The enigma of early Miocene biserial planktic foraminifera

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ABSTRACT

Small biserial foraminifera were abundant in the early Miocene (ca. 18.9–17.2 Ma) in the eastern Atlantic and western Indian Oceans, but absent in the western equatorial Atlantic Ocean, Weddell Sea, eastern Indian Ocean, and equatorial Pacific Ocean. They have been assigned to the benthic genus *Bolivina*, but their high abundances in sediments without evidence for dysoxia could not be explained. Apertural morphology, accumulation rates, and isotopic composition show that they were planktic (genus *Streptochilus*). Living *Streptochilus* are common in productive waters with intermittent upwelling. The widespread early Miocene high *Streptochilus* abundances may reflect vigorous but intermittent upwelling, inducing high phytoplankton growth rates. However, export production (estimated from benthic foraminiferal accumulation rates) was low, possibly due to high regeneration rates in a deep thermocline. The upwelled waters may have been an analog to Subantarctic Mode Waters, carrying nutrients into the eastern Atlantic and western Indian Oceans as the result of the initiation of a deep-reaching Antarctic Circumpolar Current, active Agulhas Leakage, and vigorous vertical mixing in the Southern Oceans.

Keywords: Miocene, planktic foraminifera, paleoceanography, ocean circulation, productivity, Ocean Drilling Program.

INTRODUCTION

During the relatively warm early Miocene the Antarctic ice sheet fluctuated in volume (e.g., Lear et al., 2004). In the middle Miocene deep waters cooled, latitudinal temperature gradients and water-mass stratification increased, and a permanent East Antarctic Ice Sheet formed (e.g., Zachos et al., 2001). There was a turnover in oceanic biota, possibly due to an increase in upwelling and oceanic productivity (Hallock et al., 1991). Early Miocene pCO_2 levels may have been similar to preindustrial ones (e.g., Pagani et al., 2005), and ocean circulation might have been at least a contributing factor in forcing the warm climate.

Ocean circulation probably changed during the early-middle Miocene (Ramsay et al., 1998). Deep-water exchange between the Indian and Atlantic Oceans became limited (ca. 21-19 Ma), and ended by ca. 14 Ma (e.g., Harzhauser et al., 2002). Northern Component Water (NCW, a precursor of North Atlantic Deep Water) may have started to form ca. 19 Ma and peaked ca. 17 Ma (e.g., Wright, 1998). Drake Passage, necessary for establishment of the Antarctic Circumpolar Current (ACC), which might drive NCW formation (e.g., Sijp and England, 2004), may not have opened before ca. 20 Ma (Anderson and Delaney, 2005), but estimates vary from late Miocene to middle Eocene (e.g., Barker and Thomas, 2004).

Information on the distribution of foraminifera may help in elucidating circulation patterns. An enigmatic feature of early Miocene (ca. 18.9–17.2 Ma) oceanography is the socalled High Abundance of Bolivinid (HAB) event (Thomas, 1986; Smart and Murray, 1994; Smart and Ramsay, 1995; Ramsay et al., 1998), when biserial foraminifera assigned to the benthic genus *Bolivina* were abundant at depths of 1000–2500 m in the eastern Atlantic and western Indian Oceans (Fig. 1). In the modern oceans such high relative abundances of bolivinids occur only where an oxygen minimum zone impinges on the seafloor (e.g., Bernhard and Sen Gupta, 1999), and there is no evidence for dysoxia (e.g., lamination, high organic carbon) during the HAB.

We used morphological, isotopic, and accumulation rate data in samples from Walvis Ridge, southeastern Atlantic Ocean (Ocean Drilling Program [ODP] Leg 208, Sites 1264 and 1265) (Zachos et al., 2004), to document that the lower Miocene biserial forms were planktic, and speculate on possible explanations for their abundance.

MATERIAL AND METHODS

Sites 1264 and 1265 are on Walvis Ridge, in the oligotrophic subtropical gyre in the southeastern Atlantic Ocean (Fig. 1; GSA Data Repository Table DR1¹), outside the area of coastal upwelling (e.g., Garzoli et al.,

¹GSA Data Repository item 2006227, Tables DR1 and DR2, occurrences of biserial planktics, oxygen and carbon isotope data, is available online at www.geosociety.org/pubs/ft2006.htm, or on request from editing@geosociety.org or Documents Secretary, GSA, P.O. Box 9140, Boulder, CO 80301, USA.



