Emendation of the genus *Streptochilus* Brönnimann and Resig 1971 (Foraminifera) and new species from the lower Miocene of the Atlantic and Indian Oceans

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ABSTRACT: Three new species of *Streptochilus*, a biserial planktic foraminiferal genus, were recognized in the lower Miocene of the eastern Atlantic and western Indian Oceans. These species had been formerly thought to be benthic species of the genus *Bolivina*, but evidence on their apertural morphology and stable isotopic composition indicates that they lived as plankton and should be assigned to the genus *Streptochilus*. The observation that three morphological species occurred in different regions of the oceans during the same short period of time (18.9-17.2 Ma) suggests that these biserial planktic species may have evolved polyphyletically, either from biserial planktic or from benthic ancestors, possibly in response to the occurrence of relatively eutrophic environmental conditions caused by intermittent upwelling, leading to high algal growth rates but low transport efficiency of organic matter to the sea floor. The new species of *Streptochilus* are described, illustrated and named: *S. rockallkiddensis* sp. nov. (from the northeastern Atlantic), *S. cetacensis* sp. nov. (from the equatorial and southeastern Atlantic) and *S. mascarenensis* sp. nov. (from the western equatorial Indian Ocean) and the description of the genus is emended.

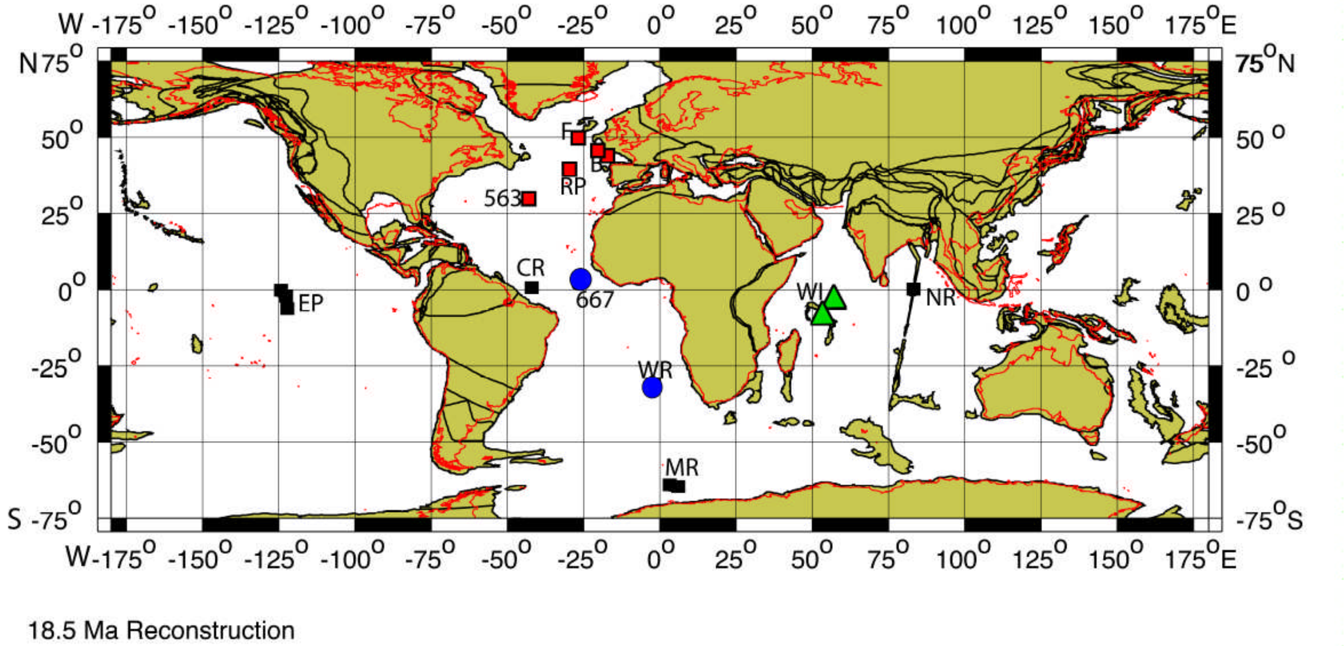
INTRODUCTION

High abundances of small biserial foraminifera assigned to the benthic genus *Bolivina* have been observed in lower Miocene sediments in the northeastern Atlantic and western Indian Oceans (~18.9-17.2 Ma) (Thomas 1986, 1987; Smart 1992; Smart and Murray 1994; Smart and Ramsay 1995). The early Miocene 'High Abundance of Bolivinid (HAB) event', as it was called, was not observed in sediments in the western equatorial Atlantic, eastern equatorial Pacific Ocean (Thomas 1985) and the Weddell Sea (Thomas 1990), although the correct size fraction and time interval were studied (text-fig. 1). These foraminifera occur dominantly in the small size fraction (>63μm) which has not been studied at many locations. At DSDP Site 608 (Northern Atlantic Ocean), Pagani et al. (1999, 2000) identified an increase in the carbon isotopic composition of alkenones coeval with the HAB event. This increase was interpreted as resulting from increased algal growth rates, possibly in response to increased local availability of nutrients. The calcareous nannoplankton record for that site (Olafsson 1991) shows a peak in the relative abundance of the *incertae sedis* marker species *Sphenolithus belemnos* coeval with the lower part of the event and of *Sphenolithus heteromorphus* in its higher part. Nannofossil events have been dated in the orbitally tuned Neogene time scale (Lourens et al. 2004), with the Lowest Occurrence (LO) of *S. belemnos* at 18.92 Ma, its Highest Occurrence (HO) at 17.89 Ma and the LO of *S. heteromorphus* at 17.66 Ma (Zachos et al. 2004).

The HAB event was hard to explain. In the modern oceans such high abundances of bolivinids occur only where an oxygen minimum zone impinges on the sea floor, e.g., under upwelling regions along continental margins and in silled basins (e.g., Bernhard 1986; Bernhard and Sen Gupta 1999). Thomas (1986, 1987), Smart (1992) and Smart and Murray (1994) speculated that the HABs could have occurred in a period of low oxygen conditions associated with sluggish circulation, although the sites are in the open ocean, and there is no sedimentological evidence for dysoxic conditions (e.g., high organic carbon concentration, laminated sediment). Smart and Ramsay (1995) and Ramsay et al. (1998) suggested that the event was associated with an oxygen depleted water mass restricted to the Atlantic and western Indian Oceans. How did the early Miocene world look during the HAB event?

During the early Miocene a continental ice sheet was present on East Antarctica, and possibly on Greenland (Eldrett et al. 2007). The volume of the East Antarctic Ice Sheet fluctuated (Lear et al. 2004; Hannah 2006; Pekar and DeConto 2006), with smallest ice volume and highest temperatures towards the end of the early Miocene (text-fig. 2), followed by deep-water cooling, increasing latitudinal temperature gradients (e.g., Nikolaev et al. 1998), increasing vertical water mass stratification, and the transition to a permanent, continent-wide East Antarctic Ice Sheet (e.g., Zachos et al. 2001; Miller et al. 2005; Vlastelic et al. 2005). These changes were accompanied by turnover in oceanic biota, possibly due to increasing vigor of upwelling, increased nutrient levels and oceanic productivity (e.g., Hallock et al. 1991; Halfar and Mutti 2005). Early Miocene pCO_2 levels may have been similar to pre-industrial ones, as estimated from alkenone carbon isotopes (Pagani et al. 1999), boron isotopes (Pearson and Palmer 2000), and leaf stomates (Royer et al. 2001), suggesting ocean circulation might have been at least a contributing factor in forcing the warm climate.

Substantial changes in circulation, oceanic productivity and the oceanic carbon cycle may have occurred during the early-middle Miocene (e.g., Woodruff and Savin 1989; Ramsay et al.



TEXT-FIGURE 1
Occurrence of early Miocene biserial foraminifera. Red squares: *S. rockallkiddensis* at F: Feni Drift (DSDP Site 610); B: Bay of Biscay (DSDP Sites 400, 548); RP: Rockall Plateau (DSDP Site 608); 563: DSDP Site 563. Blue circles: *S. cetacensis* at 667: ODP Site 667; and WR: Walvis Ridge (DSDP Site 529; ODP Sites 1264, 1265). Green triangles: *S. mascarenensis* at WI: Western Indian Ocean (DSDP Site 237, ODP Site 709). No biserial foraminifera (black squares): CR: Ceara Rise (ODP Site 926) (Smart, unpub. data); MR: Maud Rise (ODP Sites 689, 690) (Thomas 1990); NR: Ninetyeast Ridge (ODP Site 758) (Thomas, unpub. data); EP: Equatorial Pacific Ocean (DSDP Sites 573, 574, 575) (Thomas 1985). http://www.odsn.de/odsn/services/paleomap/paleomap.html. (Modified after Smart and Thomas 2006).

1998; Sykes et al. 1998; Wright 1998; Wright and Miller 1996; Lear et al. 2003, 2004; Poore et al. 2006). Benthic foraminiferal carbon isotope values shifted to more positive values starting at ~19 Ma, peaking between ~16.3 and ~13.5 Ma (Zachos et al. 2001; text-fig. 2). This positive excursion has been linked to organic carbon deposition in marine sediments around the Pacific Rim ('Monterey Event', Vincent and Berger 1985), or in lignites on land (Föllmi et al. 2005). Biogenic silica deposition moved from the Atlantic to the Pacific Ocean near the end of the early Miocene (Baldauf and Barron 1990). Deep-water exchange between the Indian and Atlantic Oceans through the eastern Mediterranean became limited at ~21-19 Ma, with a shallow connection persisting until ~17 Ma (Harzhauser et al. 2002), and closed by ~14 Ma (Woodruff and Savin 1989). The closure of the eastern Mediterranean has been argued to have ended the influx of warm, relatively salty Tethyan Outflow Water (TOW, Wright et al. 1992; called Tethyan/Indian Saline Water [TISW] by Woodruff and Savin 1989) into the northwestern Indian Ocean, with the possible effect of global cooling, but the existence of a significant volume of such outflow has not been confirmed (Smart et al. 2007).

Formation of Northern Component Water (NCW, a precursor of North Atlantic Deep Water) has been alleged to have started at ~19 Ma and reached an early peak at about ~17 Ma (Flower et al. 1997; Wright and Miller 1996; Wright 1998), but there is serious doubt about its significant presence before about 12 Ma (Zachos et al. 2001; Poore et al. 2006). The opening of Drake Passage and subsequent establishment of the Antarctic Circumpolar Current (ACC) has been linked to the middle Miocene global cooling (e.g., Pagani et al. 2000; Vlastelic et al. 2005). A deep-reaching ACC may be necessary for the formation of NCW (e.g., Sijp and England 2004), and may not have existed before ~20 Ma (Anderson and Delaney 2005). Age estimates for the initiation of the ACC, however, vary from late Miocene to middle Eocene (e.g., Barker and Thomas 2004).

In conclusion, there is no agreement on early-middle Miocene ocean circulation patterns and the cause of the rapid middle Miocene intensification of glaciation. Recent papers argue that orbitally driven changes in insolation may have been the main trigger (Abels et al. 2005; Holbourn et al. 2005), reinforcing the effects of declining levels of atmospheric greenhouses gases (Holbourn et al. 2005). Presently available records of such gases do not confirm this hypothesis (Pagani et al. 1999; Zachos et al. 2001), possibly because of their lack of time resolution (Holbourn et al. 2005).

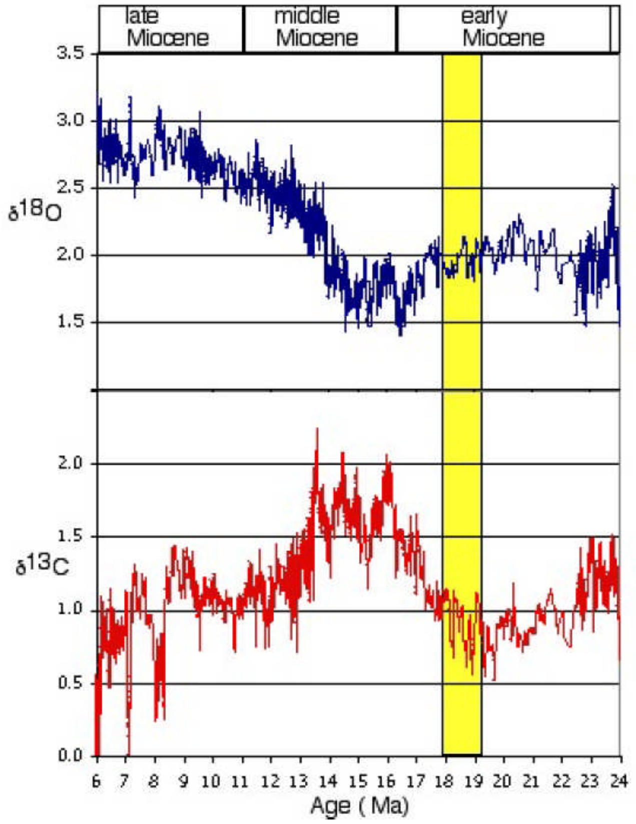
We (Smart and Thomas 2006) used information on apertural morphology, accumulation rates and isotopic composition of the tests to show that the abundant early Miocene biserial foraminifera, assigned to the benthic genus *Bolivina*, are in fact planktic foraminifera and should be assigned to the genus *Streptochilus*. We suggested that the widespread, but not global, events during which the *Streptochilus* were abundant may reflect vigorous but variable upwelling of nutrient-rich waters, inducing high growth rates of phytoplankton. Export production as estimated from benthic foraminiferal accumulation rates, however, was low during episodes of abundant *Streptochilus*, possibly because of high regeneration rates of organic matter in an expanded thermocline. The upwelled waters may have been an analog to the present 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 and active Agulhas Leakage, thus vigorous vertical mixing of nutrient-rich waters in the Southern Oceans, while there was no significant, continuous inflow of NCW (Poore et al. 2006).

In this paper we compile information on fossil and living species of *Streptochilus*, describe the morphology of the early Miocene biserial planktic species in detail, and recognize several species, each with a restricted geographic distribution. The early Miocene biserial foraminifera described here have apertures similar to those of species described as *Streptochilus*, with an internal plate formed by the infolding and downward extension of one margin of the rimmed aperture (Brönnimann and Resig 1971; Resig and Kroopnick 1983; Poore and Gosnell 1985; Resig 1989). Their walls are relatively smooth to somewhat granular in the earlier chambers and their chambers are less globose than in all described species of *Streptochilus*. Their morphology varies between sites in the North Atlantic and Indian Oceans, and we consider them to belong to three morphological species that, until now, have not been described.

