

Supporting Information

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SI Text

Notes on Taxonomy, Morphology, and Mode of Life. Occurrence of biserial and triserial benthic and planktic species. *Streptochilus globigerus* in our samples grew as a surface water dweller in pelagic environments, but is the same biological species as *Bolivina variabilis*, a shallow to intermediate infaunal dweller. This species was first described from the shelf seas around the U.K. (1), but is common worldwide in mesotrophic to eutrophic environments, from the intertidal zone to the upper slope, but most abundant on the shelf (2–8). Our observation confirms longstanding doubts about ancestor–descendant relations in biserial and triserial planktic foraminifera (9, 10).

Traditional taxonomy is, in principle, based on morphology, but lifestyle is used to separate the genera *Bolivina* and *Streptochilus*, which are placed in widely separated clades, with the genus *Bolivina* in the Order Buliminida (Superfamily Bolivinacea, Family Bolivinidae) and the genus *Streptochilus* in the Order Globigerinida (Superfamily Heterohellicae, Family Chiloguembelinidae) (11). The Superfamily Heterohellicae includes the mainly Cretaceous Family Heterohellicidae, which originated in the late Aptian to Albian (12, 13), to which are assigned the Cretaceous biserial genera *Heterohelix* and *Laeviheterohelix* (14), as well as the latter's descendant genus *Zeauvigerina*, ranging from the early late Maastrichtian through the middle Eocene (15). The Cenozoic Family Chiloguembelinidae includes the Paleocene–middle Oligocene biserial genus *Chiloguembelina* and its middle Eocene–Recent biserial descendant genus *Streptochilus* (9, 16). The Cenozoic biserial genera did not descend from a Cretaceous biserial genus, but from the triserial end-Cretaceous survivor *Guembelitria cretacea*, Family Guembelitriidae (17, 18), which originated in the late Albian (19). Families within the Superfamily Heterohellicae thus are paraphyletic (18). The Cenozoic genera (including *Streptochilus*) have been thought to be monophyletic (16, 20–22), although doubts have been expressed (9, 10, 21).

Many of the Cretaceous and Cenozoic biserial and triserial taxa described as planktic are unusual for planktic species: they have long stratigraphic ranges like benthic rather than planktic taxa (23) and a patchy distribution in space and time (e.g., refs. 9, 10, 13, 14, 19, 20, and 21). Their oxygen isotope values are lighter than those in deep-dwelling planktic and benthic forms in the same samples, suggesting they calcified in surface waters. Their $\delta^{13}\text{C}$ values are consistently lighter than those of coexisting planktic groups with nearly the same $\delta^{18}\text{O}$ value. This light $\delta^{13}\text{C}$ signature could reflect “vital effects” similar to those in spiral planktic species and/or short-term upwelling of $\delta^{13}\text{C}$ -depleted waters (9, 13, 24–28). In addition to isotopic evidence, distributional data have been used to argue for planktic lifestyle, because very abundant species are almost always planktic (10, 14, 15, 20, 25). A planktic lifestyle for the genus *Zeauvigerina*, for instance, has been refuted on morphological grounds (29) but accepted on distributional and isotope data (9).

Abundant occurrences of all biserial and triserial planktic taxa ranging from Cretaceous through Recent have been linked to high productivity, variable conditions, or disturbed environments, such as are commonly found in epicontinental, marginal, or shelf seas, living as neritic-plankton, possibly at depths from <100 m to a few hundreds of meters (13, 19, 30–32), in intense oxygen minimum zones in upwelling areas (24, 25) or generally high-productivity regions (10, 28). They are described as opportunistic taxa, able to survive strongly fluctuating and/or adverse conditions, including these after the end-Cretaceous asteroid

impact (13, 19, 33, 34). The benthic genus *Bolivina* likewise is most common in regions with high productivity, and can persist and thrive under low-oxygen conditions (35).