18.5 Ma Reconstruction

Figure 1. Abundant early Miocene biserial foraminifera (green circles): F—Feni Drift (Deep Sea Drilling Project [DSDP] Site 610); B—Bay of Biscay (DSDP Sites 400, 548); RP—Rockall Plateau (DSDP Site 608); 563—DSDP Site 563; 667—Ocean Drilling Program (ODP) Site 667; WR—Walvis Ridge (DSDP Site 529; ODP Sites 1264, 1265); WI—Western Indian Ocean (DSDP Site 237, ODP Site 709). No biserial foraminifera (black squares): CR—Ceara Rise (ODP Site 926) (Smart, unpublished data); MR—Maud Rise (ODP Sites 689, 690) (Thomas, 1990); NR—Ninetyeast Ridge (ODP Site 758) (Thomas, unpublished data); EP—equatorial Pacific Ocean (DSDP Sites 573, 574, 575) (Thomas, 1985). http://www.odsn.de/odsn/services/paleomap/paleomap.html.

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Figure 2. Scanning electron microscope micrographs of *Streptochilus* sp. (A–D) and *Bolivina plicata* (E). A: Oblique view (scale bar 50 μ m). B: Detail of aperture (scale bar 10 μ m) (Ocean Drilling Program 208–1264B–21–1, 78–80 cm, Walvis Ridge). C: Oblique view (scale bar 50 μ m). D: Detail of aperture (scale bar 10 μ m) (Deep Sea Drilling Project 24–237–18–6, 69–71 cm, western Indian Ocean). E: Aperture of type specimen of *Bolivina plicata*, type species of genus *Bolivina* (magnification ×500 in original figure) (from Loeblich and Tappan, 1987, their plate 547; Fig. 3).

1996). Age control is based on microfossil datum levels and paleomagnetic data (Zachos et al., 2004), with numerical ages according to Lourens et al. (2004). The lower boundary of abundant biserial forms is slightly above the lowest occurrence (LO) of *Sphenolithus belemnos*, as at northeastern Atlantic Ocean Site 608 (Olafsson, 1991; I. Raffi, 2005, personal commun.); the upper boundary is slightly above the LO of *Sphenolithus heteromorphus*.



Figure 3. Accumulation rates (numbers/cm² × k.y.⁻¹) of biserial planktic foraminifera (solid lines) and total benthic foraminifera (dashed lines) at Ocean Drilling Program Sites 1264 and 1265 (Walvis Ridge, southeastern Atlantic Ocean), calculated according to NF x LSR x DBD, where NF is number of foraminifera per gram of dry sediment, LSR is linear sediment rate (cm/k.y.), and DBD is dry bulk density (g/cm³) of sediment.

More than 250 foraminifers were picked from the $>63 \ \mu m$ size fraction of each sample. Accumulation rates (numbers/cm² \times k.y.⁻¹) of benthic foraminifera and biserial planktics were calculated. For stable isotope analyses ~100 monospecific biserial specimens were picked from the 63-150 µm size fraction, 10-20 Globigerinoides quadrilobatus were picked from the 250-355 µm size fraction, 10-20 Globoquadrina venezuelana were picked from the 250–355 μ m and >355 µm size fractions, and 10-15 Cibicidoides kullenbergi and Cibicidoides sp. were picked from the $>63 \ \mu m$ size fraction (Table DR2; see footnote 1). Stable isotope analyses were performed on a VG PRISM mass spectrometer (Godwin Laboratory, University of Cambridge, UK). Results are reported with refer-



ence to the international standard Vienna Peedee Belemnite calibrated through the NBS19 standard (Coplen, 1995); precision is better than $\pm 0.06\%$ for ${}^{13}C/{}^{12}C$ and better than $\pm 0.08\%$ for ${}^{18}O/{}^{16}O$.