BISERIAL PLANKTIC FORAMINIFERA

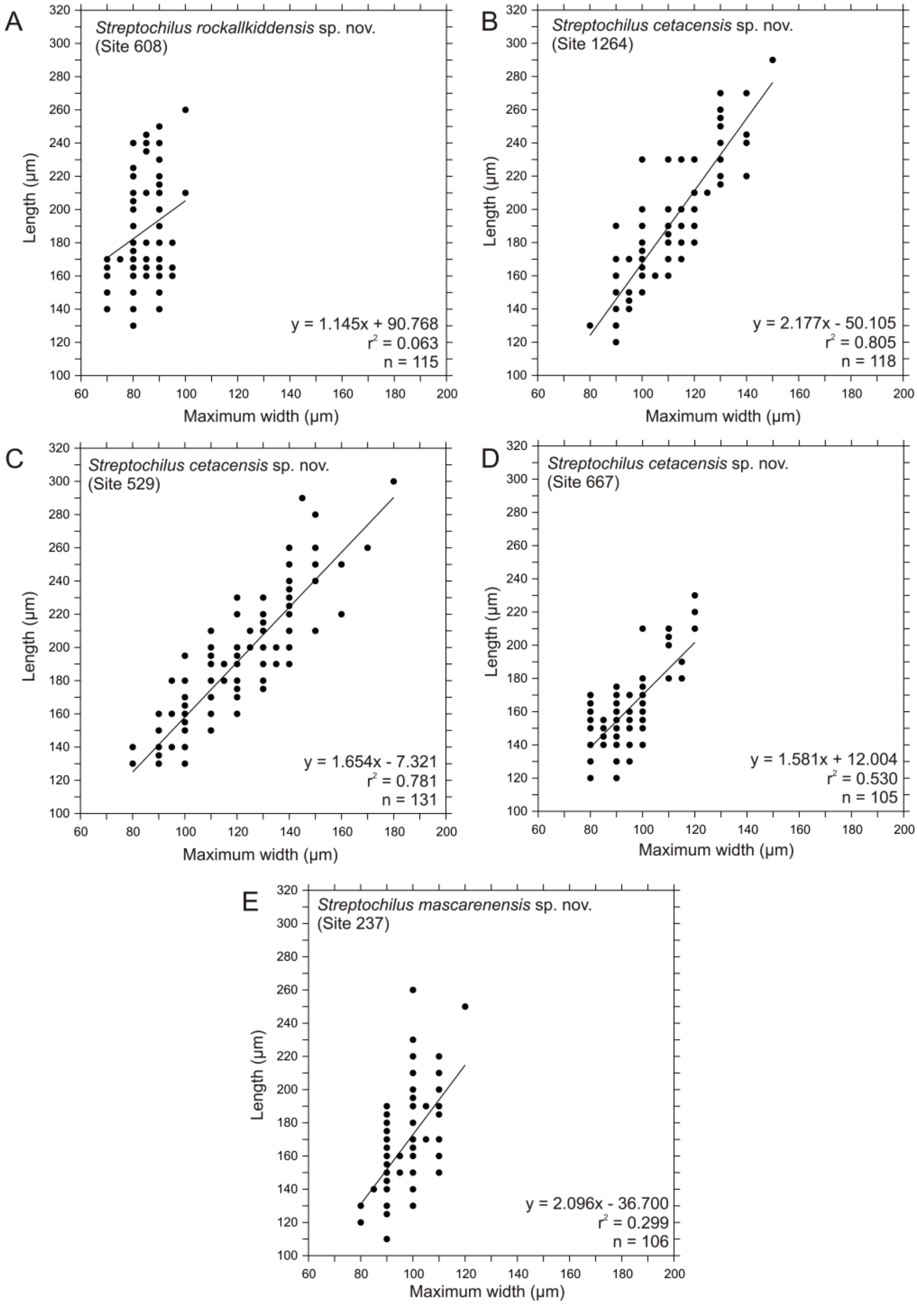
Bi- and triserial planktic foraminifera were common during the Late Cretaceous, with triserial forms among the rare survivors of the end Cretaceous mass extinction (e.g., Kroon and Nederbragt 1990; Olsson et al. 1999). Biserial forms, usually assigned to the genus *Chiloguembelina*, were common to abundant in the Paleogene (e.g., Olsson et al. 1999; Huber et al. 2006), and abundant occurrence of such taxa is commonly seen as reflecting relatively high productivity (e.g., Hallock et al. 1991). The genus *Chiloguembelina* was generally considered to have become extinct during the Oligocene, and the genus *Streptochilus* was seen as its descendant (Kennett and Srinivasan 1983), ranging from late early Miocene through Pleistocene (Brönniman and Resig 1971; Resig 1989). Poore and Gosnell (1985), however, argued that some species usually assigned to *Chiloguembelina* (e.g., *C. martini*) should be included in *Streptochilus* because of the presence of a toothplate (see below), as agreed by Huber et al. (2006) and Sexton et al. (2006). Huber at al. (2006) suggested that *Streptochilus martini* evolved in the middle Eocene from *Chiloguembelina ototara*. There is a stratigraphic gap in the upper Oligocene from which no biserial planktics have been described (Kennett and Srinivasan 1983; De Klasz et al. 1989).

The relations of the genus *Streptochilus* to other genera are not clear, however, and there is a remarkable morphological resemblance between the forms of *Streptochilus* described below and the Maastrichtian species *Zeauvigerina waiparaensis*, especially the forms called *Z. waiparaensis* sensu stricto (Huber and Boersma 1994). There is great similarity in the ontogenetic chamber morphologies, the adult and pre-adult apertural morphologies, the toothplate, and the stable isotopic signature. In addition, *Z. waiparaensis* is, as the *Streptochilus* species described below, characterized by high morphological variability and an unusually limited geographic distribution for a planktic form. If the species *Z. waiparaensis* with an earliest described occurrence in the middle Maastrichtian (Huber and Boersma 1994) should be assigned to the genus *Streptochilus*, the genus would have a much longer history than recorded by e.g. Huber et al. (2006). Alternatively, the phylogeny might be more complicated, and evolution of biserial planktic species might have been polyphyletic (see below).



TEXT-FIGURE 2
Duration of the high abundance of biserial foraminifera event (yellow bar), plotted over carbon and oxygen data in Zachos et al. (2001), using the time scale of Berggren et al. (1995). Age of abundant biserial event at Site 608 using the time scale of Lourens et al. (2004): 18.9-17.2 Ma (Lowest Occurrence [LO] of *Sphenolithus belemnos* at 18.92 Ma, Highest Occurrence at 17.89 Ma; LO of *S. heteromorphus* at 17.66 Ma (Zachos et al. 2004); using the time scale of Berggren et al. (1995): 19.3-17.6 Ma.

Several Mio- and Pliocene *Streptochilus* species were originally described as *Bolivina*, until isotope and distributional data were collected indicating a planktic mode of life, and the name *Streptochilus* was used for planktic species, the names *Bolivina* and *Brizalina* reserved for benthic ones (Brönnimann and Resig 1971; Resig and Kroopnick 1983; Resig 1989). Late Eocene *Streptochilus* species have stable isotopic signatures similar to those of the Miocene ones (Sexton et al. 2006), and are characterized by light oxygen isotope values indicating high (surface) water temperatures. Carbon isotope values, however, are also light, even lighter than those of benthics in the same samples (Smart and Thomas 2006). Resig and Kroopnick (1983) argued that this isotope signature indicated a 'deep planktonic habitat within the oxygen minimum layer', but in such a habitat $\delta^{18}O$ values would be much more positive than observed. Nikolaev et al. (1998) classified *Streptochilus* as an intermediate-dwelling species (75–150 m depth). Smart and Thomas (2006) explained the light carbon isotope signature as resulting from rapid calcification in a region with variable upwelling conditions, as such isotope signatures are seen in Recent surface dwellers in regions with intermittent upwelling, e.g. monsoonal areas in the Ara-



TEXT-FIGURE 3
Scatter plots of length versus maximum width of the three new *Streptochilus* spp. measured in random samples. Regression lines, equations of lines, coefficients of determination (r^2) and number (n) of specimens examined are also shown.

TABLE 1
Lower Miocene occurrences of high abundances of *Streptochilus* spp.

Hole	**Latitude**	**Longitude**	**Present water depth (m)**	**Size-fraction (µm)**	**Ref.**	***Streptochilus* new species names**
Atlantic Ocean						
400A	47°22'N	09°11'W	4399	>63	1	*S. rockallkiddensis*
529	28°55'S	02°46'E	3035	>63	1, 2	*S. cetacensis*
548A	48°54'N	12°09'W	1251	>74	3	*S. rockallkiddensis*
563	33°38'N	43°46'W	3786	>63	1	*S. rockallkiddensis*
608	42°50'N	23°05'W	3534	>63	4, 5	*S. rockallkiddensis*
610	53°13'N	18°53'W	2427	>63	4, 5	*S. rockallkiddensis*
667A	04°34'N	21°54'W	3529	>63	1	*S. cetacensis*
1264A, B	28°31'S	02°50'E	2505	>63	6	*S. cetacensis*
1265A	28°50'S	2°38'E	3060	>63	6	*S. cetacensis*
Indian Ocean						
237	07°05'S	58°08'E	1623	>63	7	*S. mascarenensis*
709C	03°54'S	60°33'E	3040	>63	7	*S. mascarenensis*

References: 1 = Smart and Murray (1994), 2 = Smart (1992), 3 = Poag and Low (1985), 4 = Thomas (1986), 5 = Thomas (1987), 6 = Zachos et al. (2004), 7 = Smart and Ramsay (1995).

bian Sea (e.g., Kroon and Ganssen 1989; Naidu and Niitsuma 2004). Such a habitat would be in agreement with inferences that Paleogene biserial forms generally indicate eutrophic conditions (e.g., Hallock et al. 1991; Smart and Thomas 2006).

Streptochilus was thought to be extinct when the genus was first described (Brönnimann and Resig 1971), but found to be common (up to 15%) as living forms in plankton tows south of India, where intermittent upwelling causes highly variable conditions close to the shelf edge (Kroon and Nederbragt 1990). The spatial and temporal distribution of living *Streptochilus* are poorly known because they are minute and their size fraction rarely studied. They were found as rare specimens in plankton tows in the northern Atlantic and Caribbean (Hemleben et al. 1989; Schmuker and Schiebel 2002). According to Hemleben et al. (1989), *Streptochilus globigerus* is a deep-dwelling species in highly productive, commonly coastal waters, but also occurs as rare forms in the northern Atlantic near Bermuda, where they consume diatoms, being warm-temperate forms (Hemleben et al. 1989). Schmuker and Schiebel (2002) listed *S. globigerus* as rare in the higher productivity regions of the eastern Caribbean. Miocene *Streptochilus* spp. have been described as tropical to warm-subtropical (Brönnimann and Resig 1971; Kennett and Srinivasan 1983; Resig 1989), but they are abundant in few samples (thus reflecting a limited time-range) from the northernmost Atlantic Ocean (Flower 1999) through the Bahama Bank (Kroon et al. 2000), the equatorial western Pacific (Premoli-Silva and Violanti 1981; Resig 1989) and the eastern Indian Ocean (Resig 1989).

Biserial planktic foraminifera have been said to be represented by only one living species, *Streptochilus globigerus* (Hemleben et al. 1989), but there might be more than one morphological species. Some *Streptochilus* species have a fairly smooth wall (e.g., the type species of the genus, *S. globulosus*). Others have a macroperforate, cancellate wall, with large pores inside a hexagonal system of ridges (e.g., *S. globigerus*). An extinct species, *S. subglobigerum*, was described as being partially cancellate-walled, but having smooth-walled later chambers (Resig 1989). Note that the description of macroperforate species as belonging to the genus *Streptochilus* (Hemleben et al. 1989) could be seen as problematic, since the genus is classified as microperforate (Huber et al. 2006). Kroon and Nederbragt (1990) observed living species (*Streptochilus* spp.) south of India, but they were not named, not described at the species level, and not figured. De Klasz et al. (1989) named that species *S. globulosus*, a smooth-walled species, which had been thought to have a Plio-Pleistocene range (Kennett and Srinivasan 1983; Resig 1989). In contrast, Hemleben et al. (1989) and Schmuker and Schiebel (2002) state that there is only one living species, which they call *S. globigerus*, a macroperforate species with a cancellate wall, originally said to have a Mio-Pliocene range (Kennett and Srinivasan 1983; Resig 1989). None of these authors shows a picture or includes a detailed description, and it thus is not clear whether there is one living morphological species or at least two, one smooth-walled and one cancellate. Living *Streptochilus* specimens collected in the Indian Ocean by K. Darling (pers. comm., 2005) have a cancellate wall and are macroperforate, and thus should be assigned to the species *S. globigerus*.

In conclusion, we argue that the present taxonomic status of the genus *Streptochilus* is not satisfactory, and that there is uncertainty regarding the taxonomic and/or habitat status of biserial species that have not been studied in detail. It is thus surprisingly difficult to ascertain whether biserial foraminifera are planktic or benthic based on morphology only. Most biserial planktics have more inflated chambers than benthics, and possess a wide, arched aperture without an internal toothplate, as in *Chiloguembelina.* The genus *Streptochilus,* however, is characterized by an aperture bordered by a collar, with a connecting internal plate superficially resembling the bolivinid toothplate (e.g., Huber et al. 2006), but this toothplate in *Streptochilus* does not extend freely outside the aperture (Brönnimann and Resig 1971; Resig and Kroopnick 1983; see also Smart and Thomas 2006). The name *Streptochilus* was derived from *streptos*, Greek (στρεπτοσ) for 'twisted' and *cheilos*, Greek (χειλοσ) for 'lip', indicating the change to an inward directed lip (Brönnimann and Resig 1971). The exact nature of the toothplate, however, is not easily observed in a light microscope because of the small size. In addition, in some specimens the toothplate is missing, and many published figures do not show this feature. Brönnimann and Resig (1971) did not specify a wall-type for the genus, and Resig (1989) included both smooth and cancellate-walled species in the genus. Huber et al. (2006) said that 'smooth to granular, rather than pustulose to costate surface texture' belongs to the distinguishing feature of the genus, but since they describe only the Eocene-Oligocene *S. martini* they do not discuss the exclusively Neogene cancellate wall type.

We are of the opinion that there is no solid evidence that a planktic or benthic lifestyle reflects phylogenetic relationships of biserial taxa. Non-morphological (e.g., stable isotopic) information on lifestyle, as described above, possibly should not be used in assigning biserial species to a genus, and morphology might not always be a foolproof way of defining lifestyle. Many biserial taxa have been assigned to the genera *Bolivina* or *Brizalina*, and thus are assumed to be benthic forms by definition, not because of the existence of evidence that they actually live or have lived in a benthic environment. Biserial forms thought to have been planktic have been seen as a monophyletic group, with all Cenozoic forms descended from a survivor group of the Cretaceous-Paleogene extinction (e.g., Kennett and

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PLATE 1

Scanning electron micrographs of *Streptochilus rockallkiddensis* sp. nov.; 1 holotype; 2-13 paratypes.
Note smooth wall in 2 and 4-7, and varying degrees of granular surface texture in 3, 8-13.
Note parallel-sided shape of 4-6 and 11, and tending to uniserial in 13.

1 a, Side view of holotype, reg. no. BM(NH) PF 67972, uncoated, note half of test with granular surface texture and parallel-sided shape, scale bar = 50µm; b, detail of wall, scale bar = 10µm (DSDP 94-608-37X-4, 38-40cm, 343.78 mbsf).

2-13 Side views of paratypes, all uncoated, all scale bars = 50µm;

2 reg. no. BM(NH) PF 67973, from DSDP 94-608-37X-6, 38-40cm, 346.78 mbsf

3 reg. no. BM(NH) PF 67974, from DSDP 94-608-37X-4, 38-40cm, 343.78 mbsf

4 reg. no. BM(NH) PF 67975, from DSDP 94-608-37X-6, 38-40cm, 346.78 mbsf

5 reg. no. BM(NH) PF 67976, from DSDP 94-608-37X-4, 38-40cm, 343.78 mbsf

6 reg. no. BM(NH) PF 67977, from DSDP 94-608-37X-6, 38-40cm, 346.78 mbsf

7 reg. no. BM(NH) PF 67978, from DSDP 94-608-37X-6, 38-40cm, 346.78 mbsf

8 reg. no. BM(NH) PF 67979, from DSDP 94-608-37X-6, 38-40cm, 346.78 mbsf

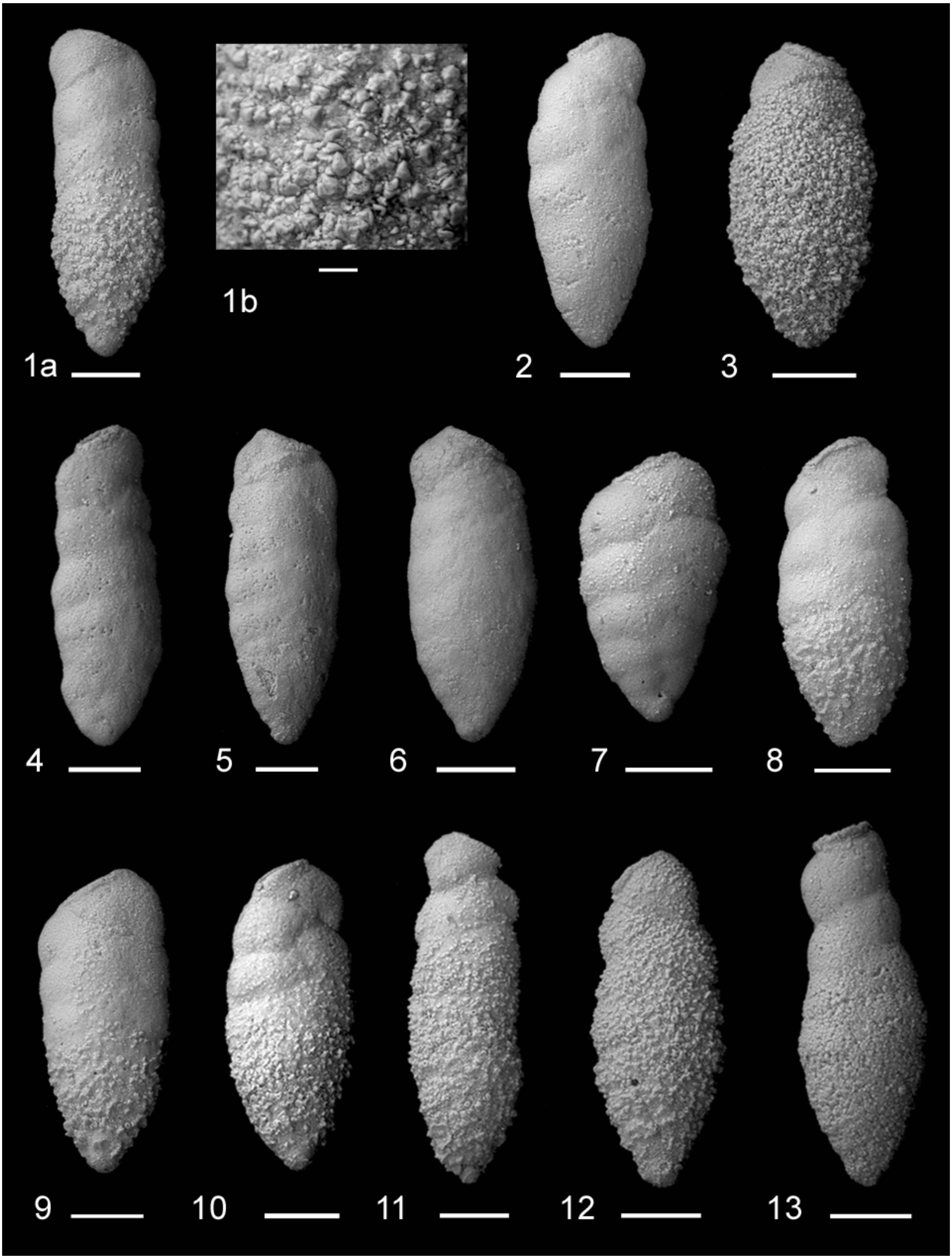
9 reg. no. BM(NH) PF 67980, from DSDP 94-608-37X-4, 38-40cm, 343.78 mbsf;

