calcification of ostracode carapaces (Benson, 1975; Peyrouquet et al., 1988). Ostracodes cannot store materials needed for calcification internally, so that these must be taken from the environment during moulting (Turpen and Angell, 1971). The energy costs of this process vary with the ambient availability of carbonate (i.e., the balance between the supply of organic carbon and oxygen). Fluctuations in this availability result in polyphenic variation in many taxa, ranging from "degraded" (minimally calcified) to "aggraded" (excessively calcified) morpho-

Figure 2. Ostracode and stable isotope data for uppermost Paleocene at Site 689. Calcareous nannoplankton and benthic foramin zones given in Thomas et al. (1990). Age model (right vertical margin) after Thomas and Shackleton (1996), using stratigraphic interpretation of Aubry et al. (1996). Stable isotopes are based on species of benthic foraminifer *Lenticulina* (Thomas and Shackleton, 1996). OTG is operational taxonomic group.



types, representing respectively hydrochemical regimes unfavorable to, and favorable to, biomineralization (Peypouquet et al., 1988; Carbonnel and Tolderer-Farmer, 1988). We use the “aggradation-degradation” model to relate ostracode morphology and calcification to water-mass geochemistry. Samples 12 to 6 are dominated by large, robustly calcified taxa (0.8–1.7 mm adult length; *Kriihe*, OTG 6) with conspicuously aggraded and/or stereotypically massive carapaces. Benthic foraminiferal assemblages from this interval also are dominated by large, heavily calcified taxa (Thomas, 1990b, 1996; Thomas and Shackleton, 1996). Such ostracode assemblages resemble those from shallow, tropical shelves, where waters are close to supersaturation in carbonate, favorable for calcification (high O₂, low CO₂, high pH), and warmer than those in present-day deep oceans. In the Paleocene, intermediate to deep waters were much warmer than they are today, at 10–15 °C (Zachos et al., 1993).

Samples 3 to 1 contain moderately sized taxa with mass-limited designs (OTG 4) and larger taxa (maximum 0.8 mm adult length) with degraded carapaces. Three Lazarus taxa (OTG 5) show thinner walls, subdued epirelief, and/or smaller shells after the faunal crisis, suggesting an environment less favorable for biomineralization (higher concentrations of dissolved CO₂, lower O₂ levels, lower pH). Long-lived benthic foraminiferal taxa present in these samples (e.g., *Nuttallides truempyi*) were also smaller and thinner walled at this time (Thomas, 1996).

Samples 4 and 5 are composed of diminutive forms (OTG 2 and 3) and moderately sized taxa (0.5–0.6 mm adult length) with thin and/or weakly calcified carapaces (e.g., *Cytheropteron* s.l., “*Propontocypris*”). Such “dwarfed” assemblages have not been described previously and are thus difficult to explain by existing models. They might reflect an increase in the corrosivity of deep waters (e.g., Thomas, 1996), but it is then unclear how so many delicate shells survived burial.

OSTRACODES AND PALEOCEANOGRAPHY

Changes in the uppermost Paleocene ostracode assemblages at Site 689 occur coeval with changes in the benthic foraminiferal and stable isotope record (Kennett and Stott, 1991; Thomas, 1990; Thomas and Shackleton, 1996). The persistent and uniform *Kriihe*/OTG 6 assemblage represents an environmentally stable interval, indicating that Maud Rise was bathed by the same water mass from 56.37 to 55.50 Ma. The presence of robustly calcified, epifaunal ostracodes and benthic foraminifers indicates

that this water mass was oxygen rich and nutrient limited; that is, it had only been recently isolated from the surface. These observations support the hypothesis that deep waters formed at high southern latitudes at this time (Miller et al., 1987).

Without evidence of prior decline, the *Kriihe*/OTG 6 assemblage was abruptly terminated at 55.50 Ma, simultaneous with a strong decrease in benthic foraminiferal $\delta^{18}\text{O}$ that represents an increase of 4–6 °C in the temperature of deep waters (Kennett and Stott, 1991; Thomas and Shackleton, 1996). During this crisis, previously dominant, heavily calcified, chiefly epifaunal genera declined or disappeared, while smaller, thinly calcified and previously rare forms survived and diversity and abundance values fell to their lowest recorded levels. The pattern of change in benthic foraminifera is similar (Thomas, 1996). This common fabric of change in two unrelated phyla is most likely the result of a rapid environmental perturbation, possibly the arrival of much warmer, oxygen-depleted waters derived from the subtropics, which were richer in dissolved CO₂ and less favorable for biomineralization (e.g., Thomas, 1990a; Kennett and Stott, 1991).

Recovery was lengthy and punctuated by rapid turnover and large fluctuation in generic proportions and sample diversity, similar to the situation in benthic foraminifera. The first stage is marked by the “*Propontocypris*” fauna, which cooccurred with a benthic foraminiferal fauna dominated by species believed to tolerate or prefer oxygen-limited conditions (Thomas and Shackleton, 1996). Comparable foraminiferal faunas occur at many other locations (e.g., Kaiho, 1994; Ortiz, 1995) in postcrisis sediments.

