

Disappearance of *Stilostomella lepidula* (Schwager) across the mid-Pleistocene Transition and its palaeoceanographic implication

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Stilostomella lepidula (Schwager), an infaunal benthic foraminifer, is an important component of the deep-sea environment, showing wide geographical distribution and variation in test morphology. The ecological preference and timing of its disappearance across the mid-Pleistocene Transition (MPT) is widely debated. To understand the ecological preference, and timing and cause(s) of disappearance of *S. lepidula*, we analysed Neogene record of this taxon from Ocean Drilling Programme and Deep Sea Drilling Project sites located at bathyal to abyssal depths in the Atlantic and Indian oceans. Population plots of this species at various sites reveal that this taxon showed a substantial increase during the warm late Oligocene to the middle Miocene and suffered a major decline across the middle Miocene cooling event (15–13 Myr). *S. lepidula* disappeared at ~0.6 Myr very close to the MPT (0.9–0.8 Myr) from the Indian and Atlantic oceans, coinciding with a change from a 40 to 100 Kyr world with amplified ice-age cycles. We suggest that high-amplitude glacial cycles, frigid deep-water temperatures and strong circulation drove *S. lepidula* to nearly disappear across the MPT.

Keywords: Late Oligocene, mid-Pleistocene Transition, palaeoceanographic implication, *Stilostomella lepidula*.

BENTHIC foraminifera provide significant information about deep-sea environments and play an important role in efforts to understand changes in these environments. Indeed, much of the recent research by geologists on modern deep-sea faunas has been driven by a desire to identify reliable tools for reconstructing bottom-water palaeoceanography. *Stilostomella lepidula* (Schwager), originally described under the name *Nodosaria lepidula* by Schwager¹, a deep-infaunal, uniserial, elongated, cylindrical species (Figure 1), has been an important component of the deep-sea ecosystem since the Cretaceous and globally disappeared across the mid-Pleistocene Transition (MPT)^{2–8}. The ecological preference of this species is also not well constrained. This taxon has been suggested to

live in both organic carbon-rich and oxygen-depleted as well as low productivity environments^{2,3,9–12}.

Numerous extinction events (not taxonomically restricted) have been observed throughout the history of the earth, both on the continents and in the oceans. Fossil record of deep-ocean organisms shows a slow turnover (appear-

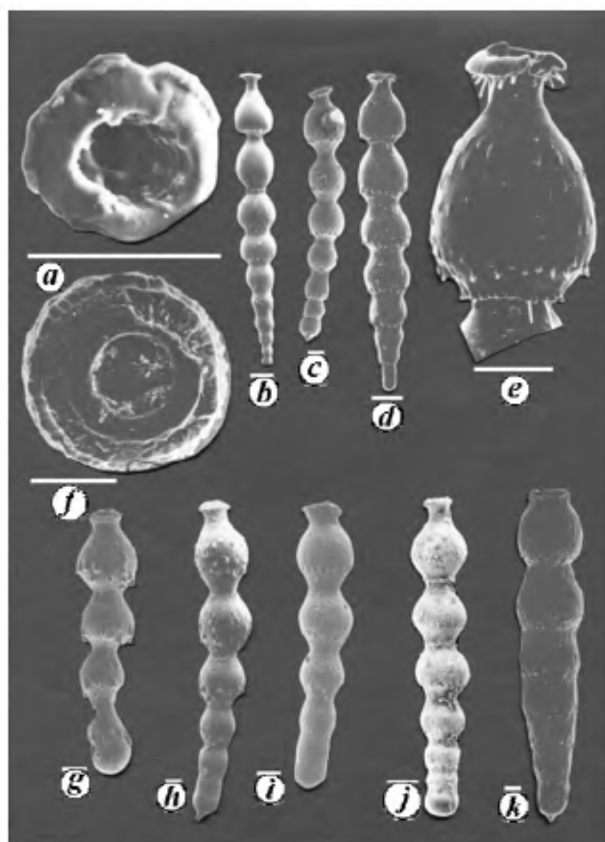


Figure 1. Scanning electron micrographs (scale bars = 50 μ m) of different specimens of *Stilostomella lepidula* from the northwest Atlantic and Indian oceans. Figure 1 a–e are from Hole 991A (sample 2H-6, 55–57, 1.06 Myr), f and k from Hole 995A (sample 16H-7, 148–150, 2.57 Myr), j, from ODP Hole 994C (sample 35X-1, 0–2, 3.79 Myr), and g–i are from Hole 757B (samples 12H-1, 17–18, 23.9 Myr and 10H-6, 1–3, 15.55 Myr).