Morphology. There are no simple morphological arguments to place the genera *Bolivina* and *Streptochilus* in widely separated clades. *Streptochilus* species were originally placed in the genus *Bolivina* because of the similarity in morphology, including *Streptochilus globulosus*, the type species of the genus *Streptochilus* (20, 21, 24, 36) as well as several Miocene *Streptochilus* species (10). Most biserial planktics have more inflated chambers than benthics, but there is a very large intraspecific variability in the degree of inflation of chambers, such as documented for *Zeauvigerina waiparensis* (15) and *Heterohelix moremani* (14). There are large interspecific differences, as shown for *Streptochilus* species (24), and several Cretaceous *Laeviheterohelix* species are compressed rather than inflated (14, 30). The type figures of *Streptochilus globigerus* (37) and *S. globulosus* (38) show strongly inflated chambers. These figures are, however, not of good quality, and the holotype of *S. globulosus* in the Smithsonian Museum of Natural History is somewhat less inflated than suggested by the type figure (observation by E.T.). We document the morphology of specimens belonging to the 2 species of *Streptochilus* as recovered in the Indian Ocean (Figs. S1–S3), and show the similarity in morphology (including wall structure and apertural structure and toothplate) of *S. globigerus* (Fig. S1) and *B. variabilis* (Fig. S4).

Our figures agree well with high-quality published figures (16, 20, 21, 24, 36) and show similar intraspecific variability. *B. variabilis* and *S. globigerus* both have a cancellate wall structure (Figs. S1, S2, and S4), with pores surrounded by hexagonal ridges (1, 37). Similar wall structures occur in some trochospiral planktic forms (9, 18, 39).

Most genera in the Superfamily Buliminacea possess a tooth plate, a contorted plate running from an intercameral foramen to an aperture, and attached to both (Fig. S2–S4). It separates the main chamber lumen partly or completely from the apertural depression and may be shaped to form a single, double, or spiral fold (or “tongue”) with a free, often serrated, distal end protruding into the aperture (40–42). The detailed configuration of tooth plates has been used extensively in taxonomy of the Buliminacea (40), and some authors limit the designation “tooth plate” to the apertural structure within that superfamily (41, 42). The tooth plate in Buliminacea is described as “a piece of inner lining drawn out from under the axial-most part of the aperture into the chamber lumen and attached to the septum, close to the foramen,” and it is a monolamellar part of the septum between the last and fore-last chamber, intergrown with the bilamellar imperforate rim or collar around the aperture (41, 42). The genus *Streptochilus* is described as having an aperture “bordered by a collar. 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” (36). *Streptochilus* was said to have evolved from *Chiloguembelina*, which has no tooth plate, by infolding of the inner margin of the aperture. This structure in *Streptochilus* was described as not a true tooth plate, missing its internal monolamellar part (28).

It is not easy to evaluate the exact nature of the tooth plate, especially in small species, and the exact nature of the tooth plate has been documented for relatively few species, whether planktic or benthic (29, 38). The species *cubensis*, for instance, has been assigned to *Streptochilus* because of the presence of a tooth plate

(43) but to *Chiloguembelina* because of its absence (9). The type species of *Bolivina* (*B. plicata*) shows a serrated tooth plate protruding from the aperture, whereas the aperture is fully rimmed, whereas *Streptochilus* shows a structure formed by an infolded part of the rim of the aperture, with a clear adapertural depression (10, 28). A very similar aperture is present in other planktic taxa, including some specimens of *Guembelitra cretacea* as well as its Cenozoic biserial descendant genus *Woodringina*.

We argue that there is no solid evidence that there is a true structural difference in the tooth plates of *Streptochilus* and *Bolivina*, because there is considerably more intrageneric (and even intraspecific) than intergeneric variability. The imperforate rim around the aperture develops to a varying extent into a collar, becomes folded along part of the aperture, extends downwards within the lumen of the last chamber to connect to the aperture of an earlier chamber (foramen), and develops more or fewer “teeth.” Figures of *Bolivina* as well as other benthic species in the Buliminacea and Heterohelicacea show a wide variety of tooth plates, some apparently identical to the structure in *Streptochilus*, in which the rim or collar does not fully surround the aperture, and, in part, is infolded within the chamber lumen, forming a clear adapertural depression (Figs. S2 and S3). A similar adapertural structure is present in some *Zeauvigerina* species (15). The tooth plate may or may not protrude from the aperture and may have serrated edges (2, 3) (Figs. S1–S4). In Recent (44) as well as extinct (10, 15) species of Buliminacea, the configuration of the tooth plate changes during ontogeny, so that one specimen may have differently shaped tooth plates during its life (Fig. S2). We do not know whether some or all taxa in the Buliminacea and Heterohelicea have a complex intergrowth of parts of the adapertural rim and part of the last chamber septum as contrasted with a structure formed from infolding of the rim only, but in view of the variability of the structure, we consider the tooth plate not as a synapomorphic character, in agreement with molecular phylogenies which assign genera with similar tooth plates (*Bulimina*, *Bolivina*) traditionally placed within the Buliminida (42) to different clades (45). **Ecology.** Both benthic and planktic biserial taxa are most common in high-food, low-oxygen environments (25, 35, 46). The serrated tooth plates in our specimens of *Streptochilus* (Figs. S2 and S3) strongly resemble those in the adapertural structures of *Bulimina elegantissima* and *Stainforthia fusiformis*, benthic biserial species that use these teeth to break open diatoms and liberate their chloroplasts (46, 47). Such chloroplasts are not immediately digested and may keep performing photosynthesis if the foraminifer lives in the photic zone (chloroplast husbandry). They also remain undigested in foraminifera below the photic zone, where they may be used in an unknown adaptation to dysoxic environments, or in the assimilation of inorganic nitrogen (48), a potentially useful feature for a planktic organism living in surface waters that are commonly nitrogen-depleted. *Streptochilus globulosus* is reported to feed on diatoms (49), and one could speculate that planktic biserial forms behave like benthic ones, use the teeth to open diatom frustules, and sequester chloroplasts (kleptochloroplasts).