10 reg. no. BM(NH) PF 67981, from DSDP 94-608-37X-6, 38-40cm, 346.78 mbsf

11 reg. no. BM(NH) PF 67982, from DSDP 94-608-37X-6, 38-40cm, 346.78 mbsf

12 reg. no. BM(NH) PF 67983, from DSDP 94-608-37X-6, 38-40cm, 346.78 mbsf

13 reg. no. BM(NH) PF 67984, from DSDP 94-608-37X-6, 38-40cm, 346.78 mbsf.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Srinivasan 1983; De Klasz et al. 1989; Olsson et al. 1999; Huber et al. 2006). Benthic biserial specimens assigned to the genus *Bolivina*, however, are commonly seen in plankton tows (Lidz 1966; Hueni et al. 1978, D. Kroon, pers. comm.. 2005; R. Schiebel, pers. comm. 2005), and are abundant among species transported off the shelves into open ocean during storms (e.g., Brunner and Biscaye 1997). Some of the shelf dwelling *Bolivina,* e.g., *Bolivina variabilis* (Williamson 1858) have cancellate walls resembling those of *S. globigerus*, with large pores in hexagonal depressions. The exact shape of the aperture of this species and its toothplate have not been described, because the type figure of *B. variabilis* shows an aperture without a toothplate: either the figure is incorrect or the toothplate has been broken. A plesiotype at the Smithsonian Museum of Natural History (Washington DC, USA; Cushman Collection # 23807) also lacks the toothplate. This species therefore could be a *Streptochilus* rather than a *Bolivina*, with its apertural structure strongly resembling that of *Streptochilus* in photographs of some specimens assigned to this species (Murray 1971; Boltovskoy et al. 1980). Since details of toothplates have not been commonly described, biserial benthic species might have different types of toothplate, and the toothplate type described in the type species of *Streptochilus* could thus possibly occur in some benthic species. The genus *Laterostomella* has an aperture similar to that of *Streptochilus*, and at least some species placed in this genus have a macro-perforate, cancellate wall (De Klasz et al. 1989). Loeblich and Tappan (1987) considered *Laterostomella* to be a morphological synonym of *Streptochilus*, but oxygen isotope data indicate it had a benthic life style, the reason for De Klasz et al. (1989) to argue that this name can not be synonymous to the planktic *Streptochilus*.

As mentioned above, we are not fully convinced that this argument from habitat (rather than from morphology) is valid. It could be speculated that at least some bolivinids might live tychopelagically as some diatom species do, rather than exclusively as part of the benthos. If this is correct, benthic specimens of *Bolivina* swept out to the open ocean might survive and live and even reproduce within the planktic habitat, hence having a planktic lifestyle as indicated by their oxygen isotopic and trace element signature. Such bolivinids, a group generally adapted to high-food conditions (e.g., Jorissen et al., in press), would be expected to be most successful in survival in regions with a high food supply, i.e., upwelling regions. One taxonomic group (e.g., *Bolivina*) would then have either a benthic or a planktic lifestyle, depending upon the circumstances. One could go a step further in speculation, and argue that a planktic-living population could survive and evolve into a purely planktic species. In that case, there might be no close phylogenetic linkage between different biserial planktic groups, with polyphyletic evolution of planktic from benthic biserial groups occurring several times, thus explaining such a feature as the lack of biserial taxa in the late Oligocene. If such were true, taxonomic affiliation may not give clear information on planktic or benthic status. We argue that more detailed, morphological as well as stable isotopic investigations are needed, in addition to genetic investigations of

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PLATE 2

Scanning electron micrographs of *Streptochilus rockallkiddensis* sp. nov.; paratypes.

1 Side view of paratype (reg. no. BM(NH) PF 67985), uncoated, note elongate shape becoming uniserial, scale bar = 50µm (DSDP 94-608-37X-4, 38-40cm, 343.78 mbsf).

2 Side view of paratype (reg. no. BM(NH) PF 67986), uncoated, note becoming uniserial towards apertural end, scale bar = 50µm (DSDP 94-608-37X-4, 38-40cm, 343.78 mbsf).

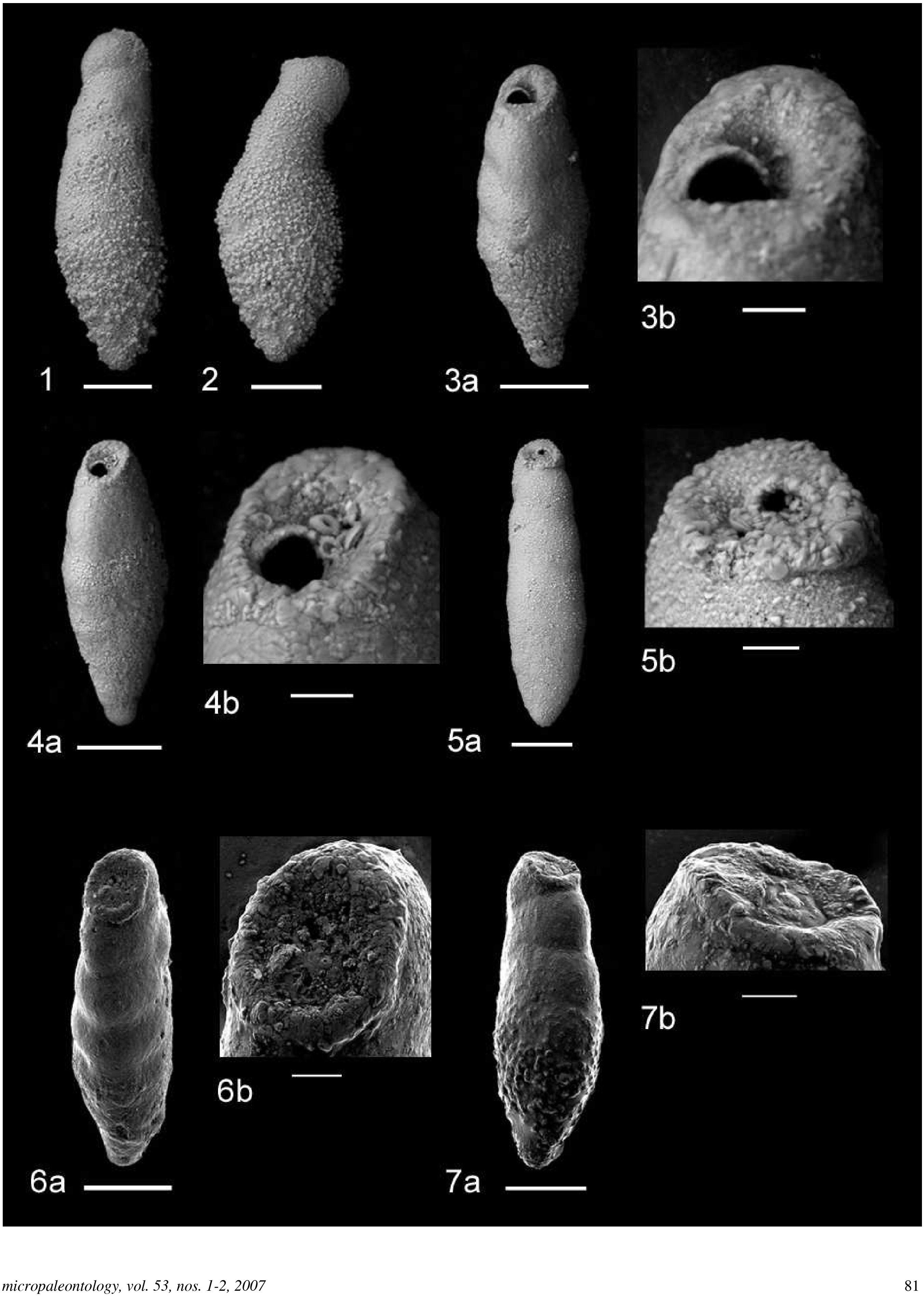
3 a, Edge view of paratype (reg. no. BM(NH) PF 67987), uncoated, showing aperture, scale bar = 50µm; b, detail of aperture showing infolded rimmed margin, scale bar = 10µm (DSDP 94-608-37X-6, 38-40cm, 346.78 mbsf).

4 a, Edge view of paratype (reg. no. BM(NH) PF 67988), uncoated, showing aperture, scale bar = 50µm; b, detail of aperture, scale bar = 10µm (DSDP 94-608-37X-6, 38-40cm, 346.78 mbsf).

5 a, Edge view of paratype (reg. no. BM(NH) PF 67989), uncoated, showing aperture, scale bar = 50µm; b, detail of aperture, note thickened rim of final chamber, scale bar = 10µm (DSDP 94-608-37X-6, 38-40cm, 346.78 mbsf).

6 a, Edge view of paratype (reg. no. BM(NH) PF 67990), gold coated, showing aperture, scale bar = 50µm; b, detail of aperture, note aperture obscured by thickening and thickened rim of final chamber, scale bar = 10µm (DSDP 94-608-37X-6, 38-40cm, 346.78 mbsf).

7 a, Oblique view of paratype (reg. no. BM(NH) PF 67991), gold coated, showing aperture, scale bar = 50µm; b, detail of aperture, note aperture obscured by thickening and thickened rim of final chamber, scale bar = 10µm (DSDP 94-608-37X-6, 38-40cm, 346.78 mbsf).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living biserial taxa, in order to solve the question of phylogenetic relations between biserial taxa, and whether biserial planktic foraminifera constitute a monophyletic group. Such information is also needed in order to solve the question whether detailed morphological information can be sufficient to determine the planktic or benthic lifestyle of biserial taxa, or whether this must be resolved by non-morphological (e.g., stable isotopic) data.

METHODS

For each sample, foraminifers were picked from the >63µm size-fraction, because *Streptochilus* spp. are absent in larger size-fractions. A random sample of specimens was chosen for size measurements. Specimen length, width and thickness were determined using a micrometer eyepiece (accuracy 10µm) fitted to a reflected-light microscope. For scanning electron microscope (SEM) analysis, specimens were mounted on small metal stubs with gummed adhesives and, in some cases, were sputter-coated with a thin layer of gold. Specimens were studied and photographed using a JEOL JSM-5600LV SEM at the University of Plymouth, UK. Gold-coated specimens were observed in high vacuum mode and uncoated specimens were examined in low vacuum mode. Specimens to be sectioned were embedded in epoxy resin and set. They were then manually polished and studied in low vacuum mode under the SEM.

Light photograph digital images were taken of various specimens by A. S. Henderson at the Natural History Museum, London. High-resolution digital photography and an image manipulation application are used to produce focused (and color) composite images of specimens. This technique (known as *PalaeoVision*), developed at the Natural History Museum, London, UK, provides detailed digital images that closely represent how the specimens look under a light microscope (e.g., Holbourn and Henderson 2002). Apart from one specimen (plate 7, fig. 11b), the specimens were too small to obtain clear focused images. All type specimens are deposited in the Department of Palaeontology, The Natural History Museum, Cromwell Road, London, UK.

SYSTEMATIC DESCRIPTIONS

The suprageneric classification scheme follows Loeblich and Tappan (1992).

Class FORAMINIFEREA Lee 1990
Order GLOBIGERINIDA Lankester 1885 (as Globigerinidea; nom. corr. Calkins 1909)
Superfamily HETEROHELICACEA Cushman 1927
Family CHILOGUEMBELINIDAE Reiss 1963

Genus ***Streptochilus*** Brönnimann and Resig 1971, emend. Smart and Thomas this paper

We propose that the original description of *Streptochilus* given by Brönnimann and Resig (1971) should be emended as follows, due to features of the new species *S. rockallkiddensis* (see below), i.e. the test may become staggered uniserial, and the aperture may be obscured by a thickening of the wall including the rim of the aperture:

PLATE 3

Scanning electron micrographs of *Streptochilus rockallkiddensis* sp. nov.; paratypes.

1 a, Oblique view of paratype (reg. no. BM(NH) PF 67992), gold coated, showing aperture, scale bar = 50µm; b, detail of aperture, note aperture obscured by thickening and thickened rim of final chamber, scale bar = 10µm (DSDP 94-608-37X-6, 38-40cm, 346.78 mbsf).

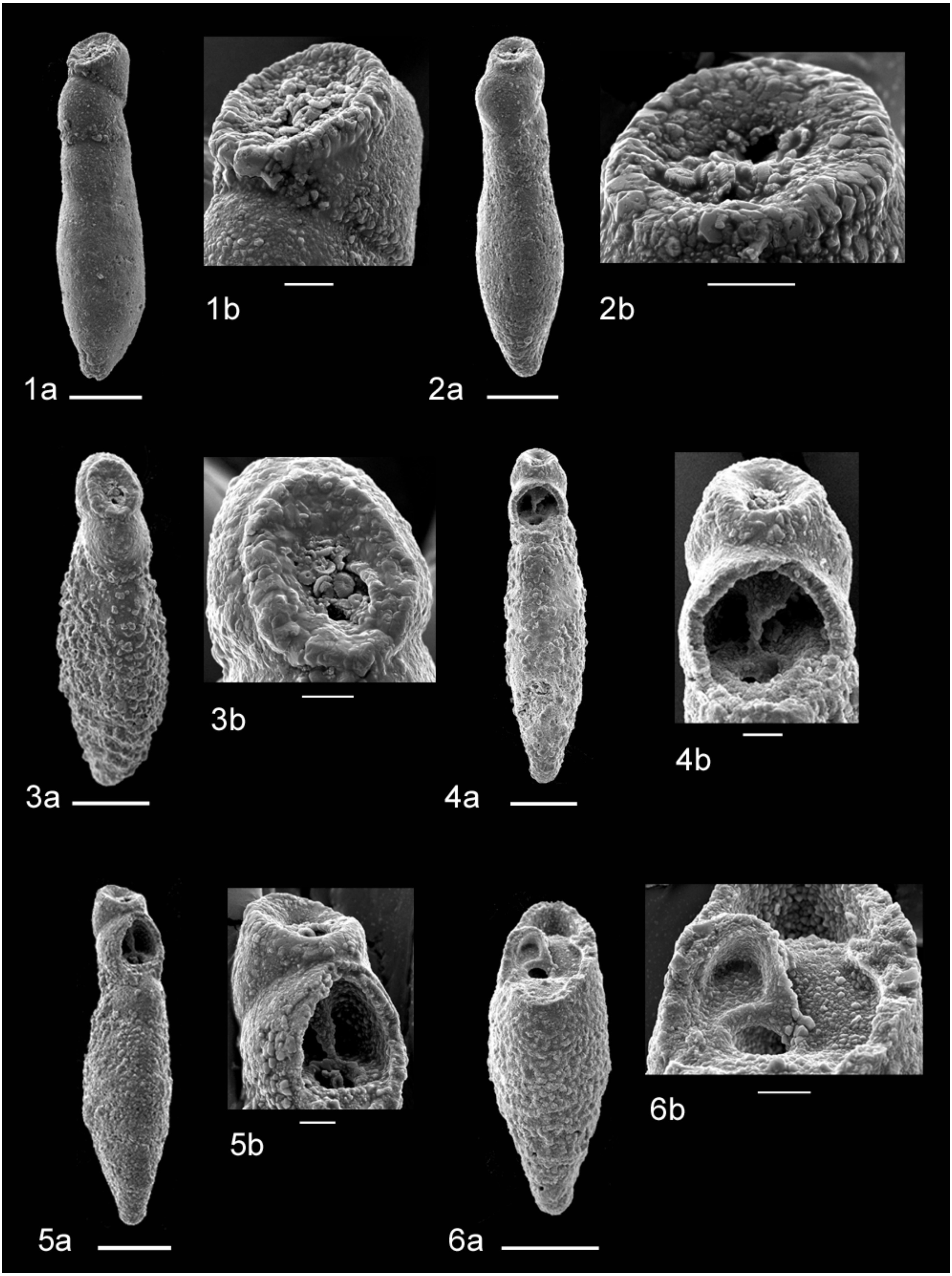
2 a, Edge view of paratype (reg. no. BM(NH) PF 67993), gold coated, showing aperture, scale bar = 50µm; b, detail of aperture, note aperture obscured somewhat by thickening and thickened rim of final chamber, scale bar = 10µm (DSDP 94-608-37X-6, 38-40cm, 346.78 mbsf).