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ances and disappearances) rate of 2% per million year¹³. In the Cenozoic, Thomas¹⁴ and Miller *et al.*¹⁵ recognized three shifts in deep-sea benthic foraminiferal populations: (1) the Paleocene/Eocene turnover during which time 30–50% of foraminiferal species disappeared due to circulation of oxygen-poor, warm, corrosive bottom-water coupled with changes in surface productivity^{16,17}; (2) the Eocene/Oligocene turnover, mainly due to changes in bottom-water circulation along with gradual global cooling¹⁵ and (3) the middle Miocene turnover driven by a change either in deep-water source and/or surface ocean productivity¹⁵. The last major extinction event, popularly known as *Stilostomella* Extinction, occurred during the MPT, close to the Brunhes–Matuyama boundary^{3,6–8,18}. The term *Stilostomella* Extinction event in the middle Pleistocene, is applicable to the mass extinction of benthic foraminifera (including *S. lepidula*), most of which include the elongated uniserial or biserial taxa with cribrate, hooded, two-toothed or secondary toothed apertures^{5–8}. However, a study by Rai and Singh¹⁹ suggests that different specimens of *Stilostomella* are recorded from the younger/recent sediments in the Indo-Pacific region.

In the early to middle Pleistocene (1.2 to 0.6 Myr), the earth experienced a new vigour of global cooling that allowed extensive sea-ice cover in both the hemispheres, coinciding with a change in glacial cycles from a rhythm of shorter, small amplitude, symmetric 41 Kyr to 100 Kyr period²⁰. The time of strengthening of the 100 kyr cycles in different records is not exactly the same. For instance, according to de Garidel-Thoron *et al.*²⁰, the transition time is about 850 Kyr before the Present, whereas according to Mudelsee and Statterger²¹, the MPT is a multiple-transition phenomenon that occurred in the intervals between 942 and 650 Kyr. These authors suggest that 100 Kyr glacial cycles started abruptly around 0.65 Myr.

In this article, we examine the spatial as well as bathymetric distribution of *S. lepidula* during the late Oligocene to middle Pleistocene interval in the Indian and northwest Atlantic oceans. We attempt to analyse ecological preference, and timing and causes of *S. lepidula* disappearance in the Indian and Atlantic oceans, using data from Deep Sea Drilling Project (DSDP) Site 214 and Ocean Drilling Programme (ODP) Holes 752A, 757B and 758A (all from the eastern and central Indian Ocean), ODP Holes 991A, 994C, 995A, 997A (all from the NW Atlantic Ocean) and DSDP Site 219 (NW Indian Ocean) during the past 25 Myr.

Site description

DSDP Site 219 is located on the crest of the Laccadive–Chagos Ridge near an upwelling zone in the northwestern Indian Ocean, which is a major linear feature in the Indian Ocean (Figure 2, Table 1). Except Site 219, all other sites/holes from the Indian Ocean (214, 752A,

757B, 758A) are located in the eastern and southeastern parts (Figure 2, Table 1). Site 214 is located on the crest of the Ninetyeast Ridge near the transition between Equatorial water and Central water. Hole 752A lies on the Broken Ridge, whereas Hole 757B is located in the central part of the Ninetyeast Ridge below the equatorial divergence zone on the northern edge of the subtropical gyre and somewhat south of the South Equatorial Current (SEC). ODP Hole 758A lies on the northern tip of the Ninetyeast Ridge, eastern equatorial Indian Ocean.

ODP Holes 991A, 994C, 995A and 997A are located on the Blake Outer Ridge, ~200 km off the east coast of the USA, northwest Atlantic under the profound influence of the North Atlantic Deep Water²² (NADW; Figure 3 and Table 1).