Ostracode faunas from modern and ancient oxygen-limited environments contain typical bathyal taxa, but with enhanced numbers of genera such as *Cytherella*, *Bairdia*, and *Kriihe* (Cronin, 1983; Dingle et al., 1989), and thus do not resemble the “*Propontocypris*” assemblage. Ostracode faunas from Cretaceous anoxic events in the western European Cenomanian and Turonian typically are monogeneric and consist of *Cytherella*, an infaunal filter feeder (Horne et al., 1990; Jarvis et al., 1988), whose reproductive and feeding strategies enable it to survive in an oxygen-limited setting (Whatley, 1992). This genus occurs rarely in samples 12 to 6, but does not increase in abundance in the “*Propontocypris*” assemblage. We therefore conclude that low-oxygen conditions cannot account for the presence of the “*Propontocypris*” association, and thus may not explain the occurrence of

the equally distinctive benthic foraminiferal assemblage either.

What could explain the brief presence of such an unusual ostracode assemblage? *Propontocypris* and its relatives are very rare to absent in assemblages from food-limited environments in the deep sea. They are restricted to ephemeral high-nutrient sites (wood falls, hydrothermal vents) and demonstrate the capacity for effective long-distance dispersal (Maddocks and Steineck, 1987; Steineck et al., 1990). At Site 689, the form referred to herein as “*Propontocypris*” is absent in older samples but shows explosive postcrisis population growth and an equally rapid decline when typical bathyal genera return (Fig. 2). These observations suggest that deep-sea *propontocyprids* employ an opportunistic life strategy and have an affinity for food-rich environments. Carbon isotopic records suggest that Site 689 was characterized by upwelling of deep waters and enhanced local primary productivity during the interval in which the “*Propontocypris*” association was present (Thomas and Shackleton, 1996). We therefore propose that the no-analogue assemblage is a “disaster-fauna” (e.g., Vermeij, 1987), composed of stress-tolerant and/or opportunistic constituents which dominate when typical bathyal ostracode genera disappear. Opportunistic taxa usually occupy a biotope for a short time only, so they do not normally appear in the fossil record (Levinton, 1970; Grassle and Grassle, 1974). It is possible that the isolated location and physiography of Maud Rise delayed recolonization, so that the “disaster-fauna” survived long enough (about 25–40 k.y., Table 1) to leave a fossil record. At Site 689, the benthic foraminifers *A. aragonensis* and *T. selmensis* show stratigraphic abundance variations similar to those of the “*Propontocypris*” assemblage, and thus may have similar ecological characteristics (Thomas, 1996).

The second phase of recovery occurred when typical bathyal taxa returned between 55.48 and 55.45 Ma (samples 4 and 3). Subsequent assemblages (samples 1 to 3) are characterized by taxa with mass-limited and/or degraded carapaces, suggesting that the ambient conditions were not favorable for calcification. Such water-mass characteristics could develop as a result of a high flux of organic matter from the surface waters, or as a result of the presence of a water mass that has traveled far from the location where it sank from the surface water. We therefore suggest that at this time a warm, oxygen-depleted and carbonate-poor water mass was present from low latitudes at intermediate depths at Maud Rise.

CONCLUSIONS

In the latest Paleocene, major changes in the geochemistry and circulation of the world ocean precipitated a global mass extinction in deep-sea benthic foraminifers. At Maud Rise in the Weddell Sea this extinction was accompanied by an equally calamitous turnover in ostracodes. Important elements of a long-ranging and hitherto stable fauna were suddenly replaced by opportunistic and generalist taxa typical of "disaster-faunas." This novel association, together with an equally distinctive benthic foraminiferal assemblage, persisted for 25 k.y. After this time, typical bathyal taxa returned to Maud Rise. Our data suggest that intermediate waters were dominantly derived from higher southern latitudes prior to the major faunal turnover, from subtropical latitudes for at least some time after the extinction.

APPENDIX. COMPOSITION OF OPERATIONAL TAXONOMIC GROUPS (OTG)

OTG 1

Hemiparacytheridea
Eucythere
Argilloecia
Triniciacythere

Cytheropteron s.l.

Cytheropteron
Aversovalva
Rimacytheropteron
Kobayashina

OTG 2

Cretaceratina
Glyphidocythere
Palmoconcha
"Bythoceratina"

OTG 3

Pedicythere
Aratrocypris
Typhloocytherura
Munseyella
"Pectocythere"

OTG 4

Messinella
Platyleberis
Flexuocythere

OTG 5*

Dutoitella
Oertiella
Pelecocythere

OTG 6#

Abyssocypris (infaunal)
Veenia (epifaunal)
Abyssocythere (epifaunal)
Dutoitella (epifaunal)
Oertiella (epifaunal)
Pelecocythere (epifaunal)

*Degraded morphotypes found in postcrisis samples.

#Aggraded morphotypes occurring in precrisis samples.

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