3 a, Edge view of paratype (reg. no. BM(NH) PF 67994), gold coated showing aperture, note slight twisting, scale bar = 50µm; b, detail of aperture, note thickened rim of final chamber, scale bar = 10µm (DSDP 94-608-37X-6, 38-40cm, 346.78 mbsf).

4 a, Edge view of paratype (reg. no. BM(NH) PF 67995), dissected specimen, gold coated, scale bar = 50µm; b, detail of aperture, note internal plate connecting with apertural rim, scale bar = 10µm (DSDP 94-608-37X-6, 38-40cm, 346.78 mbsf).

5 a, Oblique view of paratype (reg. no. BM(NH) PF 67996), dissected specimen, gold coated, scale bar = 50µm; b, detail of aperture, note internal plate connecting with apertural rim, scale bar = 10µm (DSDP 94-608-37X-6, 38-40cm, 346.78 mbsf).

6 a, Edge view of paratype (reg. no. BM(NH) PF 67997), dissected specimen, gold coated, scale bar = 50µm; b, detail of aperture, note internal plate connecting with apertural rim, scale bar = 10µm (DSDP 94-608-37X-6, 38-40cm, 346.78 mbsf).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Test biserial, may become staggered uniserial, sometimes twisted; wall calcareous, perforate; aperture a high arch, eccentric in position, extending from the base of the last chamber onto the apertural face. On the outside margin, a collar borders the aperture. Near the base of the inside margin, the collar and apertural edge are turned inward, producing a plate-like connection with the proximal margin of the collar of the previous aperture. Aperture may be obscured by a thickening of the wall including the rim of the aperture. The length of the test varies between 75 and 300µm.

Streptochilus rockallkiddensis Smart and Thomas **n. sp.**
Plates 1-5

Bolivina sp. 9 – POAG and LOW 1985, pl. 1, figs. 16-18
Bolivina spathulata (Williamson). – THOMAS 1987, Tables 1-2
Bolivina sp. – SMART AND MURRAY 1994, fig. 2, no. 1. – SMART and RAMSAY 1995, fig. 2

Diagnosis. Test small, elongate, laterally slightly compressed, biserial becoming staggered uniserial, commonly rectilinear and often narrower towards apertural end, aperture with thickened rim and often obscured, surface ornamentation varying from smooth to granular.

Description. Test small, elongate, laterally slightly compressed, periphery rounded and non-lobulate, shape variable, commonly elongate, parallel-sided and rectilinear, occasionally flared, in some elongate specimens the later formed part of the test may narrow towards the apertural end, biserial tending to staggered uniserial in some elongate specimens, rarely twisted; most specimens have 6 pairs of chambers but the number of pairs varies from 5-8 or more, chambers increase regularly in size as added, slightly wider than high, initial chambers small and often obscured by granular surface ornamentation; sutures slightly curved and depressed; final chamber often has thickened rim; aperture low-arch shaped, offset to one side of test, with an internal plate formed by the infolding and downward extension of one margin of the rimmed aperture, often small and obscured by thickening; wall uniformly very finely perforate, surface ornamentation varies from smooth to finely granular to coarsely granular and, where present, ornamentation constitutes half or more of the test occurring from proloculus towards apertural end; no obvious differences between micro- and megalospheric specimens.

Dimensions. Length, 260-130µm (mean 187µm, St. Dev. 28, n = 115); maximum width, 100-70µm (mean 84 µm, St. Dev. 6, n = 115); thickness, 70-60µm (mean 63 µm, St. Dev. 4, n = 20).

Etymology. Named after the area where it has been found, i.e. Rockall Plateau, NE Atlantic Ocean and in honor of the late Professor Robert B. Kidd (1947-1996), a marine geologist and colleague who was one of the co-chief scientists on DSDP Leg 94 responsible for drilling DSDP Site 608, the site from which the highest abundances of the species have been reported to date.

Type locality and distribution. Lower Miocene, NE Atlantic Ocean, DSDP Site 608. Also reported from North Atlantic DSDP Sites 400, 548, 563 and 610 (Table 1).

Type specimens. The figured holotype, figured paratypes and unfigured paratypes are deposited in the Department of Palaeontology, The Natural History Museum, Cromwell Road, London, UK. The holotype (reg. no. BM(NH) PF 67972) is from DSDP 94-608-37X-4, 38-40cm, 343.78 mbsf [Deep Sea Drilling Project Leg-Hole-Core-Section-Interval, meters below sea floor] (Plate 1, Fig. 1a,b). All other examined and illustrated

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PLATE 4

Scanning electron micrographs of *Streptochilus rockallkiddensis* sp. nov.; paratypes.

1 a, Edge view of paratype (reg. no. BM(NH) PF 67998), dissected specimen, gold coated, scale bar = 50µm; b, detail of aperture, note internal plate connecting with apertural rim, scale bar = 10µm (DSDP 94-608-37X-6, 38-40cm, 346.78 mbsf).

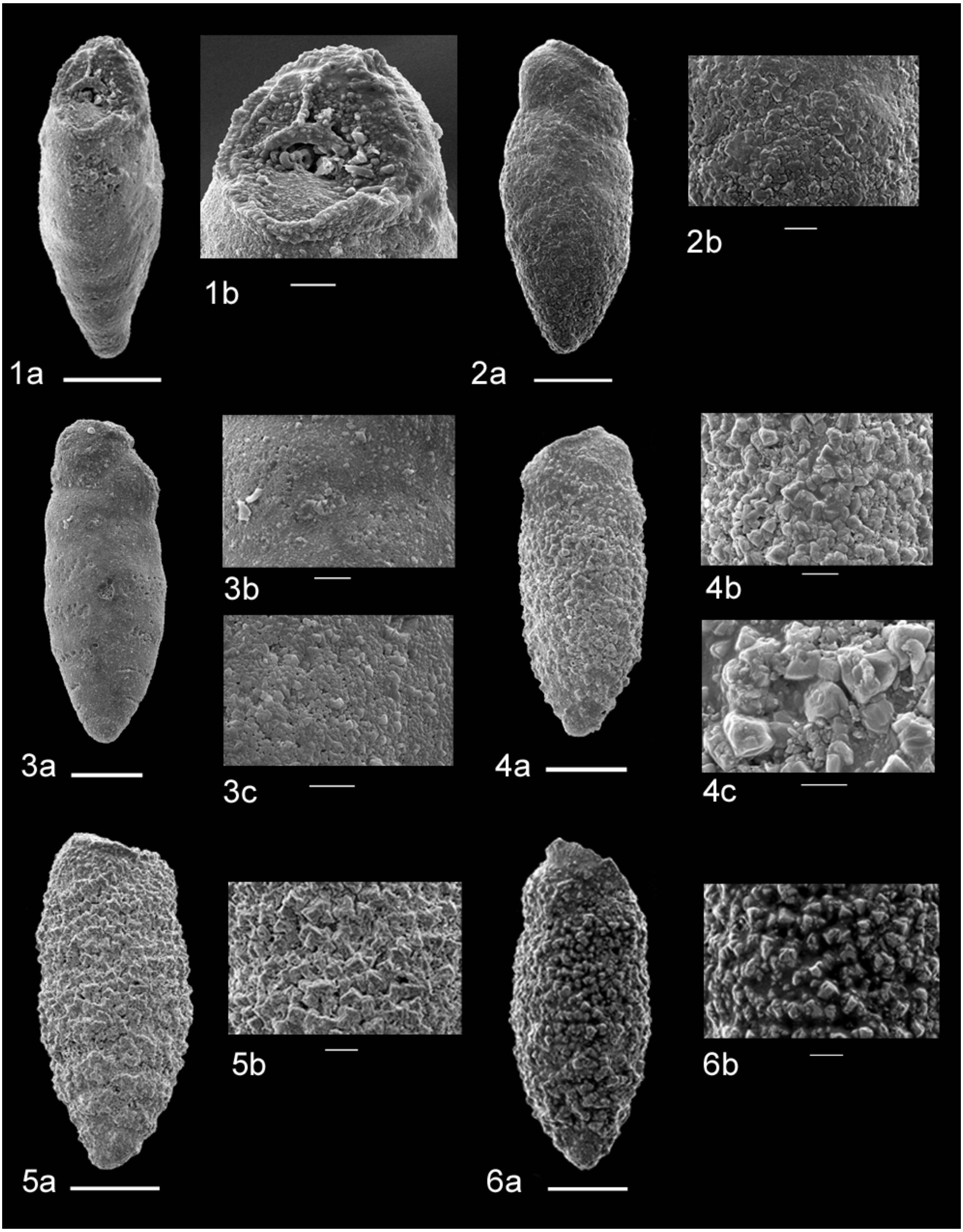
2 a, Side view of paratype (reg. no. BM(NH) PF 67999), gold coated, note smooth wall, scale bar = 50µm; b, detail of wall, scale bar = 10µm (DSDP 94-608-37X-6, 38-40cm, 346.78 mbsf).

3 a, Side view of paratype (reg. no. BM(NH) PF 68000), gold coated, note smooth wall, scale bar = 50µm; b, detail of wall, scale bar = 10µm; c, greater detail of wall showing fine pores, scale bar = 5µm (DSDP 94-608-37X-6, 38-40cm, 346.78 mbsf).

4 a, Side view of paratype (reg. no. BM(NH) PF 68001), gold coated, note coarse granular wall texture, scale bar = 50µm; b, detail of wall, scale bar = 10µm; c, greater detail of wall, scale bar = 5µm (DSDP 94-608-37X-6, 38-40cm, 346.78 mbsf).

5 a, Side view of paratype (reg. no. BM(NH) PF 68002), gold coated, note granular wall texture, scale bar = 50µm; b, detail of wall, scale bar = 10µm (DSDP 94-608-37X-6, 38-40cm, 346.78 mbsf).

6 a, Side view of paratype (reg. no. BM(NH) PF 68003), gold coated, note granular wall texture, scale bar = 50µm; b, detail of wall, scale bar = 10µm (DSDP 94-608-37X-6, 38-40cm, 346.78 mbsf).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specimens are designated paratypes (reg. no. BM(NH) PF 67973-68061, BM(NH) PF 68192-68221) and are from DSDP 94-608-37X-4, 38-40cm, 343.78 mbsf; DSDP 94-608-37X-6, 38-40cm, 346.78 mbsf; and DSDP 82-563-11-5, 19-21cm, 257.69 mbsf (Plate 1, Figs. 2-13; Plates 2-5).

Remarks. The granular surface texture displayed by a high proportion of specimens can be difficult to discern under a light microscope, but becomes clear when specimens are viewed under a SEM. The degree of roughness of the test varies from specimen to specimen and from sample to sample. In the specimens examined from Site 608, the percentage of roughened specimens varies from ~68% (sample DSDP 608-37X-4, 38-40cm, n = 110) to ~37% (sample DSDP 608-37X-6, 38-40cm, n = 115). Specimens from DSDP Sites 400 and 563 often have a roughened appearance. Typically the roughened appearance makes up half of the test, although in some specimens this may be one-third, two-thirds, three-quarters or more of the test. The number of parallel-sided and flared tests varies between specimens and between samples, although parallel-sided individuals are generally more common. The roughened appearance obscures the chambers, although these are discernible when specimen is wetted.

Streptochilus rockallkiddensis sp. nov. closely resembles *Bolivina* sp. 9 of Poag and Low (1985, pl. 1, figs 16, 17, 18) reported from DSDP Site 548. Their illustrations clearly show the variability of test roughness ranging from smooth (pl. 1, fig. 16), to one-third roughened (pl. 1, fig. 17) to three-quarters roughened (pl. 1, fig. 18).

Thomas (1986, 1987) referred to *Streptochilus rockallkiddensis* sp. nov. as *Bolivina spathulata* (Williamson). A specimen from Site 563 has been illustrated in Smart and Murray (1994, Fig. 2, 1) and Smart and Ramsay (1995, Fig. 2). For a description of the differences between the three new Miocene *Streptochilus* spp., see differential analysis (below).

Streptochilus cetacensis Smart and Thomas **n. sp.**
Plates 6-11

Bolivina sp. – SMART and MURRAY 1994, fig. 2, no. 2, – SMART and RAMSAY 1995, fig. 2
Streptochilus sp. – SMART and THOMAS 2006, fig. 2, A, B

Diagnosis. Test elongate, laterally slightly compressed, flared and typically 'triangular' in shape with curved and depressed sutures, with many specimens covered with evenly distributed pores.

Description. Test small to medium sized, elongate, increasing regularly in size, flared and typically 'triangular' in shape, laterally slightly compressed, periphery broadly rounded to somewhat lobulate, sometimes twisted, biserial; 5-8 pairs of chambers, slightly inflated, wider than high, increasing regularly in size as added; sutures curved and depressed; aperture high arch-shaped, offset slightly to one side of test, extending from the base of the last chamber onto apertural face, bordered by a thickened rim/collar along the top and outer side of the arch, the opposite side is turned inward to a plate connecting with the top of the collar and the inturned portion of the preceding foramen; wall smooth to finely granular, commonly affected by dissolution, finely perforate although mostly obscured by dissolution, chambers often show numerous, small pores evenly distributed over test, in some specimens enlarged by dissolution; no obvious differences between micro- and megalospheric specimens.

Dimensions. Specimens at the two sites (529 and 1264) on Walvis Ridge: length, 300-120µm (mean 188µm, St. Dev. 39, n = 249); maximum width, 180-80µm (mean 114µm, St. Dev. 19,

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PLATE 5

Scanning electron micrographs of *Streptochilus rockallkiddensis* sp. nov.; paratypes.

1 a, Side view of paratype (reg. no. BM(NH) PF 68004), gold coated, note granular wall texture, scale bar = 50µm; b, detail of wall, scale bar = 10µm (DSDP 94-608-37X-6, 38-40cm, 346.78 mbsf).