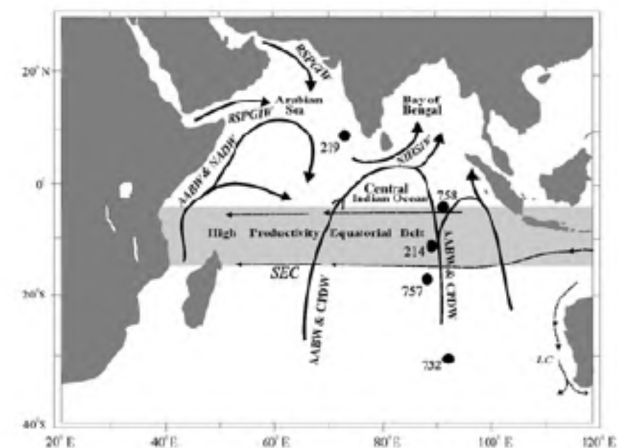


Figure 2. Location of DSDP Sites 214, 219 and ODP Sites 752, 757 and 758 in the Indian Ocean with regard to present-day South Equatorial Current and deep-water currents (modified from Kawagata *et al.*⁶). High-productivity equatorial belt in the Indian Ocean is marked by the grey shaded zone (after Gupta and Srinivasan³⁰). Thick lines indicate deep and intermediate water current, whereas segmented lines indicate surface water current. AABW, Antarctic Bottom Water; CPDW, Circumpolar Deep Water; NADW, North Atlantic Deep Water; RSPGIW, Red Sea–Persian Gulf Intermediate Water; NIHSIW, North Indian High-Salinity Intermediate Water; LC, Leeuwin Current.

Table 1. Location and water depth (m) of the studied DSDP/ODP Sites

Site/Hole	Latitude	Longitude	Water depth (m)
Indian Ocean			
DSDP Site 219	9°01'N	72°52'E	1764
ODP Hole 758A	5°23'N	91°21'E	2924
DSDP Site 214	11°20'S	88°43'E	1671
ODP Hole 757B	17°01'S	88°10'E	1652
ODP Hole 752A	30°53'S	93°34'E	1086
Atlantic Ocean			
ODP Hole 994C	31°47'N	75°32'W	2799
ODP Hole 995A	31°48'N	75°31'W	2778
ODP Hole 997A	31°50'N	75°28'W	2770
ODP Hole 991A	32°59'N	75°55'W	2567

Oceanographic settings

At present Site 219 is bathed by the high-salinity intermediate watermass commonly known as the North Indian Deep Water²³ (NIDW) or North Indian Intermediate Water²⁴ (NIIW), which is a mixture of watermass of the North Indian Ocean origin and NADW²⁵. The Antarctic Bottom Water (AABW) flows at depths below 3800 m, just below the lysocline depth²⁶. The bottom-water temperature, salinity and oxygen concentration in the area is about 3.1°C, 34.8 psu and 2.3 ml/l respectively²⁷.

In the eastern Indian Ocean the zone between 5°N and 15°S is the high-productivity belt, lying below the equatorial divergence²⁸. The intermediate and deep waters in the eastern Indian Ocean are a mixture of watermasses of the Atlantic and Southern Ocean origins. The upper 1000 m water column in the equatorial Indian Ocean is mainly influenced by the wind-driven, low-salinity, high-productivity, oxygen-poor SEC²⁸. Depths between 1000 and 4000 m are bathed by the southward-flowing NIDW²³. The well-oxygenated cold AABW (having a potential temperature 0.9–1.2°C in the Indian Ocean) lies below 4000 m depth, which originates from the Weddell Sea and the Ross Sea^{26,29}. The benthic foraminiferal lysocline lies near 3600 m (ref. 30). The deep-water temperature, salinity and oxygen concentration between 1000 and 1700 m water depth are 3–4°C, 34.5–34.8 psu and 2.6–3.5 ml/l respectively²⁷. At greater depths (Hole 758A), the deep-water temperature (~1.7°C) shows significant change, whereas the salinity and bottom-water oxygenation remain within the above-mentioned limit²⁷. The northward-moving

Indian plate shows about 13° northward movement since the Oligocene/Miocene boundary to the Present, from a colder to a relatively warmer region with a little change in the palaeodepths^{31,32}.