Benthic foraminiferal species are thought to lack buoyancy and, if expatriated from shelf to plankton in turbulent weather systems, would be expected to progressively sink out of the water column. There is, however, considerable evidence that *Bolivina* species may be expatriated for a life in the plankton. Benthic

bolivine species have commonly been observed in plankton tows (50, 51), and they are among the species most commonly observed as transported offshore during storm events (52–54).

In conclusion, there are no consistent morphological differences between at least some species placed in *Bolivina* and in *Streptochilus*. If one biological species can successfully employ planktic and benthic life strategies, “planktic” and “benthic” are not synapomorphic within foraminifera, and lifestyle cannot be used as a character in phylogenetic analysis. If Recent biserial foraminifera are able to live tychopelagically, such a lifestyle may also have been used by biserial and triserial species in the past, explaining the patchy record in space and time of such taxa. This patchiness may reflect a tychopelagic lifestyle rather than be caused by incomplete observation of small taxa in a size fraction that is commonly not studied. Triserial and biserial planktic foraminifera thus probably are not a monophyletic group, but are much more probably the result of multiple expatriation events from coastal benthos to the pelagic zone, rather than of migration of neritoplankton from the coastal zone into open ocean. The possibility to exploit both benthic and planktic life strategies may have been a major factor in their species longevity and resistance to extinction. The biserial benthic genus *Bolivina* may have an exaptation for a pelagic lifestyle in its use of kleptochloroplasts and its buoyancy. We do not know whether most occurrences of these taxa reflect a true tychopelagic lifestyle or whether some taxa evolved into one or a purely planktic species over geological time. In that case, there might be no close phylogenetic linkage between different biserial planktic groups, with polyphyletic evolution of planktic from benthic biserial groups.

Formal taxonomy: Genus *Streptochilus* Brönniman and Resig 1971.

Type Reference: P. Brönniman and J. A. Resig, A Neogene globigerinacean biochronologic timescale of the southwestern Pacific. In: E. L. Winterer et al., eds., Initial Reports of the Deep-Sea Drilling Project, vol 7, Washington DC, pt 2, p 1288.

Streptochilus globigerus (Schwager) Figs. S1 and S2.

Textularia globigera. Type reference: C. Schwager, Fossile Foraminiferen von Kar Nikobar. Novara Exped., 1857–1859, Wien, Österreich, 1866, Geol. Theil., Bd. 2, Abt. 2, p 252, pl. 7, Fig. 100.

Streptochilus globulosus (Cushman) Fig. S3.

Bolivina globulosa. Type reference: J. A. Cushman, Some new Recent Foraminifera from the tropical Pacific. Contr. Cushman Lab. Foram. Res., Sharon, MA, 1933, vol. 9, pt. 4, no., 137, p. 80, pl. 8, Figs. A, 9b.

Bolivina variabilis (Williamson) Fig. S4.

Textularia variabilis. Type reference: W. C. Williamson, On the Recent Foraminifera of Great Britain, 1858, p. 76, pl. 6, Figs. 162–163.

Cruise Track. The cruise track is shown in Fig. S6. Specimens of *Streptochilus globigerus* were collected along the cruise track in the central Arabian Sea during the summer monsoon of 2003 on the RRS *Charles Darwin* (Cruise CD148, Natural Environment Research Council, U.K.)