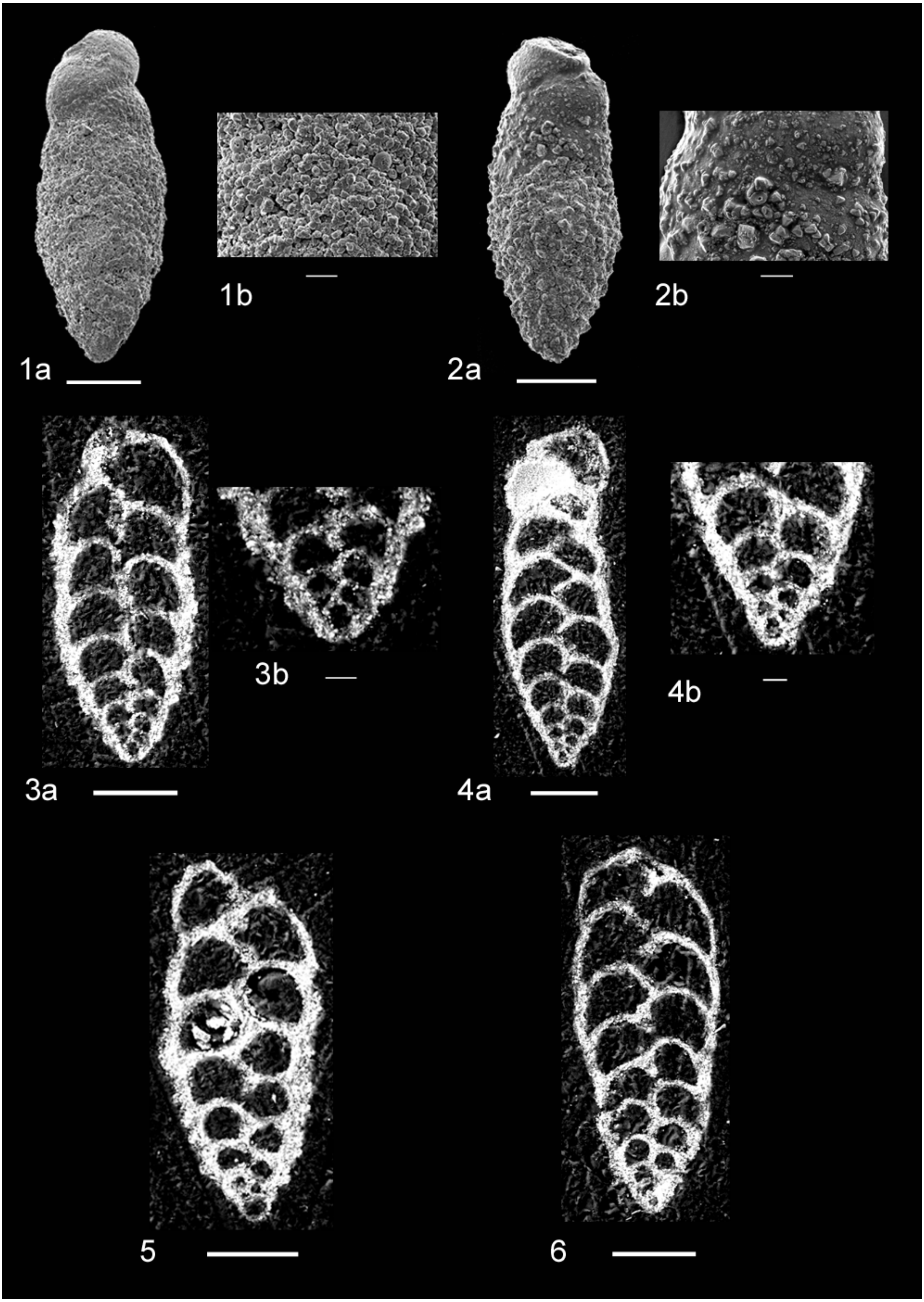
2 a, Side view of paratype (reg. no. BM(NH) PF 68005), gold coated, note granular wall texture, scale bar = 50µm; b, detail of wall, scale bar = 10µm (DSDP 94-608-37X-6, 38-40cm, 346.78 mbsf).

3 a, Side view of paratype (reg. no. BM(NH) PF 68204), polished microspheric specimen, uncoated, scale bar = 50µm; b, detail of initial part, scale bar = 10µm (DSDP 94-608-37X-4, 38-40cm, 343.78 mbsf).

4 a, Side view of paratype (reg. no. BM(NH) PF 68206), polished microspheric specimen, uncoated, scale bar = 50µm; b, detail of initial part, scale bar = 10µm (DSDP 94-608-37X-4, 38-40cm, 343.78 mbsf).

5 Side view of paratype (reg. no. BM(NH) PF 68200), polished megalospheric specimen, uncoated, scale bar = 50µm (DSDP 94-608-37X-4, 38-40cm, 343.78 mbsf).

6 Side view of paratype (reg. no. BM(NH) PF 68203), polished microspheric specimen, uncoated, scale bar = 50µm (DSDP 94-608-37X-4, 38-40cm, 343.78 mbsf).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n = 249); thickness, 75-50µm (mean 62 µm, St. Dev. 6, n = 40). Specimens at Site 667: length, 230-120µm (mean 157µm, St. Dev. 21, n = 105); maximum width, 120-80 µm (mean 91 µm, St. Dev. 10, n = 105); thickness, 65-45 µm (mean 55 µm, St. Dev. 6, n = 20).

Etymology. Named after the Latin for a large marine animal such as a whale, *cetus*, after the area where it has been found (Walvis Ridge [Walvis = Dutch for whale], SE Atlantic Ocean, ODP Sites 1264 and 1265 and DSDP Site 529).

Type locality and distribution. Lower Miocene, SE Atlantic Ocean, ODP Site 1264 (Table 1); equatorial Atlantic Ocean, ODP Site 667.

Type specimens. The figured holotype, figured paratypes and unfigured paratypes are deposited in the Department of Palaeontology, The Natural History Museum, Cromwell Road, London, UK. The holotype (reg. no. BM(NH) PF 68062) is from ODP 208-1264B-21-1, 78-80cm, 210.60 mcd [Ocean Drilling Program Leg-Hole-Core-Section-Interval, meters coring depth] (Plate 6, Fig. 1a,b). All other examined and illustrated specimens are designated paratypes (reg. no. BM(NH) PF 68063-68151, BM(NH) PF 68222-68251) and are from ODP 208-1264B-21-1, 78-80cm, 210.60 mcd; DSDP 74-529-8-4, 72-74cm, 70.72 mbsf [Deep Sea Drilling Project Leg-Hole-Core-Section-Interval, meters below sea floor]; DSDP 74-529-8-3, 74-76cm, 69.24 mbsf; and ODP 108-667A-22H-7, 6-8cm, 200.36 mbsf (Plate 6, Figs. 2-11; Plates 7-11).

Remarks. Dissolution of tests commonly obscures detail; fine pores observable in later chambers unaffected by dissolution. Specimen size is variable with some specimens being relatively large, e.g., in sample DSDP 74-529-8-3, 74-76cm (69.24 mbsf) the size of the specimens examined was: length, 300-130µm (mean 211µm, St. Dev. 38, n = 62); maximum width, 180-80µm (mean 131µm, St. Dev. 19, n = 62). In contrast, specimens in sample DSDP 74-529-8-4, 72-74cm (70.72 mbsf) were consistently smaller: length, 260-130µm (mean 168µm, St. Dev. 29, n = 69); maximum width, 140-80µm (mean 107µm, St. Dev. 17, n = 69). Specimens from Site 667 (equatorial Atlantic Ocean) are overall smaller (text-fig. 3d) than those from the Walvis Ridge sites, and tend to have pores over all chambers of the test. We have included specimens from this location in *S. cetacensis* because they resemble the specimens from Walvis Ridge strongly, and the differences in size and pore distribution and size might be due to differential dissolution. Detailed morphological information from more locations is necessary in order to evaluate whether the equatorial group could be a different morphological species, or whether the variability is within the intra-group morphological variability of the species within the larger geographic region.

Streptochilus cetacensis sp. nov. resembles *Streptochilus* sp. aff. *S. martini* (Pijpers) as illustrated in Poore and Gosnell (1985; Plate 1, figs. 8-16). *Streptochilus cetacensis* resembles *Streptochilus globulosum* (Cushman), but the latter is much more globose. Originally, the size of the holotype (Holotype USNM26172 in the Smithsonian Museum of Natural History, USA) was given as: length, 700µm; width, 400µm; thickness, 150µm (Cushman 1933), which would have been much larger than our species, but these measurements were incorrect; the size of the holotype is length, 300µm and width, 130µm (Cushman et al. 1954), as checked by E. Thomas. For a description of the differences between the three new Miocene *Streptochilus* spp., see differential analysis (below).

Streptochilus mascarenensis Smart and Thomas **n. sp.**
Plates 12-13

PLATE 6

Scanning electron micrographs of *Streptochilus cetacensis* sp. nov.; 1 holotype, 2-11 paratypes.
All specimens are from ODP 208-1264B-21-1, 78-80cm, 210.60 mcd.

1 a, Side view of holotype, reg. no. BM(NH) PF 68062, uncoated, scale bar = 50µm; b, detail of wall, scale bar = 10µm (ODP 208-1264B-21-1, 78-80cm, 210.60 mcd);

2-11 Side views of paratypes, uncoated, all scale bars = 50µm

2 reg. no. BM(NH) PF 68063;

3 reg. no. BM(NH) PF 68064;

4 reg. no. BM(NH) PF 68065, slightly curved specimen;

5 reg. no. BM(NH) PF 68066;

6 reg. no. BM(NH) PF 68067;

7 reg. no. BM(NH) PF 68068;

8 reg. no. BM(NH) PF 68069;

9 reg. no. BM(NH) PF 68070;

10 reg. no. BM(NH) PF 68071, slightly curved specimen;

11 reg. no. BM(NH) PF 68072, slightly curved specimen.


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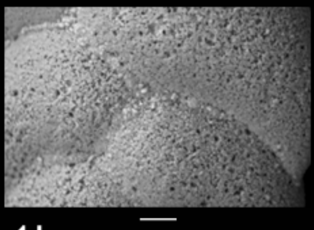
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Bolivina sp. – SMART 2002, fig. 3.1, no. 2
Streptochilus sp. – SMART and THOMAS 2006, fig. 2, C, D

Diagnosis. Test small, elongate, laterally compressed, commonly flared with distinct chambers and curved and depressed sutures.

Description. Test small, elongate, increasing regularly in size, flared and occasionally almost parallel-sided, laterally compressed, periphery broadly rounded and lobulate, rarely twisted, biserial; 5-7 pairs of chambers, wider than high, increasing gradually in size as added; sutures distinct, curved and slightly depressed; aperture high arch-shaped, offset slightly to one side of test, extending from the base of the last chamber onto apertural face, bordered by a thickened rim/collar along the top and outer side of the arch, the opposite side is turned inward to a plate connecting with the top of the collar and the inturned portion of the preceding foramen; wall smooth to finely granular, very finely perforate; no obvious differences between micro- and megalospheric specimens.

Dimensions. Length, 260-110µm (mean 169µm, St. Dev. 30, n = 106); maximum width, 120-80µm (mean 98µm, St. Dev. 8, n = 106); thickness, 60-45µm (mean 50µm, St. Dev. 3, n = 20).

Etymology. Named after the area where it has been found, i.e. the Mascarene Plateau, NW Indian Ocean (DSDP Site 237).

Type locality and distribution. Lower Miocene, NW Indian Ocean, DSDP Site 237 (Table 1). Also reported from ODP Site 709.

Type specimens. The figured holotype, figured paratypes and unfigured paratypes are deposited in the Department of Palaeontology, The Natural History Museum, Cromwell Road, London, UK. The holotype (reg. no. BM(NH) PF 68152) is from DSDP 24-237-18-6, 69-71cm, 166.69 mbsf [Deep Sea Drilling Project Leg-Hole-Core-Section-Interval, meters below sea floor] (Plate 12, Figs. 1a,b,c). All other examined and illustrated specimens are designated paratypes (reg. no. BM(NH) PF 68153-68191, BM(NH) PF 68252-68279) and are from DSDP 24-237-18-3, 72-74cm, 162.22 mbsf; and DSDP 24-237-18-6, 69-71cm, 166.69 mbsf (Plate 12, Figs. 2-8; Plate 13).

Remarks. *Streptochilus mascarenensis* sp. nov. was called *Bolivina* sp. and specimens from DSDP Site 237 are illustrated in Smart (2002, Fig. 3.1, 2) and Smart and Thomas (2006, fig. 2, C, D). For a description of the differences between the three new Miocene *Streptochilus* spp., see differential analysis (below).

DIFFERENTIAL ANALYSIS

Early Miocene *Streptochilus* spp. occurred coevally at various sites in the Atlantic and Indian Oceans, but the species differ morphologically from site to site. *Streptochilus rockallkiddensis* sp. nov. is the most variable species and differs from all other species in its typically parallel-sided/rectilinear shape which often narrows towards the apertural end, the tendency to become staggered uniserial, and thickening of the wall including the rim of the aperture which may obscure the aperture. The variability of surface ornamentation is a feature of this species which varies from smooth to granular, the granular nature constituting typically half or more of the test occurring from proloculus to apertural end.

Streptochilus mascarenensis sp. nov. closely resembles *Streptochilus cetacensis*, but *Streptochilus mascarenensis* sp. nov. is consistently more laterally compressed (thickness 50µm compared with 62µm), its periphery is more lobulate, and its pores are smaller. *Streptochilus cetacensis* sp. nov. is typically 'triangular' in shape and flared, and is clearly different from *S.*

PLATE 7

Scanning electron micrographs of *Streptochilus cetacensis* sp. nov.; paratypes.

1 Side view of paratype (reg. no. BM(NH) PF 68073), uncoated, slightly twisted specimen, scale bar = 50µm (ODP 208-1264B-21-1, 78-80cm, 210.60 mcd).

2 Side view of paratype (reg. no. BM(NH) PF 68074), uncoated, twisted specimen, scale bar = 50µm (ODP 208-1264B-21-1, 78-80cm, 210.60 mcd).

3-11 Side views of paratypes, all uncoated, all scale bars = 50µm;

3 reg. no. BM(NH) PF 68075, from DSDP 74-529-8-4, 72-74cm, 70.72 mbsf;

4 reg. no. BM(NH) PF 68076, from DSDP 74-529-8-4, 72-74cm, 70.72 mbsf;

5 slightly twisted specimen, reg. no. BM(NH) PF 68077, from DSDP 74-529-8-4, 72-74cm, 70.72 mbsf;

6 reg. no. BM(NH) PF 68078, from DSDP 74-529-8-4, 72-74cm, 70.72 mbsf;

7 reg. no. BM(NH) PF 68079, from DSDP 74-529-8-4, 72-74cm, 70.72 mbsf;

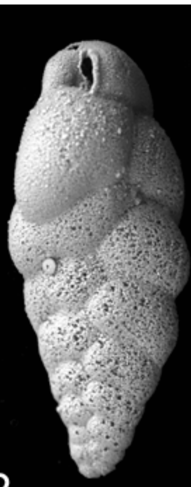
8 reg. no. BM(NH) PF 68080, from DSDP 74-529-8-3, 74-76cm, 69.24 mbsf;

9 reg. no. BM(NH) PF 68081, from DSDP 74-529-8-3, 74-76cm, 69.24 mbsf;

10 curved specimen, reg. no. BM(NH) PF 68082, from DSDP 74-529-8-4, 72-74cm, 70.72 mbsf;

11 a, SEM micrograph and b, light photograph (using *PalaeoVision* System) of same specimen; reg. no. BM(NH) PF 68083, from DSDP 74-529-8-4, 72-74cm, 70.72 mbsf.


1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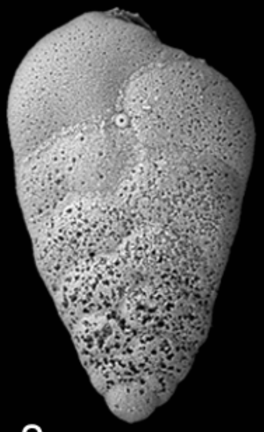
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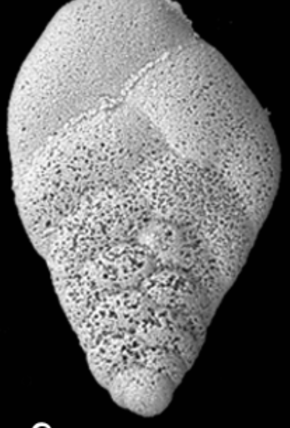
9


10


11a


11b

rockallkiddensis sp. nov. (text-fig. 3). Specimens of *S. cetacensis* at Site 667 are overall smaller than those from the southeastern Atlantic (Sites 529 and 1264) (text-fig. 3), and have distinctive pores over all chambers of the test. The differences in pore distribution and size of *S. cetacensis* between the equatorial Atlantic specimens (Site 667) and southeastern Atlantic specimens might be due to differential dissolution. *Streptochilus cetacensis* sp. nov. closely resembles *S. mascarenensis* sp. nov., but *S. cetacensis* sp. nov. is consistently less laterally compressed (thickness 62μm compared with 50μm), becomes thicker towards the apertural end, its periphery is less lobulate, and is more 'triangular' in shape. *S. mascarenensis* sp. nov. is clearly different from *S. rockallkiddensis* sp. nov. in its general shape, its more pronounced chambers, and absence of a coarsely roughened test. For all three new species, differentiating between microspheric and megalospheric specimens in non-sectioned specimens is often unclear and speculative, although in sectioned/polished specimens it is possible to distinguish between specimens that have relatively small (microspheric) or large (megalospheric) proloculi.