The Blake Ridge, NW Atlantic underlies the periphery of the subtropical central gyre and is under the profound influence of the northerly flowing, warm, saline Gulf Stream surface current as well as the southerly flowing Western Boundary Undercurrent³³. The modern lysocline in the area lies between 4000 and 4350 m water depths³⁴. At the deepest level of the North Atlantic, AABW flows northward and mixes with several other water masses in the deep recirculating gyres to form southerly flowing true NADW. The NADW is initially oxygen-rich (5.2 to 5.6 ml/l) and nutrient-poor³⁵, with temperatures of 2.2–3.5°C and salinities ranging from 34.9 to 35 psu. The Blake Ridge has been a tectonically inactive setting since the late Cenozoic³⁶. The only tectonic event that has occurred adjacent to this area is the closing of the Panama Isthmus around 4 Ma, which drove significant changes in the thermohaline circulation of the North Atlantic³⁷.

Materials and methods

In the present study, we have used partially published data from Sites 214 (5.2 Myr to Recent)³, Hole 757B (25 to 5.3 Myr)¹¹ and published data from Site 219 (2.36 Myr to Recent)³. *S. lepidula* census data from Holes 752A and 758A (Indian Ocean) and 991A, 994C, 995A and 997A (NW Atlantic) is unpublished. A total of 211, 71, 142, 194, 270, 141, 442, 299 and 246 samples were analysed from Sites 214 (24.25 Myr to Recent), 219 (2.36 to Recent), 752 (24.56 to Recent), 757 (24.8 Myr to Recent), 758 (24.37 Myr to Recent), 991 (5 Myr to Recent), 994 (5 Myr to Recent), 995 (3.64 Myr to Recent) and 997 (5 Myr to Recent) respectively. Samples were processed using the method described in Gupta and Thomas⁴. Each sediment sample of 10 cubic cm volume was soaked for 8–12 h in a solution of water with 4–5 drops of H₂O₂ and washed over 63 µm-size sieve. Residual samples were dried in an electric oven at ~50°C temperature and then transferred into Borosil glass vials. The oven-dried samples were dry-sieved over a 125 µm-size sieve for microscopic examinations. Samples were split into suitable aliquots to obtain 250–300 specimens of benthic foraminifera. Relative abundances of all the benthic foraminiferal species were calculated. Scanning electron micrographs were taken to understand the morphological variations in *S. lepidula* from different sites (Figure 1).

Ages were calculated on the basis of the nannofossil age datums following Berggren *et al.*^{38,39} and updated by Okada⁴⁰ for Sites 994, 995 and 997. In case of site 991, ages were adopted from Rodriguez and Paull⁴¹. For Sites 752, 757 and 758 we applied the age model of Peirce *et al.*³². For Sites 214 and 219 age models of von der Borch *et*

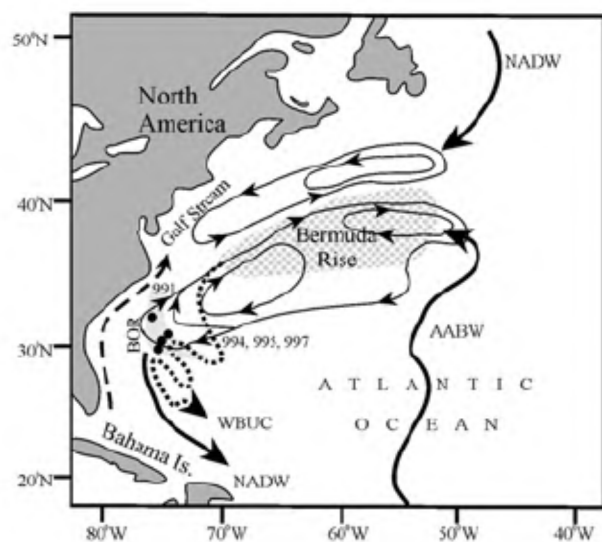


Figure 3. Location map of ODP Sites 991, 994, 995 and 997 on the Blake Ridge in the NW Atlantic. Thick lines (continuous and broken) indicate deep-ocean current and thin lines indicate subtropical central gyre (after Paull *et al.*²² and Ikeda *et al.*³³). AABW, Antarctic Bottom Water; NADW, North Atlantic Deep Water and WBUC, Western Boundary Undercurrent.

*al.*⁴², Fleisher⁴³ and Srinivasan and Singh⁴⁴ were adopted. All the ages for samples from the Indian Ocean were updated to the timescale of Berggren *et al.*^{38,39}.

We combined *S. lepidula* census data with per cent *Cibicides wuellerstorfi* from Site 214 along with global benthic oxygen isotope data⁴⁵ for the last 25 Myr and composite carbon and oxygen isotope values of *C. wuellerstorfi*^{46,47} from Hole 758A to understand the productivity and temperature changes over the past 25 Myr.