RESULTS

Most biserial planktics have more inflated chambers than benthics, and a wide, arched aperture without an internal tooth plate. Benthic biserials have a tooth plate connecting the aperture of the last chamber to that of earlier ones. Some Streptochilus species are less inflated, but all have an aperture with an internal plate formed by the infolding and downward extension of a margin of the aperture (Brönnimann and Resig, 1971). The plate resembles the bolivinid tooth plate, but is formed from the rim around the aperture rather than sticking up from the interior of the chamber (Fig. 2). Test morphology of the lower Miocene biserials varies between sites, and we consider them representatives of several undescribed species.

There is no relation between the accumulation rates of benthic species and of the biserial foraminifera in the same size fraction of the same samples (Fig. 3). The biserial planktic taxa compose 1%–2% of total foraminifera at Site 1264, comparable to late Miocene Indian Ocean *Streptochilus* abundances (Resig, 1989).

Oxygen isotope values of the biserial planktics overlap with those of surface dwelling planktic foraminifera in the same samples (Fig. 4; Table DR2 [see footnote 1]). Carbon isotope values of the biserial taxa are lighter than the values for other planktics, and overlap with, or are lighter than, those of benthics in the same samples.

> Figure 4. Oxygen and carbon isotope values of biserial planktic foraminifera (Streptochilus spp.), other planktics (shallowdwelling Globigerinoides quadrilobatus and deepdwelling Globoquadrina venezuelana), and benthic foraminifera (Cibicidoides kullenbergi and Cibicidoides sp.) at Sites 608 (northeastern Atlantic) and 1264 (southeastern Atlantic). Isotope data are not corrected for disequilibrium.

DISCUSSION

Benthic biserial species are swept out to the open sea by storms (Brunner and Biscaye, 1997) to occur as rare specimens in plankton tows (Hueni et al., 1978). The early Miocene biserials were not displaced benthics: their aperture (Fig. 2) indicates that they belong to the planktic genus *Streptochilus* and they occur at many pelagic locations (Fig. 1) over a period of \sim 2 m.y.

The oxygen isotope values of the lower Miocene biserials overlap with those of surface-dwelling planktic species in the same samples (Fig. 4). Some benthic foraminifera are offset in oxygen isotope values from equilibrium with the seawater in which they formed (vital effects), but no benthic species has such a large offset in its δ^{18} O values. *Bolivina* species do not have significant δ^{18} O vital effects (e.g., Kennett et al., 2000).

The carbon isotope values of the biserials are as low as or lower than those of benthic foraminifera, as in upper Miocene and middle Eocene Streptochilus (Resig and Kroopnick, 1983; Sexton et al., 2006). Resig and Kroopnick (1983, p. 244) argued for a "deep planktonic habitat within the oxygen minimum layer"; this would, however, result in more positive δ^{18} O values than observed. Nikolaev et al. (1998) classified late Miocene Streptochilus as an intermediate-dwelling species (75-150 m depth). We explain the low carbon isotope values as resulting from rapid calcification in a region with variable upwelling conditions, as seen in modern surface dwellers (e.g., Kroon and Ganssen, 1989). In the Arabian Sea, Globigerina bulloides (a nonsymbiont species), for example, has more depleted δ^{13} C values than benthic Uvigerina excellens, but a light oxygen isotope signature, suggesting that the light carbon isotopic signature persists when upwelled waters warm (Naidu and Niitsuma, 2004).

Little is known about the ecology of living *Streptochilus* and no isotope data have been reported. They constitute as much as 15% of assemblages in plankton tows close to the shelf in regions of high productivity, with intermittent upwelling, south of India (De Klasz et al., 1989; Kroon and Nederbragt, 1990). Hemleben et al. (1989) described them as deep dwelling in temperate to tropical, highly productive waters, but present in shallow surface waters close to upwelling in coastal regions. *Streptochilus* are rare (<1%) near Bermuda (Hemleben et al., 1989) and in the Caribbean (Schmuker and Schiebel, 2002).

High abundances of Paleogene biserial planktics are indicative of eutrophic waters (e.g., Hallock et al., 1991), and Resig (1989) correlated high abundances of Miocene–Pliocene *Streptochilus* species with high accumulation rates of foraminiferal oozes. Late Miocene *Streptochilus* spp. have been de-

scribed as tropical to warm subtropical (Resig, 1989), but are abundant in samples from the northernmost Atlantic Ocean (Flower, 1999), the Bahama Bank (Kroon et al., 2000), the equatorial western Pacific Ocean (Premoli Silva and Violanti, 1981; Resig, 1989), and the eastern Indian Ocean (Resig, 1989).