CONCLUSIONS

Several morphological species of *Streptochilus* (Foraminifera) occur in the lower Miocene in the eastern Atlantic and western Indian Oceans (18.9-17.2 Ma in the Lourens et al. 2004 time scale; 19.3-17.6 Ma in the Berggren et al. 1995 time scale). They had previously been assigned to the benthic genus *Bolivina*, but evidence on their apertural morphology, together with accumulation rate data and isotopic composition show that they lived as plankton, and should be assigned to the planktic genus *Streptochilus* (Smart and Thomas 2006). Three new species are described, illustrated and named: *S. rockallkiddensis* sp. nov. (from the northeastern Atlantic), *S. cetacensis* sp. nov. (from the equatorial and southeastern Atlantic), and *S. mascarenensis* sp. nov. (from the western equatorial Indian Oceans). The description of the genus *Streptochilus* is emended to include the observation that in some specimens of *S. rockallkiddensis* sp. nov. the test occasionally becomes staggered uniserial, typically parallel-sided/rectilinear in shape and the aperture is often obscured by a thickening of the wall including the rim of the aperture. The three species occurred in different regions of the oceans during the same short period of time (18.9-17.2 Ma) which suggests that they may have evolved (either from biserial planktic or from benthic ancestors) polyphyletically. If they evolved from benthic ancestors, e.g., from specimens swept out to sea during storms, their evolution may have been made possible by relatively eutrophic conditions in the surface waters (Smart and Thomas 2006), during which there were high algal growth rates but low transport efficiency of organic matter to the sea floor, possibly in a deep thermocline. There are no modern analog environments over such large areas of the eastern Atlantic and western Indian Oceans.

ACKNOWLEDGMENTS

CWS gratefully acknowledges financial support from a NERC/UK IODP Rapid Response Award. This research used samples provided by the Ocean Drilling Program (ODP). The ODP was sponsored by the US National Science Foundation (NSF) and participating countries (including the UK) under the management of the Joint Oceanographic Institutions (JOI), Inc. CWS would like to thank Roy Moate, Peter Bond and Glenn Harper (EM Unit, University of Plymouth, UK) for their assistance in scanning electron microscopy. ET recognizes funding by the USSSP for post-cruise research related to Leg 208. Thanks also go to Andy Henderson (Natural History Museum,

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PLATE 8

Scanning electron micrographs of *Streptochilus cetacensis* sp. nov.; paratypes.

1 a, Edge view of paratype (reg. no. BM(NH) PF 68084), uncoated, scale bar = 50μm; b, detail of aperture showing infolded rimmed margin, scale bar = 10μm (DSDP 74-529-8-4, 72-74cm, 70.72 mbsf).

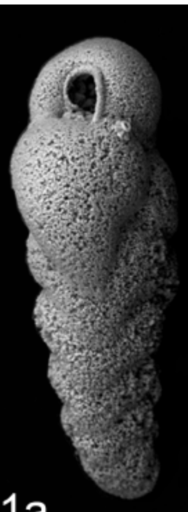
2 a, Oblique view of paratype (reg. no. BM(NH) PF 68085), uncoated, scale bar = 50μm; b, detail of aperture showing rimmed margin, scale bar = 10μm (DSDP 74-529-8-4, 72-74cm, 70.72 mbsf).

3 a, Oblique view of paratype (reg. no. BM(NH) PF 68086), gold coated, scale bar = 50μm; b, detail of aperture showing infolded rimmed margin, scale bar = 10μm; c, detail of wall showing fine granular texture and small pores, scale bar = 10μm (ODP 208-1264B-21-1, 78-80cm, 210.60 mcd).

4 a, Edge view of paratype (reg. no. BM(NH) PF 68087), dissected specimen, gold coated, scale bar = 50μm; b, detail of aperture, note internal plate connecting with apertural rim, scale bar = 10μm (ODP 208-1264B-21-1, 78-80cm, 210.60 mcd).

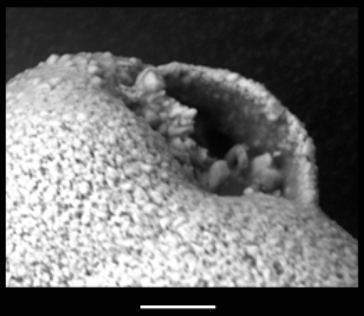
5 a, Oblique view of paratype (reg. no. BM(NH) PF 68088), dissected specimen, gold coated, scale bar = 50μm; b, detail of aperture, note internal plate connecting with apertural rim, scale bar = 10μm (ODP 208-1264B-21-1, 78-80cm, 210.60 mcd).

6 a, Side view of paratype (reg. no. BM(NH) PF 68089), uncoated, scale bar = 50μm; b, detail of wall showing fine granular texture and small pores, scale bar = 10μm (ODP 208-1264B-21-1, 78-80cm, 210.60 mcd).


1a


1b


2a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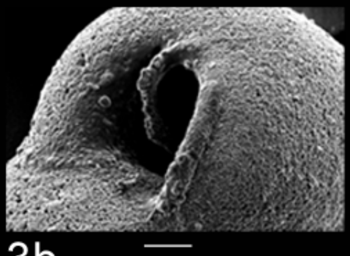
3a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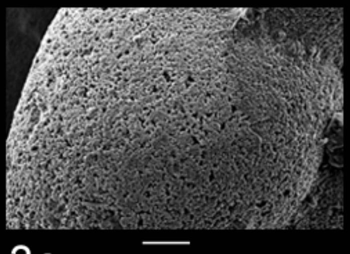
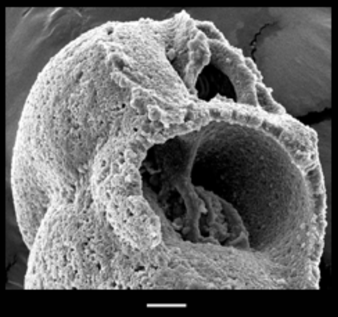

3c

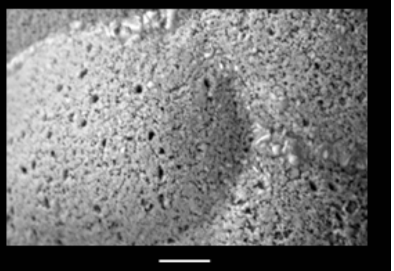

4a


4b


5a


5b


6a


6b

London) for carrying out the *PalaeoVision* images. Stefan Revets is thanked for his constructive comments on an earlier version of the manuscript. We also thank Brian Huber and Dick Olsson for their helpful comments.

REFERENCES

ABELS, H. A., HILGEN, F. J., KRIJGSMAN, W., KRUK, R. W., RAFFI, I., TURCO, E., and ZACHARIASSE, W. J., 2005. Long-period orbital control on middle Miocene global cooling: integrated stratigraphy and stronomical tuning of the Blue Clay Formation on Malta. *Paleoceanography* 20: PA4012, doi: 10.1029/2004PA001129.

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*, 20, PA3011, doi: 10.1029/2004PA001082

BALDAUF, J. G. and BARRON, J. A., 1990, Evolution of biosiliceous sedimentation patterns – Eocene through Quaternary: paleoceanographic response to polar cooling. In: Bleil, U. and Thiede, J., Eds., *Geological History of the Polar Ocean: Arctic versus Antarctic*, 575-607. Kluwer Academic Publishers, Dordrecht, Netherlands.

BARKER, P.F. and THOMAS, E., 2004. Origin, signature and palaeoclimatic influence of the Antarctic Circumpolar Current. *Earth Science Reviews*, 66: 143-162.

BERGGREN, W.A., KENT, D.V., SWISHER, C. C., III and AUBRY, M.-P., 1995. A revised Cenozoic geochronology and chronostratigraphy. In: Berggren, W.A., Kent, DV., Aubry, M.-P. and Hardenbol, J., Eds., *Geochronology, time scales and global stratigraphic correlation*, 129-212. SEPM Special Publication, 54.

BERNHARD, J. M., 1986. Characteristic assemblages and morphologies of benthic foraminifera from anoxic, organic-rich deposits. *Journal of Foraminiferal Research*, 16: 207-215.

BERNHARD, J. M. and SEN GUPTA, B.K., 1999. Foraminifera of oxygen-depleted environments. In: Sen Gupta, B.K., Ed., *Modern Foraminifera*, 141-160. Dordrecht: Kluwer Academic Publishers.

BOLTOVSKOY, E., GIUSSANI, G.; WATANABE, S. and WRIGHT, R. 1980. *Atlas of benthic shelf foraminifera of the Southwest Atlantic.* The Hague: Dr. W. Junk Publs., 147p.

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: 1235-1469. Washington, DC: US Government Printing Office, .

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*, 17: 491-508.

CALKINS, G. N., 1909. *Protozoology.* New York: Lea and Febiger.

CUSHMAN, J. A., 1927. An outline of reclassification of the Foraminifera. *Cushman Laboratory for Foraminiferal Research, Contributions*, 3 (1): 1-105.

———, 1933. Some new Recent foraminifera from the tropical Pacific. *Contributions from the Cushman Laboratory for Foraminiferal Research*, 9: 77-95.

CUSHMAN, J.A., TODD, R. and POST, R.J., 1954. Recent foraminifera of the Marshall Islands, Bikini and nearby Atolls, Part 2, Oceanography (Biologic). *US Geological Survey Professional Papers* , 260-H: 319-384.

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*, 8: 215-226.

ELDRETT, L., HARDING, I. C., WILSON, P. A. and ROBERTS, A. P., 2007. Continental ice in Greenland during the Eocene and Oligocene. *Nature* 446: 176-179.

FLOWER, B. P., ZACHOS, J. C. and MARTIN, E., 1997. Latest Oligocene through early Miocene isotopic stratigraphy and deep-water paleoceanography of the western equatorial Atlantic Sites 926 and 929. In: Shackleton, N.J., Curry, W.B., Richter, C. and Bralower, T.J., Eds., *Proceedings of the Ocean Drilling Program, Scientific Results, volume 154,* 451-461. College Station, Texas: Ocean Drilling Program.

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., Jansen, E., Blum, P. and Herbert, T. D., Eds., *Proceedings of the Ocean Drilling Program, Scientific Results, volume 162,* 19-34. College Station, Texas: Ocean Drilling Program.

FÖLLMI, K. B., BADERTSCHER, C., DE KAENEL, E., STILLE, P., JOHN, C. M., ADATTE, T. and STEINMANN, P., 2005. Phosphogenesis and organic-carbon preservation in the Miocene Monterey Formation at Naples Beach, California – The Monterey hypothesis revisited. *Geological Society America Bulletin*, 117: 589-619.

HALFAR, J. and MUTTI, M., 2005. Global dominance of coralline red-algal facies: a response to Miocene oceanographic events. *Geology*, 33: 481-484.

HALLOCK, P., PREMOLI SILVA, I. and BOERSMA, A. 1991. Similarities between planktonic and larger foraminiferal evolutionary trends through Paleogene paleoceanographic changes. *Palaeogeography, Palaeoclimatology, Palaeoecology*, 83: 49-64.

HANNAH, M.J., 2006. The palynology of ODP Site 1165, Prydz Bay, East Antarctica: a record of Miocene glacial advance and retreat. *Palaeogeography, Palaeclimatology, Palaeoecology,* 231: 120-133.

HARZHAUSER, M., PILLER, W.E. and STEININGER, F.F., 2002. Circum-Mediterranean Oligo-Miocene biogeographic evolution: the gastropods' point of view. *Palaeogeography, Palaeoclimatology, Palaeoecology*, 183: 103-133.

HEMLEBEN, Ch., SPINDLER, M. and ANDERSON, O. R., 1989. *Modern Planktonic Foraminifera*. Springer Verlag, 363 pp.

HOLBOURN, A. E. and HENDERSON, A. S., 2002. Re-illustration and revised taxonomy for selected deep-sea benthic foraminifers: *Palaeontologia Electronica*, v. 4, art. 3, 36 p.
http://palaeo-electronica.org/2001_2/foram/issue2_01.htm

HOLBOURN, A., KUHNT, W., SCHULZ, M. and ERLENKEUSER, H., 2005. Impacts of orbital forcing and atmospheric carbon dioxide on Miocene ice-sheet expansion. *Nature,* 438: 483-487.

HUBER, B. T. and BOERSMA, A., 1994. Cretaceous origination of *Zeauvigerina* and its relationship to Paleocene biserial planktonic foraminifera. *Journal of Foraminiferal Research,* 24:268-287.

HUBER, B. T., OLSSON, R. K. and PEARSON, P. N., 2006. Taxonomy, biostratigraphy and phylogeny of Eocene microperforate planktonic foraminifera (*Jenkinsina, Cassigerinelloita, Chiloguembelina, Streptochilus, Zeauvigerina, Tenuitella* and *Cassigerinella*) and problematic (*Dispidripella*). *Cushman Foundation of Foraminiferal Research, Special Publication*, 41: 461-508.

HUENI, C., MONROE, J.A., GEVIRTZ, J. and CASEY, R., 1978. Distribution of living benthonic foraminifera as indicators of oceano-

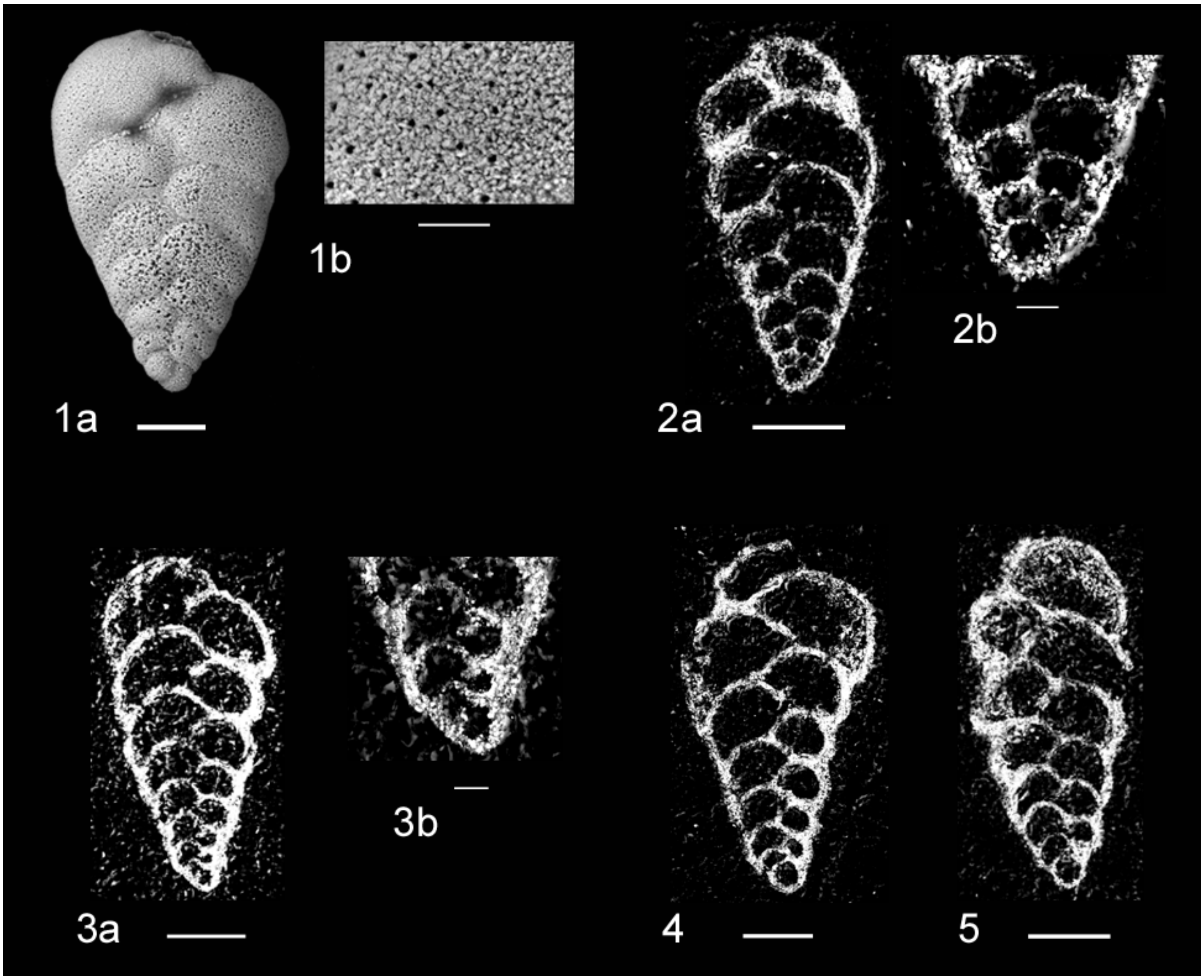


PLATE 9
Scanning electron micrographs of *Streptochilus cetacensis* sp. nov.; paratypes.