Functional morphology

Individuals of *S. lepidula* have a similarity in general outline, but show wide variation in the surface ornamentation. Test of this species is elongated, rectilinear to slightly curvilinear, uniserial, tapering towards the proloculus, spines are common at the end of proloculus, chambers spherical, circular in cross-section, seven to nine in the adult (number of chambers may vary from 6 to 16), series of short blunt spines (in one line or two lines or just scattered) cover the widest portion of the chambers, sutures prominent and deeply constricted, aperture with a phialine lip (usually with spines). Our specimens do not show any dentition within the aperture (Figure 1), whereas it is common in the specimens of *Siphonodosaria lepidula* f. *lepidula* described by Hayward⁶ (plate 3, figures 25–32). The forms described and illustrated as *S. lepidula* by Srinivasan and Sharma⁴⁸ (plate 7, figures 1–6) fall within the range of variation of our specimens. Thus we have followed the terminology of Srinivasan and Sharma⁴⁸.

The long, thin test with spines at proloculus is indicative of a shallow infaunal, static, vertical-dwelling habitat of this species that is not suitable for moving through mud. Spines at the end helped it to stay vertically in a particular place. The well-rounded, broad, terminal aperture and the vertical-dwelling nature are indicative of either suspension feeding or pseudopodia moving over the sediment surface.

Results and discussion

S. lepidula is considered to live in a low oxygen and organic carbon-rich environment^{2,3,10}. Kaiho⁹, on the contrary, inferred that such taxa could live in low-productive areas. The geographical and bathymetric distribution of *S. lepidula* shows greater abundance at the lower bathyal depths of the Indian Ocean since the early Miocene (Figure 4). On the other hand, this species has higher abundances at abyssal depths in the northwestern Atlantic Ocean (Figure 5). We do not observe any regular latitudinal variation in the abundances of *S. lepidula*. Previous records also document different species of the genus *Stilostomella* from the lower bathyal to abyssal depths in all the ocean basins^{3,6–8,12,18,49}.

The earth experienced a long-term warm spell during the late Oligocene to middle Miocene interval (25 to ~15 Myr), during which time the bathyal depths in the southeastern Indian Ocean received low food supply^{11,50,51}. The low food supply to the seafloor probably linked either to winnowing caused by intense deep-water flow resulting from the development of the Antarctic Circumpolar Current when the Drake Passage started widening⁵⁰, or low surface productivity¹¹. In the early to middle Miocene, the bottom-water was more aerated with reduced organic carbon accumulation⁵². *S. lepidula* shows maximum population in the Indian Ocean during the late Oligocene–early Miocene and sharply declines across the early–middle Miocene boundary (~15 Myr, Figure 4), at a time when Antarctic ice sheets began to grow significantly and vigour of deep-sea currents also increased substantially^{53,54}. During this period Paleogene benthic fauna was replaced