Early Miocene *Streptochilus* were abundant over a wide range of latitudes (Fig. 1). At northeastern Atlantic Ocean Site 608 an increase in the carbon isotopic composition of alkenones, coeval with the peak *Streptochilus* abundance, has been interpreted as due to high algal growth rates in response to high nutrient availability (Pagani et al., 1999). The early Miocene *Streptochilus* may thus have bloomed opportunistically in response to highly fluctuating nutrient conditions where nutrient-rich waters upwelled intermittently, as suggested by their small size and high abundance and as inferred for Paleogene biserial planktics (e.g., Hallock et al., 1991).

The blooms did not result in high export productivity. Benthic foraminiferal accumulation rates, a proxy for delivery of food to the seafloor (Herguera and Berger, 1991), are low when biserials are abundant (Fig. 3; Diester-Haass and Billups, 2005). Low export productivity occurs where the thermocline is deep and regeneration rates of organic matter are high (e.g., Fischer et al., 2003). The widespread abundant occurrence of Streptochilus would have required the occurrence of a deep thermocline, broken up intermittently, over large regions. Such a situation does not occur in the present oceans, but average thermocline depth may have been greater in the warm early Miocene (e.g., Philander and Fedorov, 2003). The small Indian Ocean area where modern Streptochilus is abundant (De Klasz et al., 1989; Kroon and Nederbragt, 1990) could be the closest modern counterpart, not comparable in geographic extent.

Why was there widespread, intermittent upwelling in the eastern Atlantic and western Indian Oceans only at 18.9–17.2 Ma? Maybe it was the circulation: NCW may have been present between 19 and 17 Ma, its formation triggered by the sinking of the Greenland-Scotland Ridge (Wright, 1998), or by the development of a deep ACC (e.g., Anderson and Delaney, 2005) leading to the formation of NCW (Sijp and England, 2004). A deep ACC causes strong mixing in the Southern Oceans, triggering increased nutrient contents in the Subantarctic Mode Waters that support global productivity (Sarmiento et al., 2004).

The closing of the Mediterranean to the Indian Ocean (Harzhauser et al., 2002) may have increased the flow of surface waters from the Indian Ocean around South Africa (Agulhas Leakage), leading to deep convection (De Ruijter et al., 2006) in the Southern Oceans, thus providing the nutrient-rich waters upwelled in the eastern Atlantic and western Indian Oceans.

Why did the high abundance of biserial planktics end ca. 17.2 Ma? Possibly, vigorous North Atlantic deep circulation ended earlier than envisaged by Wright (1998, using carbon isotope records). It is not clear why high abundances of *Streptochilus* did not resume during the middle Miocene cooling and formation of NCW, but upwelling might have become constrained to its modern locations rather than being widespread because of the overall increase of circulation vigor.

CONCLUSIONS

The early Miocene HAB events in the eastern Atlantic and western Indian Oceans were planktic events, and the biserial foraminifera belong to the genus *Streptochilus*.

During the early Miocene (19–17 Ma) large stretches of the eastern Atlantic and western Indian Oceans may have been characterized by a deep thermocline intermittently broken up by vigorous upwelling.

The high productivity in surface waters did not result in high export to the seafloor, possibly because of high regeneration in an expanded thermocline.

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REFERENCES CITED

- Anderson, L.D., and Delaney, M.L., 2005, Use of multiproxy records on the Agulhas Ridge, Southern Ocean (Ocean Drilling Project Leg 177, Site 1090) to investigate sub-Antarctic hydrography from the Oligocene to the early Miocene: Paleoceanography, v. 20, p. PA3011, doi: 10.1029/2004PA001082.
- Barker, P.F., and Thomas, E., 2004, Origin, signature and palaeoclimatic influence of the Antarctic Circumpolar Current: Earth Science Reviews, v. 66, p. 143–162, doi: 10.1016/j.earscirev. 2003.10.003.
- Bernhard, J.M., and Sen Gupta, B.K., 1999, Foraminifera of oxygen-depleted environments, *in* Sen Gupta, B.K., ed., Modern foraminifera: Dordrecht, Kluwer Academic Publishers, p. 141–160.
- Brönnimann, P., and Resig, J., 1971, A Neogene globigerinacean biochronologic time-scale of the southwestern Pacific, *in* Winterer, E., Riedel, W., et al., Initial reports of the Deep Sea Drilling Project, Volume 7: Washington, D.C., U.S. Government Printing Office, p. 1235–1469.
- Brunner, C., and Biscaye, P., 1997, Storm-driven transport of foraminifers from the shelf to the upper slope, southern middle Atlantic