1 a, Side view of paratype (reg. no. BM(NH) PF 68090), uncoated, scale bar = 50μm; b, detail of wall showing fine granular texture and small pores, scale bar = 10μm (DSDP 74-529-8-3, 74-76cm, 69.24 mbsf).

2 a, Side view of paratype (reg. no. BM(NH) PF 68224), polished megalospheric specimen, uncoated, scale bar = 50μm; 3b detail of initial part, scale bar = 10μm (ODP 208-1264B-21-1, 78-80cm, 210.60 mcd).

3 a, Side view of paratype (reg. no. BM(NH) PF 68235), polished microspheric specimen, uncoated, scale bar = 50μm; b, detail of initial part, scale bar = 10μm (ODP 208-1264B-21-1, 78-80cm, 210.60 mcd).

4-5 Side views of paratypes (4 reg. no. BM(NH) PF 68227, 5 reg. no. BM(NH) PF 68232), polished megalospheric specimens, uncoated, scale bars = 50μm (ODP 208-1264B-21-1, 78-80cm, 210.60 mcd).

graphic processes on the South Texas outer continental shelf. *Transactions of the Gulf Coast Association of Geological Societies*, 28: 193-200.

JORISSEN, F. J., FONTANIER, C. and THOMAS, E., in press, 2007. Paleoceanographical proxies based on deep-sea benthic foraminiferal assemblage characteristics. In: Hillaire-Marcel, C. and de Vernal, A., Eds., *Proxies in Late Cenozoic Paleoceanography (Pt. 2): Biological tracers and biomarkers.* Amsterdam: Elsevier.

KENNETT, J. P. and SRINIVASAN, M. S., 1983. *Neogene Planktonic Foraminifera: a phylogenetic atlas*. 265 pp.

KROON, D. and GANSSEN, G., 1989, Northern Indian Ocean upwelling cells and the stable isotope composition of living planktonic foraminifera. *Deep-Sea Research,* 36: 1219-1236.

KROON, D. and NEDERBRAGT, A.J., 1990. Ecology and paleoecology of triserial planktic foraminifera. *Marine Micropaleontology*, 16: 25-38.

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., Eberli, G. P., Malone, M. J. and Sarj, J. F., Eds., *Proceedings of the Ocean Drilling Program, Scientific Results*, volume 166:155-166. College Station, Texas: Ocean Drilling Program.

LANKESTER, E. R., 1885. *Protozoa.* In: *Encyclopaedia Britannica,* vol. 19, 9th ed.: 830-866.

LEAR, C.H., ROSENTHAL, Y. and WRIGHT, J.D., 2003. The closing of a seaway: ocean water masses and global climate change. *Earth and Planetary Science Letters*, 210: 425-436.

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*, 19, PA4015, doi: 10.1029/2004PA001039.

LEE, J. J.. 1990. Phylum Granuloreticulosa (Foraminifera). In: Margulis, L., Corliss, J.O., Melkonian, M., Chapman, D.J., Eds., *Handbook of Protoctista*, 524-548. Boston: Jones & Bartlett.

LIDZ, B., 1966. Planktonic foraminifera in the water column of the mainland shelf off Newport Beach, California. *Limnology Oceanography*, 11: 257-263.

LOEBLICH, A. R. and TAPPAN, H. 1987. *Foraminiferal genera and their classification.* New York: Van Nostrand Reinhold Company, 2nd vol., 1182 pp.

———, 1992. Present status of foraminiferal classification. In: Takayanagi, Y. and Saito, T., Eds., *Studies in Benthic Foraminifera,* 93-102. Tokyo: Tokai University Press, Japan.

LOURENS, L.J., HILGEN, F.J., LASKAR, J., SHACKLETON, N.J. and WILSON, D., 2004, The Neogene Period, *in* Gradstein, F.M., Ogg, J.G. and Smith, A.G., Eds., *A Geologic Time Scale 2004*, p. 409-440. Cambridge: Cambridge University Press.

MILLER, K. G., WRIGHT, J. D. and BROWNING, J. V., 2005. Visions of ice sheets in a greenhouse world. *Marine Geology*, 217: 215-231.

MURRAY, J. W., 1971. *An Atlas of British Recent Foraminiferids.* London: Heinemann Educational Books.

NAIDU, P. D. and NIITSUMA, N., 2004. Atypical $\delta^{13}C$ signature in *Globigerina bulloides* at the ODP Site 723A (Arabian Sea): implications of environmental changes caused by upwelling. *Marine Micropaleontology*, 53: 1-10.

PLATE 10

Scanning electron micrographs of *Streptochilus cetacensis* sp. nov.; paratypes.
All specimens are from ODP 108-667A-22H-7, 6-8cm, 200.36 mbsf.

1 a, Side view of paratype (reg. no. BM(NH) PF 68122), uncoated, scale bar = 50µm; b, detail of wall showing pores, scale bar = 10µm.

2-7 Side views of paratypes, all uncoated..

2 reg. no. BM(NH) PF 68123, scale bar = 50µm;

3 reg. no. BM(NH) PF 68124, scale bar = 50µm;

4 reg. no. BM(NH) PF 68125, scale bar = 50µm;

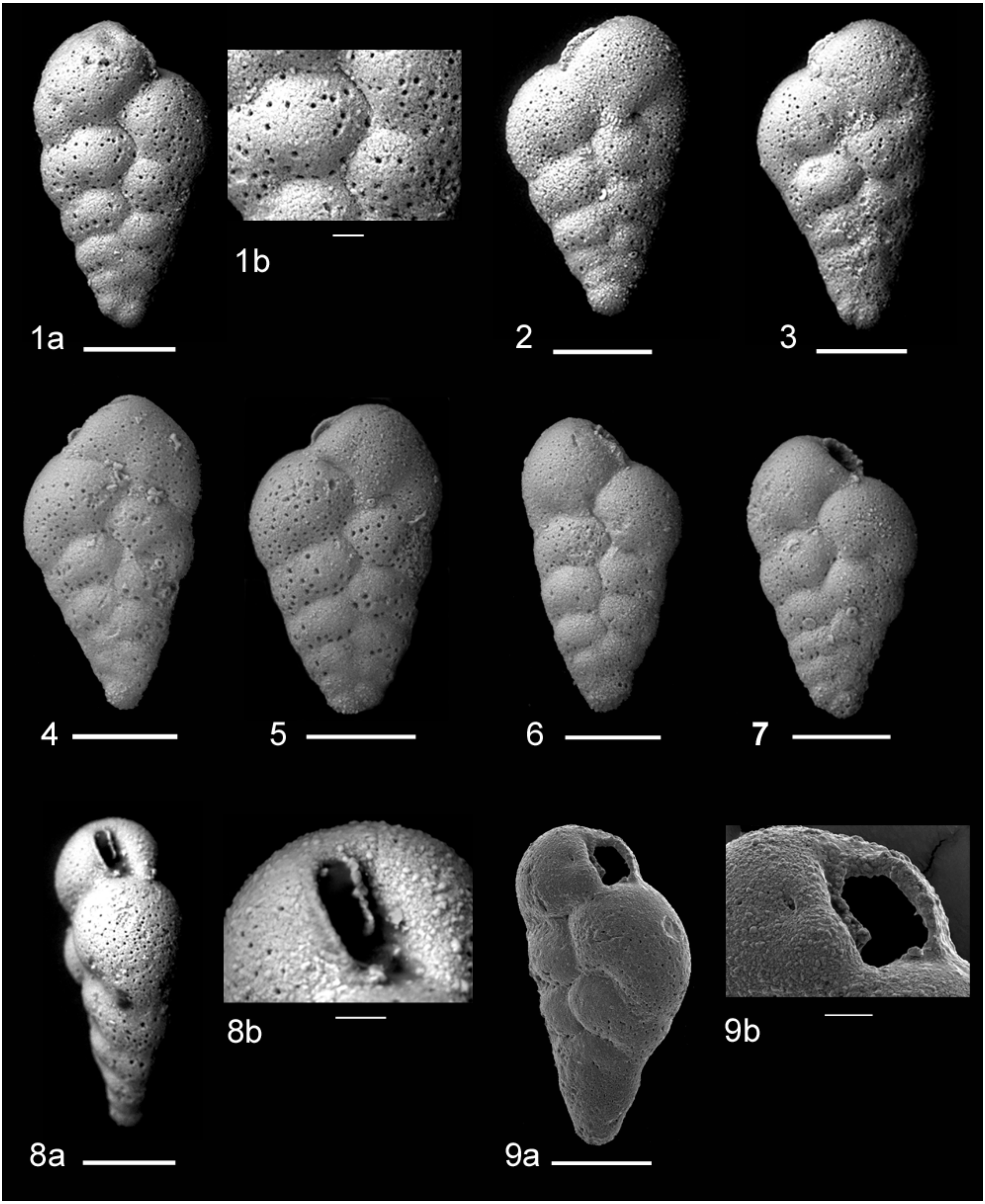
5 reg. no. BM(NH) PF 68126, scale bar = 50µm;

6 reg. no. BM(NH) PF 68127, scale bar = 50µm;

7 reg. no. BM(NH) PF 68128, scale bar = 50µm;

8 a, Edge view of paratype (reg. no. BM(NH) PF 68129), uncoated, scale bar = 50µm; b, detail of aperture showing infolded rimmed margin, scale bar = 10µm;

9 a, Oblique view of paratype (reg. no. BM(NH) PF 68130), gold coated, scale bar = 50µm; b, detail of aperture showing rimmed infolded margin, scale bar = 10µm.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1b
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9b

NIKOLAEV, S. D., OSKINA, N. S., BYLUM, N. S. and BUBENSHCHIKOVA, N. V., 1998, Neogene-Quaternary variations in the 'Pole-Equator' temperature gradient of the surface oceanic waters in the North Atlantic and North Pacific. *Global and Planetary Change*, 18: 85-111.

OLAFSSON, G., 1991. Late Oligocene through Late Miocene Calcareous Nannofossil Biostratigraphy and Biochronology. *Meddelanden från Stockholms Universitets Institution för Geologi og Geokemi*, Nr. 283, 157 p.

OLSSON, R. K., HEMLEBEN, C., BERGGREN, W. A. and HUBER, B. T., 1999. *Atlas of Paleocene Planktonic Foraminifera.* Smithsonian Contributions to Paleobiology, 85.

PAGANI, M., ARTHUR, M. A. and FREEMAN, K. H., 1999. The Miocene evolution of atmospheric carbon dioxide. *Paleoceanography*,14: 273-292.

PAGANI, M., ARTHUR, M. A. and FREEMAN, K. H., 2000. Variations in Miocene phytoplankton growth rates in the southwest Atlantic: Evidence for Changes in Ocean Circulation: *Paleoceanography*, 15: 486-496.

PEARSON, P. N. and PALMER, M. R., 2000. Atmospheric carbon dioxide concentrations over the past 60 million years. *Nature*, 406: 695-699.

PEKAR, S. F. and DECONTO, R. M., 2006. High-resolution ice-volume estimates for the early Miocene: evidence for a dynamic ice sheet on Antarctica. *Palaeogeography, Palaeclimatology, Palaeoecology,* 231: 101-109.

POAG, C. W. and LOW, D., 1985. Environmental trends among Neogene benthic foraminifers at DSDP Site 548, Irish continental margin, *in* GRACIANSKY, P. C. de, POAG, C. W. and others, Eds., *Initial Reports of the Deep Sea Drilling Project*, 80: 489-503. Washington, DC: US Government Printing Office.

POORE, H. R., SAMWORTH, R., WHITE, N. J., JONES, S.M. and MCCAVE, I. N., 2006. Neogene overflow of Northern Component water at the Greenland-Scotland Ridge. *Geochemistry, Geophysics, Geosystems*, 7: QO6010, doi: 10.1029/GC001085.

POORE, R. Z. and GOSNELL, L. B., 1985. Apertural features and surface texture of upper Paleogene biserial planktonic foraminifers: links between *Chiloguembelina* and *Streptochilus*. *Journal of Foraminiferal Research*, 15: 1-5.

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, SCHLANGER, S. O., eds, *Initial Reports of the Deep Sea Drilling Project*, *Volume 61*, p. 397-422. US Government Printing Office, Washington, DC.

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., Macleod, C. J., Lee, S. V. and Jones, E. J. W., Eds., *Geological evolution of ocean basins: results from the Ocean Drilling Program,* 55-70. Geological Society, London, Special Publication No. 131.

REISS, Z., 1963. Reclassification of perforate foraminifera. *State of Israel Geological Survey Bulletin*, 35: 1-111.

RESIG, J., 1989. Stratigraphic distribution of late Neogene species of the planktonic foraminifer *Streptochilus* in the Indo-Pacific. *Micropaleontology*, 35: 49-62.

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*, 8: 235-248.

ROYER, D. L., WING, S. L., BEERLING, D. J., JOLLEY, D. W., KOCH, P. L., HICKEY, L. J. and BERNER, R. A. 2001. Palaeo-

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PLATE 11

Scanning electron micrographs of *Streptochilus cetacensis* sp. nov.; paratypes.
All specimens are from ODP 108-667A-22H-7, 6-8cm, 200.36 mbsf.

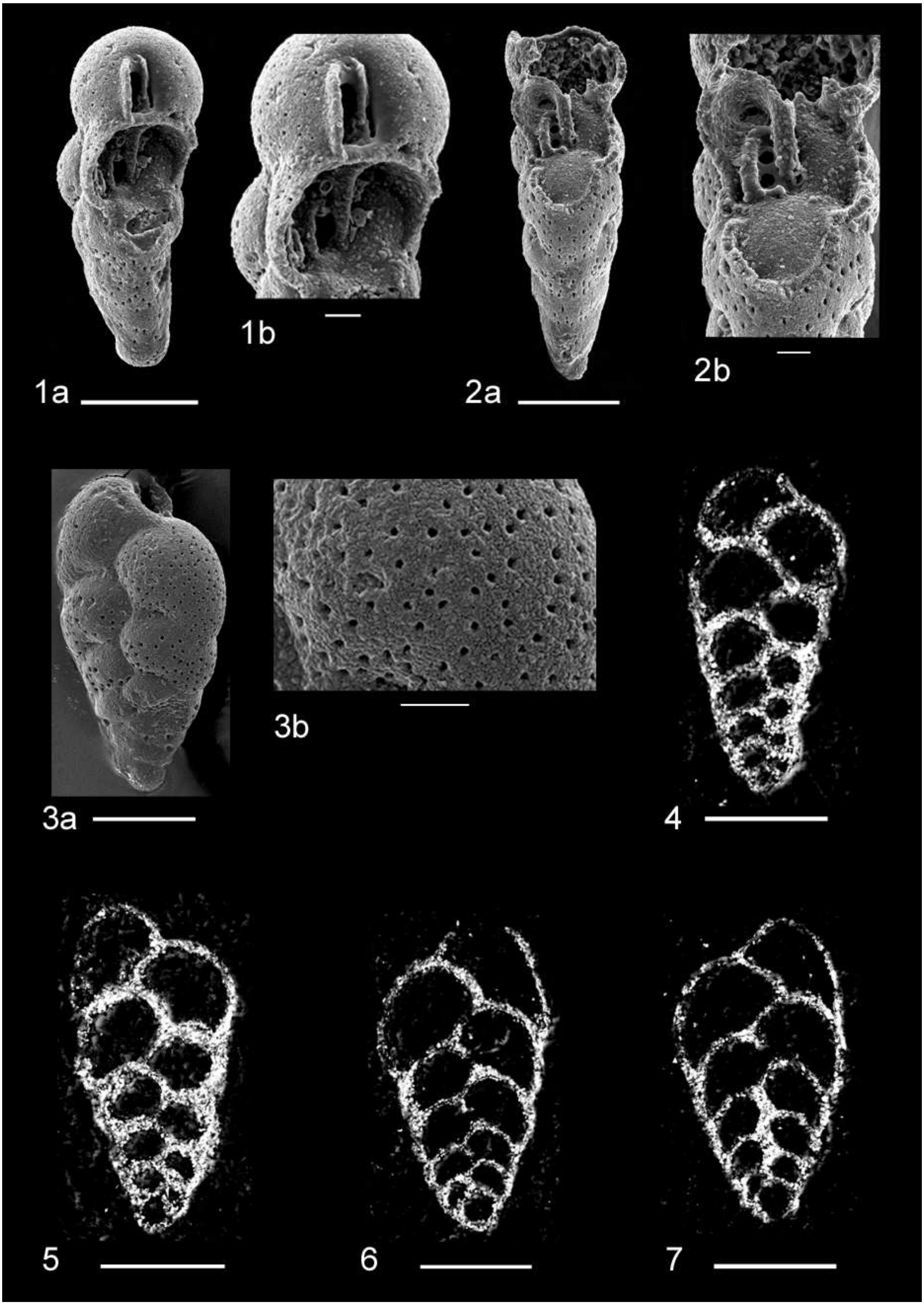
1 a, Edge view of paratype (reg. no. PF 68131), dissected specimen, gold coated, scale bar = 50µm; b, detail of aperture, note internal plate connecting with apertural rim, scale bar = 10µm;

2 a, Edge view of paratype (reg. no. PF 68132), dissected specimen, gold coated, scale bar = 50µm; b, detail of aperture, note internal plate connecting with apertural rim, scale bar = 10µm;

3 a, Oblique view of paratype (reg. no. PF 68133), gold coated, scale bar = 50µm; b, detail of wall showing pores, scale bar = 10µm;

4 Side view of paratype (reg. no. PF 68244), polished specimen (probably microspheric), uncoated, scale bar = 50µm;

5-7 Side views of paratypes (5 reg. no. PF 68243, 6 reg. no. PF 68246, 7 reg. no. PF 68248), polished megalospheric specimens, uncoated, scale bars = 50µm.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botanical evidence for near present-day levels of atmospheric CO_2 during part of the Tertiary. *Nature*, 292: 2310-2313.