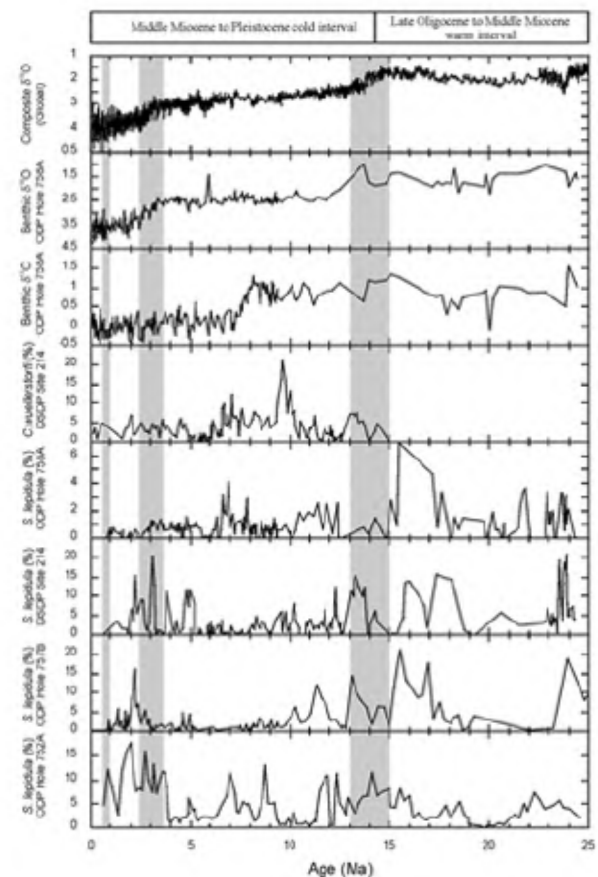


Figure 4. Distribution of *Stilostomella lepidula* over the last 25 Myr at different locations in the Indian Ocean. Also shown are *Cibicides wuellerstorfi* percentages. Grey bar at 15–13 Myr indicates middle Miocene southern hemisphere cooling event and at 3.6–2.5 Myr indicates strengthening of Northern Hemisphere Glaciation (NHG), whereas at 0.9–0.6 Myr the bar indicates the mid-Pleistocene Transition (MPT). Global oxygen isotope data are adapted from Zachos *et al.*⁴⁵. Oxygen and carbon isotope data for ODP site 758 are from Gupta *et al.*⁴⁷ and Chen *et al.*⁴⁶.

by the modern benthic fauna contemporaneous with the well-known positive oxygen isotopic shift indicating the presence of cold, more oxygenated bottom-water. On the other hand, decline in *S. lepidula* population in the middle Miocene coincides with the advent of *C. wuellerstorfi* at Site 214, which prefers to live in high energetic, oligotrophic conditions in epibenthic microhabitat (Figure 4). Abrupt decrease in carbon isotopic values around 8 Myr coincides with the latest Miocene–early Pliocene ‘biogenic bloom’ during which time the Indian Ocean was more productive and less oxygenated⁵⁵. *S. lepidula* finally disappeared between 0.8 and 0.6 Myr, nearly coinciding with the increased amplitude of glacial cycles and abrupt beginning of 100 Kyr cycles around 0.65 Myr (Figure 5)²¹.

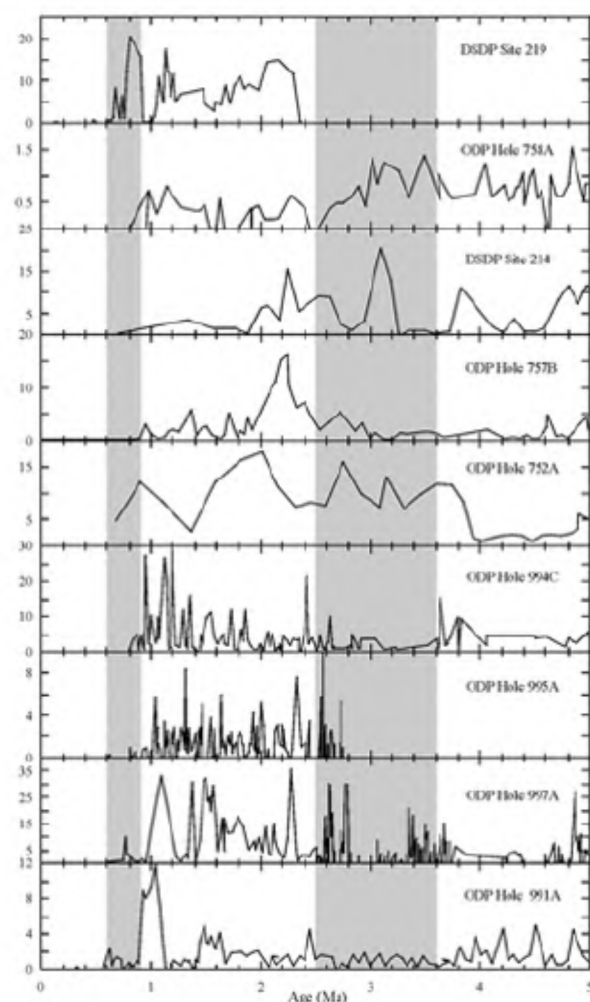


Figure 5. Per cent distribution of *S. lepidula* in the Indian and Atlantic oceans during the last 5 Myr. The species shows extinction across the MPT. Grey bar between 3.6 and 2.5 Myr coincides with major increase in the NHG, whereas grey bar between 0.9–0.6 Myr correlates with the MPT showing a major decline and final disappearance of *S. lepidula*.