Bight: Continental Shelf Research, v. 17, p. 491–508, doi: 10.1016/S0278-4343(96) 00043-X.

- Coplen, T.B., 1995, New IUPAC guidelines for the reporting of stable hydrogen, carbon, and oxygen isotope-ratio data: National Institute of Standards and Technology Journal of Research, v. 100, p. 285.
- De Klasz, I., Kroon, D., and van Hinte, J.E., 1989, Notes on the foraminiferal genera *Laterostomella* de Klasz and Rerat and *Streptochilus* Brönnimann and Resig: Journal of Micropaleontology, v. 8, p. 215–226.
- De Ruijter, W.P.M., Brummer, G.J., Drijfhout, S.S., Lutjeharms, J.R.E., Peeters, F., Ridderinkhof, H., van Aken, H., and van Leeuwen, P.J., 2006, Observations of the inter-ocean exchange around South Africa: Eos (Transactions, American Geophysical Union), v. 87, p. 97, 99, 101.
- Diester-Haass, L., and Billups, K., 2005, Miocene global carbon isotope shifts and marine biological productivity: Eos (Transactions, American Geophysical Union), v. 86, Fall meeting supplement, abs. PP51B–0588.
- Fischer, G., Wefer, G., Romero, O., Dittert, N., Ratmeyer, V., and Donner, B., 2003, Transfer of particles into the deep Atlantic and the global ocean: Control of nutrient supply and ballast production, *in* Wefer, G., et al., eds., The South Atlantic in the late Quaternary: reconstruction of material budgets and current systems: Berlin, Springer Verlag, p. 21–46.
- Flower, B.P., 1999, Data report: Planktonic foraminifers from the subpolar North Atlantic and Nordic Sea: Sites 980–987 and 907, *in* Raymo, M.E., et al., Proceedings of the Ocean Drilling Program, Scientific results, Volume 162: College Station, Texas, Ocean Drilling Program, p. 19–34.
- Garzoli, S.L., Gordon, A.L., Kamenkovich, V., Pillsbury, D., and Duncombe-Rae, C., 1996, Variability and sources of the south eastern Atlantic circulation: Journal of Marine Research, v. 54, p. 1039–1071, doi: 10.1357/ 0022240963213763.
- Hallock, P., Premoli Silva, I., and Boersma, A., 1991, Similarities between planktonic and larger foraminiferal evolutionary trends through Paleogene paleoceanographic changes: Palaeogeography, Palaeoclimatology, Palaeoecology, v. 83, p. 49–64, doi: 10.1016/ 0031-0182(91)90075-3.
- Harzhauser, M., Piller, W.E., and Steininger, F.F., 2002, Circum-Mediterranean Oligo-Miocene biogeographic evolution: The gastropods' point of view: Palaeogeography, Palaeoclimatology, Palaeoecology, v. 183, p. 103–133, doi: 10.1016/S0031-0182(01)00464-3.
- Hemleben, C., Spindler, M., and Anderson, O.R., 1989, Modern planktonic foraminifera: Heidelberg, Germany, Springer Verlag, 363 p.
- Herguera, J.C., and Berger, W.H., 1991, Paleoproductivity from benthic foraminifer abundance: Glacial to postglacial change in the west equatorial Pacific: Geology, v. 19, p. 1173–1176, doi: 10.1130/0091-7613(1991)019<1173: PFBFAG>2.3.CO;2.
- Hueni, C., Monroe, J.A., Gevirtz, J., and Casey, R., 1978, Distribution of living benthonic foraminifera as indicators of oceanographic processes on the South Texas outer continental shelf: Gulf Coast Association of Geological Societies Transactions, v. 28, p. 193–200.
- Kennett, J.P., Cannariato, K.G., Hendy, I.L., and Behl, R.J., 2000, Carbon isotopic evidence for methane instability during Quaternary interstadials: Science, v. 288, p. 128–133, doi: 10.1126/science.288.5463.128.
- Kroon, D., and Ganssen, G., 1989, Northern Indian