SCHMUKER, B. and SCHIEBEL, R., 2002. Planktic foraminifera and hydrography of the eastern and northern Caribbean Sea. *Marine Micropaleontology*, 46: 387-403.

SEXTON, P. E., WILSON, P. A. and PEARSON, P. N., 2006. Palaeoecology of late middle Eocene planktic foraminifera and evolutionary implications. *Marine Micropaleontology*, 60: 1-16.

SIJP, W.P. and ENGLAND, M., 2004. Effect of the Drake Passage Throughflow on global climate. *Journal of Physical Oceanography*, 34: 1254-1266.

SMART, C.W., 1992. Early to middle Miocene benthic foraminiferal faunas from DSDP Sites 518 and 529, South Atlantic: preliminary investigations. In: Takayanagi, Y. and Saito, T., Eds., *Studies in Benthic Foraminifera*, 245-248. Tokyo: Tokai University Press.

———, 2002. Environmental applications of deep-sea benthic foraminifera. In: Haslett, S. K., Ed., *Quaternary Environmental Micropalaeontology*, 14-58. Arnold.

SMART, C.W. and MURRAY, J.W., 1994. An early Miocene Atlantic-wide foraminiferal/ palaeoceanographic event. *Palaeogeography, Palaeoclimatology, Palaeoecology*, 108: 139-148.

SMART, C. W. and RAMSAY, A. T. S., 1995. Benthic foraminiferal evidence for the existence of an early Miocene oxygen-depleted oceanic water mass? *Journal of the Geological Society, London*, 152: 735-738.

SMART, C. W. and THOMAS, E., 2006. The enigma of early Miocene biserial planktic foraminifera. *Geology*. 34: 1041-1044.

SMART, C. W., THOMAS, E. and RAMSAY, A. T. S., 2007. Middle-late Miocene benthic foraminifera in a western equatorial Indian Ocean depth transect: Paleoceanographic implications. *Palaeogeography, Palaeoclimatology, Palaeoecology,* 247: 402-420. doi:10.1016/j.palaeo.2006.11.003

SYKES, T. J. S., RAMSAY, A. T. S. and KIDD, R. B., 1998. *Southern hemisphere Miocene bottom water circulation: a paleobathymetric analysis*, 43-54. In: Cramp, A., MacLeod, C.J., Lee, S.V. and Jones, E.J.W., Eds., Geological Society of London, Special Publication 131.

THOMAS, E., 1985. Late Eocene to Recent deep-sea benthic foraminifera from the central equatorial Pacific Ocean. In: Mayer, L., Theyer, F. and others, Eds., *Initial Reports of the Deep Sea Drilling Project*, *volume 85,* 655-694. Washington, DC: US Government Printing Office.

———, 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*, 205-218. Geological Society, London, Special Publication, 21.

———, 1987. Late Oligocene to Recent benthic foraminifers from Deep Sea Drilling Project Sites 608 and 610, northeastern North Atlantic, In: Ruddiman, W. F., Kidd, R. B., Thomas, E. and others, Eds., *Initial Reports of the Deep Sea Drilling Project*, v. 94: 997-1031. Washington, DC: US Government Printing Office.

———, 1990. Late Cretaceous through Neogene deep-sea benthic foraminifers (Maud Rise, Weddell Sea, Antarctica). In: Barker, P.F., Kennett, J.P., et al., Eds., *Proceedings Ocean Drilling Program, Scientific Results*, *volume 113,* 571-594. College Station, Texas: Ocean Drilling Program.

VINCENT, E. and BERGER, W. H., 1985. Carbon dioxide and polar cooling: The Monterey Hypothesis. In: Sundquist, E. T. and Broecker, W. S., Eds., *The carbon cycle and atmospheric CO_2, natural variations Archaean to Present,* 455-468. American Geophysical Union, Monographs, 32.

PLATE 12

Scanning electron micrographs of *Streptochilus mascarenensis* sp. nov.; 1 holotype, 2-8 paratypes.

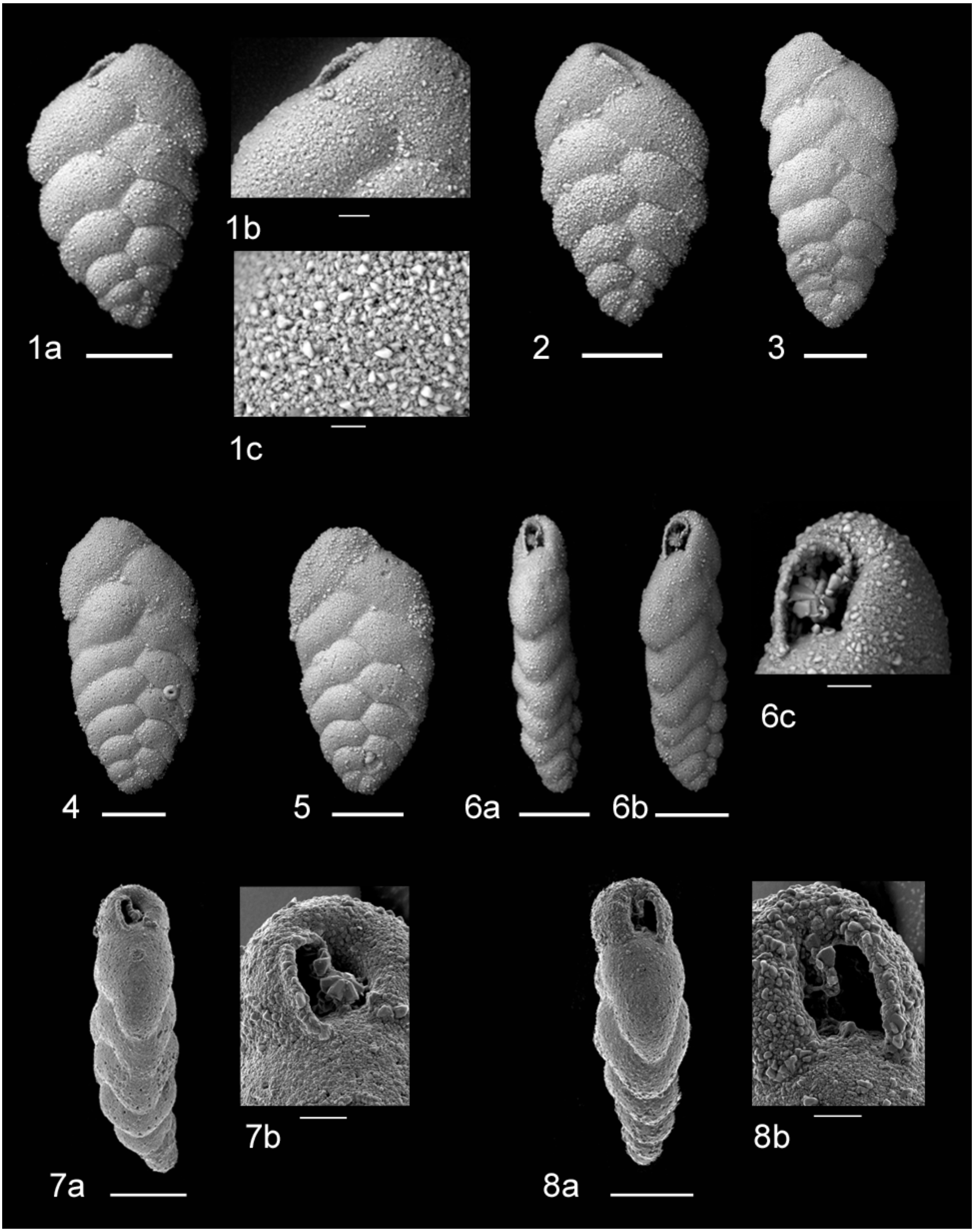
1 a, Side view of holotype (reg. no. BM(NH) PF 68152), uncoated, scale bar = 50µm; b, detail of wall, scale bar = 10µm; c, greater detail of wall showing granular texture and small pores, scale bar 5µm (DSDP 24-237-18-6, 69-71cm, 166.69 mbsf)

2-5 Side views of paratypes, all uncoated, all scale bars = 50µm; 2 (reg. no. BM(NH) PF 68153), 3 (reg. no. BM(NH) PF 68154), 4 (reg. no. BM(NH) PF 68155), 5 (reg. no. BM(NH) PF 68156) (all from DSDP 24-237-18-6, 69-71cm, 166.69 mbsf).

6 a, Edge view of paratype (reg. no. BM(NH) PF 68157), uncoated, scale bar = 50µm; b, oblique view, scale bar = 50µm; c, detail of aperture showing infolded rimmed margin, scale bar = 10µm (DSDP 24-237-18-6, 69-71cm, 166.69 mbsf).

7 a, Edge view of paratype (reg. no. BM(NH) PF 68158), gold coated, scale bar = 50µm; b, detail of aperture showing infolded rimmed margin, scale bar = 10µm (DSDP 24-237-18-3, 72-74cm, 162.22 mbsf).

8 a, Edge view of paratype (reg. no. BM(NH) PF 68159), gold coated, scale bar = 50µm; b, detail of aperture showing infolded rimmed margin, scale bar = 10µm (DSDP 24-237-18-3, 72-74cm, 162.22 mbsf).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VLASTELIC, I., CARPENTIER, M. and LEWIN, E., 2005. Miocene climate change recorded in the chemical and isotopic (Pb, Nd, Hf) signature of Southern Ocean sediments. *Geochemistry, Geophysics, Geosystems*, 6, QO3003, doi: 10.1029/2004GC000819.

WILLIAMSON, W. C., 1858. *On the Recent Foraminifera of Great Britain.* London, England: Ray Society, 1- 107.

WOODRUFF, F. and SAVIN, S.M., 1989. Miocene deepwater oceanography. *Paleoceanography*, 4: 87-140.

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*, 192-211. Oxford University Press.

WRIGHT, J. D., MILLER, K. G. and FAIRBANKS, R. G., 1992. Early and middle Miocene stable isotopes: implications for deepwater circulation and climate. *Paleoceanography*, 7: 357-389.

WRIGHT, J. D. and MILLER, K. G., 1996. Control of North Atlantic deep water circulation by the Greenland-Scotland Ridge. *Paleoceanography,* 11: 157-170.

ZACHOS, J., PAGANI, M., SLOAN, L., THOMAS, E. and BILLUPS, K., 2001. Trends, rhythms and aberrations in global climate: 65 Ma to present. *Science*, 292: 686-693.

ZACHOS, J. C., KROON, D., BLUM, P. et al., 2004. *Proceedings of the Ocean Drilling Program, Initial Reports,* 208 [CD-ROM]. Available from: Ocean Drilling Program, Texas A&M University, College Station TX 77845-9547, USA.

Manuscript received July 28, 2006
Manuscript accepted March 3, 2007

PLATE 13

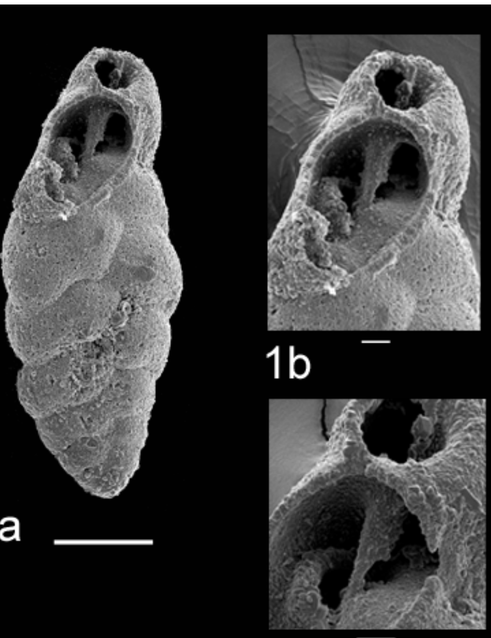
Scanning electron micrographs of *Streptochilus mascarenensis* sp. nov.; paratypes.

1 a, Edge view of paratype (reg. no. BM(NH) PF 68160), dissected specimen, gold coated, scale bar = 50µm; b, detail of aperture, note internal plate connecting with apertural rim, scale bar = 10µm; greater detail of aperture, scale bar = 10µm (DSDP 24-237-18-3, 72-74cm, 162.22 mbsf).

2 a, Side view of paratype (reg. no. BM(NH) PF 68161), uncoated, scale bar = 50µm; 2b, detail of wall showing fine granular texture and small pores, scale bar = 10µm (DSDP 24-237-18-6, 69-71cm, 166.69 mbsf).

3 a, Side view of paratype (reg. no. BM(NH) PF 68258), polished megalospheric specimen, uncoated, scale bar = 50µm; 3b, detail of initial part, scale bar = 10µm (DSDP 24-237-18-3, 72-74cm, 162.22 mbsf).

4-7 Side views of paratypes (4 reg. no. BM(NH) PF 68260, 5 reg. no. BM(NH) PF 68264, 6 reg. no. BM(NH) PF 68265, 7 reg. no. BM(NH) PF 68271), polished microspheric specimens, uncoated, all scale bars = 50µm; 4 is from DSDP 24-237-18-3, 72-74cm, 162.22 mbsf; 5-7 are from DSDP 24-237-18-6, 69-71cm, 166.69 mbsf.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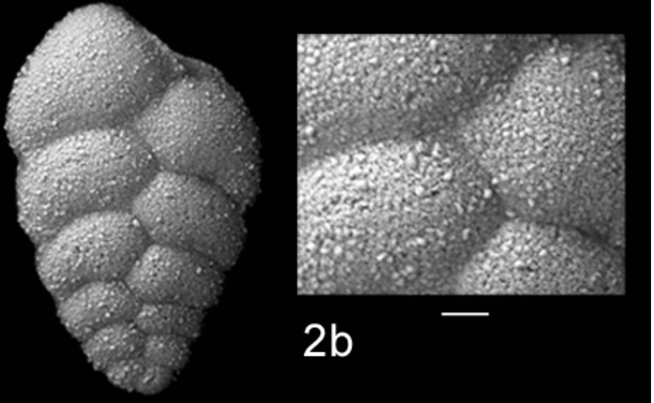
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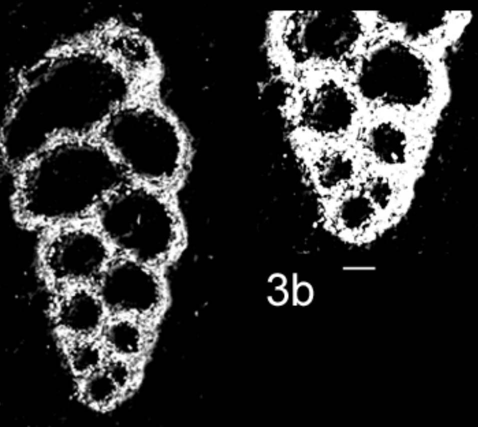
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