The middle Miocene transition is marked by an increased glaciation in the southern hemisphere and intense bottom-water circulation with no major change in productivity. Since the middle Pleistocene, the deep Indian Ocean became well-oxygenated with pulsed to strongly pulsed supply of organic material along with active deep-ocean currents^{4,56}. In the northwest Atlantic a change from high to low productivity was noticed during the middle Pleistocene, which could be related to the decreased upwelling in the subtropical central gyre^{33,40}. The disappearance of *S. lepidula* across the MPT has been implicated to the presence of more oxygenated water, increased food supply or their apertural feature^{5,6}. More recently, Kawagata *et al.*^{7,8} related this disappearance event (they used extinction) to the increased cooling, high increasing oxygen content of the deep water and increasing global ocean circulation. Gupta and Thomas⁵⁶, and Thomas and Gooday⁵⁷ suggested that elongated forms like *S. lepidula*, had apertural characteristics that were not suitable for fluctuating food supply to the seafloor. Our findings suggest that frigid deep-water temperature, strong deep-sea currents and fluctuating food supply (increase in bottom-water oxygenation) during the high-amplitude glacial cycles caused the disappearance of *S. lepidula* across the MPT. It appears that *S. lepidula* was less adaptive to sudden changes in the deep-sea environment and was unable to migrate from stressful to equable environment. The elongate test and deep infaunal microhabitat probably did not allow *S. lepidula* to migrate to more productive areas during these climate extremes.

Conclusion

The distribution pattern of *S. lepidula* in the Indian and Atlantic oceans shows higher abundances of this species in the late Oligocene to early Miocene. This species suffered a major decrease in its relative abundance across

Appendix 1. Systematic description of *S. lepidula* (Schwager)

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|-------------|--|
| Superfamily | : STILOSTOMELLACEA Finlay 1947 (ref. 58) |
| FAMILY | : STILOSTOMELLIDAE Finlay 1947 (ref. 58) |
| SUBFAMILY | : STILOSTOMELLINAE Finlay 1947 (ref. 58) |
| GENUS | : Stilostomella Guppy 1894 (ref. 59) |
- Nodosaria lepidula* Schwager¹, p. 210, plate 5, figures 27, 28.
Sagrina virgula Brady. Brady⁶⁰, plate 76, figures 8–10.
Nodosaria antillea Cushman⁶¹, p. 583, plate 14, figure 9.
Nodogenerina lepidula (Schwager)⁶², plate 14, figures 15–16.
Stilostomella bradyi (Cushman)⁶³, p. 159, plate 76, figures 9, 10.
Stilostomella adolphina (d'Orbigny)⁶⁴, p. 108.
Stilostomella ex.gr. S. lepidula (Schwager)⁶⁵, p. 170, plate 7, figures 32–46.
Stilostomella antillea (Cushman)⁶⁶, plate 28, figure 339.
Stilostomella lepidula (Schwager)⁴⁸, p. 46, plate 7, figures 1–6.
Stilostomella sp.¹⁸, p. 117, figure 3A.
Nodogenerina adolphina (d'Orbigny)⁶⁷, plate 2, figure 1.
Siphonodosaria lepidula f. *lepidula* (Schwager)⁶, p. 305, plate 3, figures 25–32.

the early–middle Miocene boundary (15 Myr) and finally disappeared across the MPT (0.8–0.6 Myr) from the examined sites. The two events are related to increased glacial activity at higher latitudes – during the earlier event Antarctic ice sheets grew significantly causing a decrease in bottom-water temperatures, whereas during the latter event the climate switched to an increased intensity of glacial cycles. Our study corroborates the global nature of this disappearance event (so-called ‘*Stilostomella* extinction’), which has earlier been reported at numerous sites^{3,5–8}. The fact that this species disappeared with the beginning of high-amplitude glacial cycles and a change from a 40 to 100 Kyr world, allows us to link this disappearance event to the cooling of deep waters and strong deep-ocean currents across the MPT. It is likely that *S. lepidula* preferred shallow infaunal static mode of life in a low-energy environment and was less adaptive to sudden changes in the deep-sea environment.

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ACKNOWLEDGEMENTS. We thank the Ocean Drilling Program (ODP) for providing core samples. A.K.G. thanks DST and CSIR, New Delhi for financial support. We also thank the two anonymous reviewer for suggestions.

Received 11 April 2007; revised accepted 30 January 2008