Ocean upwelling cells and the stable isotope composition of living planktonic foraminifers: Deep Sea Research, v. 36, p. 1219–1236, doi: 10.1016/0198-0149(89)90102-7.

- Kroon, D., and Nederbragt, A.J., 1990, Ecology and paleoecology of triserial planktic foraminifera: Marine Micropaleontology, v. 16, p. 25–38, doi: 10.1016/0377-8398(90)90027-J.
- Kroon, D., Williams, T., Pirmez, C., Spezzaferri, S., Sato, T., and Wright, J.D., 2000, Coupled early Pliocene–middle Miocene bio-cyclostratigraphy of Site 1006 reveals orbitally induced cyclicity patterns of Great Bahama Bank carbonate production, *in* Swart, P.K., et al., Proceedings of the Ocean Drilling Program, Scientific results, Volume 166: College Station, Texas, Ocean Drilling Program, p. 155–166.
- Lear, C., Rosenthal, Y., Coxall, H.K., and Wilson, P.A., 2004, Late Eocene to early Miocene ice sheet dynamics and the global carbon cycle: Paleoceanography, v. 19, p. PA4015, doi: 10.1029/2004PA001039.
- Loeblich, A.R., and Tappan, H., 1987, Foraminiferal genera and their classification: New York, Van Nostrand Reinhold, 1182 p.
- Lourens, L.J., Hilgen, F.J., Laskar, J., Shackleton, N.J., and Wilson, D., 2004, The Neogene Period, *in* Gradstein, F.M., et al., eds., A geologic time scale 2004: Cambridge, Cambridge University Press, p. 409–440.
- Naidu, P.D., and Niitsuma, N., 2004, Atypical δ¹³C signature in *Globigerina bulloides* at the ODP site 723A (Arabian Sea): Implications of environmental changes caused by upwelling: Marine Micropaleontology, v. 53, p. 1–10, doi: 10.1016/j.marmicro.2004.01.005.
- Nikolaev, S.D., Oskina, N.S., Bylum, N.S., and Bubenshchikova, N.V., 1998, Neogene-Quaternary variations of the 'Pole-Equator' temperature gradient of the surface oceanic waters in the North Atlantic and North Pacific: Global and Planetary Change, v. 18, p. 85–111, doi: 10.1016/S0921-8181(98) 00009-5.
- Olafsson, G., 1991, Late Oligocene through late Miocene calcareous nannofossil biostratigraphy and biochronology: Meddelanden från Stockholms Universitets Institution för Geologi og Geokemi, no. 283, 157 p.
- Pagani, M., Arthur, M.A., and Freeman, K.H., 1999, The Miocene evolution of atmospheric carbon dioxide: Paleoceanography, v. 14, p. 273–292, doi: 10.1029/1999PA900006.
- Pagani, M., Zachos, J.C., Freeman, K.H., Tipple, B., and Bohaty, S., 2005, Marked decline in atmospheric carbon dioxide concentrations during the Paleogene: Science, v. 309, p. 600–603, doi: 10.1126/science.1110063.
- Philander, S.G., and Fedorov, A.V., 2003, Role of tropics in changing the response of Milankovich forcing some three million years ago: Paleoceanography, v. 18, p. 1045, doi: 10.1029/ 2002PA000837.
- Premoli Silva, I., and Violanti, D., 1981, Cenozoic planktonic foraminifer biostratigraphy of the Deep Sea Drilling Project Hole 462, Nauru Basin (Western Equatorial Pacific), and distribution of the pelagic components, *in* Larson, R.L., and Schlanger, S.O., Initial reports of the Deep Sea Drilling Project, Volume 61: Washington, D.C., U.S. Government Printing Office, p. 397–422.
- Ramsay, A.T.S., Smart, C.W., and Zachos, J.C., 1998, A model of early to middle Miocene deep ocean circulation for the Atlantic and Indian oceans, *in* Cramp, A., et al., eds., Geological evolution of ocean basins: Results from the Ocean Drilling Program: Geological Society [London] Special Publication 131, p. 55–70.

- Resig, J., 1989, Stratigraphic distribution of late Neogene species of the planktonic foraminifer *Streptochilus* in the Indo-Pacific: Micropaleontology, v. 35, p. 49–62, doi: 10.2307/ 1485536.
- Resig, J., and Kroopnick, P., 1983, Isotopic and distributional evidence of a planktonic habitat for the foraminiferal genus *Streptochilus* Brönnimann and Resig, 1971: Marine Micropaleontology, v. 8, p. 235–248, doi: 10.1016/0377-8398(83)90026-9.
- Sarmiento, J.L., Gruber, N., Brzezinski, M.A., and Dunne, J.P., 2004, High-latitude controls of thermocline nutrients and low latitude biological productivity: Nature, v. 427, p. 56–60, doi: 10.1038/nature02127.
- Schmuker, B., and Schiebel, R., 2002, Planktic foraminifera and hydrography of the eastern and northern Caribbean Sea: Marine Micropaleontology, v. 46, p. 387–403, doi: 10.1016/ S0377-8398(02)00082-8.
- Sexton, P.E., Wilson, P.A., and Pearson, P.N., 2006, Palaeoecology of late middle Eocene planktic foraminifera and evolutionary implications: Marine Micropaleontology, v. 60, p. 1–16, doi: 10.1016/j.marmicro.2006.02.006.
- Sijp, W.P., and England, M., 2004, Effect of the Drake Passage Throughflow on global climate: Journal of Physical Oceanography, v. 34, p. 1254–1266, doi: 10.1175/1520-0485(2004) 034<1254:EOTDPT>2.0.CO;2.
- Smart, C.W., and Murray, J.W., 1994, An early Miocene Atlantic-wide foraminiferal/ palaeoceanographic event: Palaeogeography, Palaeoclimatology, Palaeoecology, v. 108, p. 139–148, doi: 10.1016/0031-0182(94)90026-4.
- Smart, C.W., and Ramsay, A.T.S., 1995, Benthic foraminiferal evidence for the existence of an early Miocene oxygen-depleted oceanic water mass?: Geological Society [London] Journal, v. 152, p. 735–738.
- Thomas, E., 1985, Late Eocene to Recent deep-sea benthic foraminifers from the central equatorial Pacific Ocean, *in* Mayer, L., Theyer, F, et al., Initial reports of the Deep Sea Drilling Project, Volume 85: Washington, D.C., U.S. Government Printing Office. p. 655–694
- Government Printing Office, p. 655–694.
 Thomas, E., 1986, Early to middle Miocene benthic foraminiferal faunas from DSDP sites 608 and 610, North Atlantic, *in* Summerhayes, C.P., and Shackleton, N.J., eds., North Atlantic Palaeoceanography: Geological Society [London] Special Publication 21, p. 205–218.
- Thomas, E., 1990, Late Cretaceous through Neogene deep-sea benthic foraminifers (Maud Rise, Weddell Sea, Antarctica), *in* Barker, P.F., Kennett, J.P., et al., Proceedings of the Ocean Drilling Program, Scientific results, Volume 113: College Station, Texas, Ocean Drilling Program, p. 571–594.
- Wright, J.D., 1998, Role of the Greenland-Scotland Ridge in Neogene climate, *in* Crowley, T.J., and Burke, K.C., eds., Tectonic boundary conditions for climatic reconstructions: New York, Oxford University Press, p. 192–211.
- Zachos, J., Pagani, M., Sloan, L., Thomas, E., and Billups, K., 2001, Trends, rhythms, and aberrations in global climate: 65 Ma to present: Science, v. 292, p. 686–693, doi: 10.1126/ science.1059412.
- Zachos, J.C., and 26 others, 2004, Proceedings of the Ocean Drilling Program, Initial reports, Volume 208: College Station, Texas, Ocean Drilling Program: http://www-odp.tamu.edu/ publications/208_IR/208ir.htm (July 2006).

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