Conductivity, Temperature, Depth (CTD) Profile. The CTD profile is shown in Fig. S5.

***B. variabilis* (Kenya) Isolates and *S. globigerus* (Arabian Sea) Clone Sequences.** The clone sequences are presented in SI Appendix.

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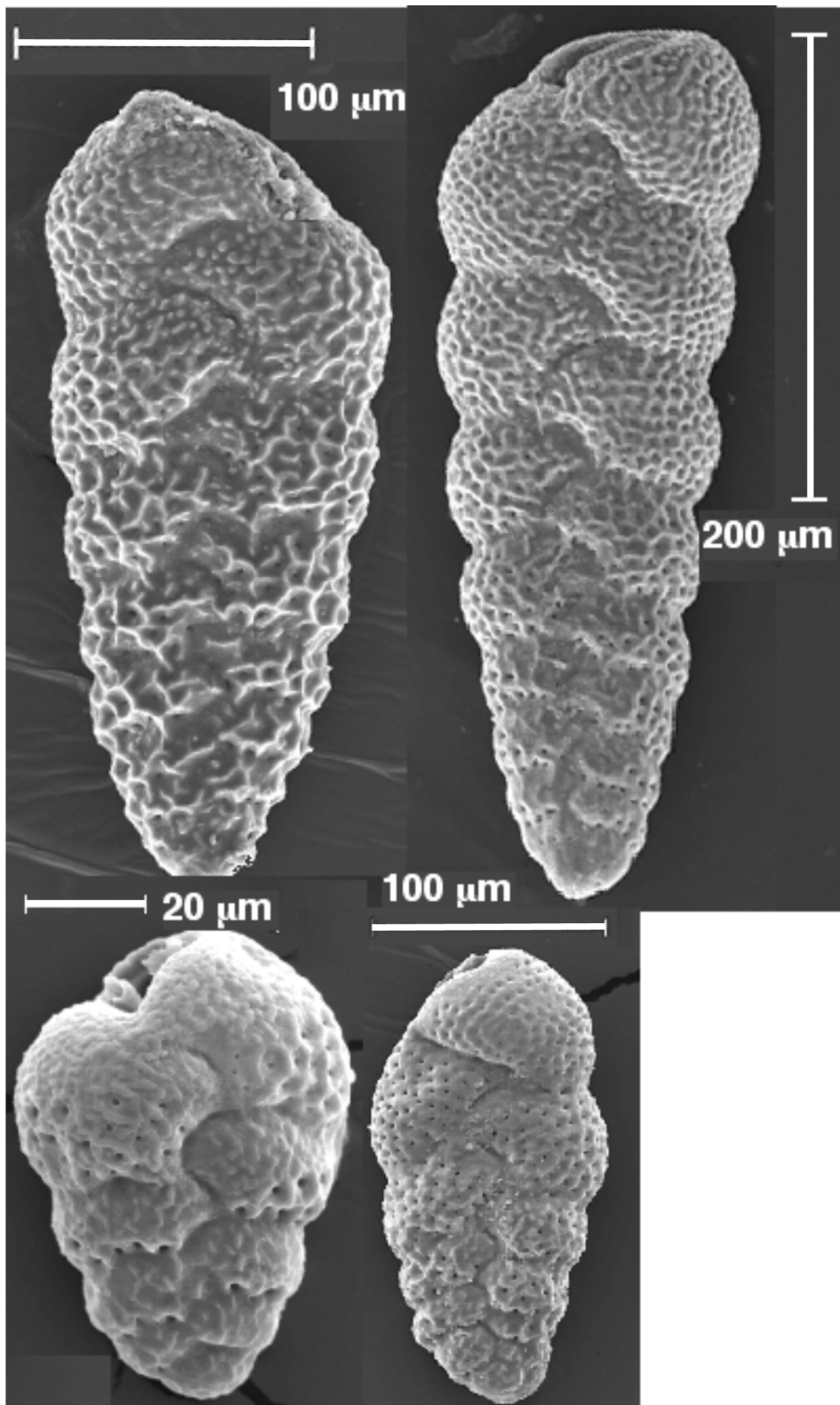


Fig. S1. Morphology of adult (*Upper*) and juvenile (*Lower*) specimens of *S. globigerus* as collected in the Indian Ocean. Note variability in the degree of globosity of the chambers, and the pronounced cancellate wall.

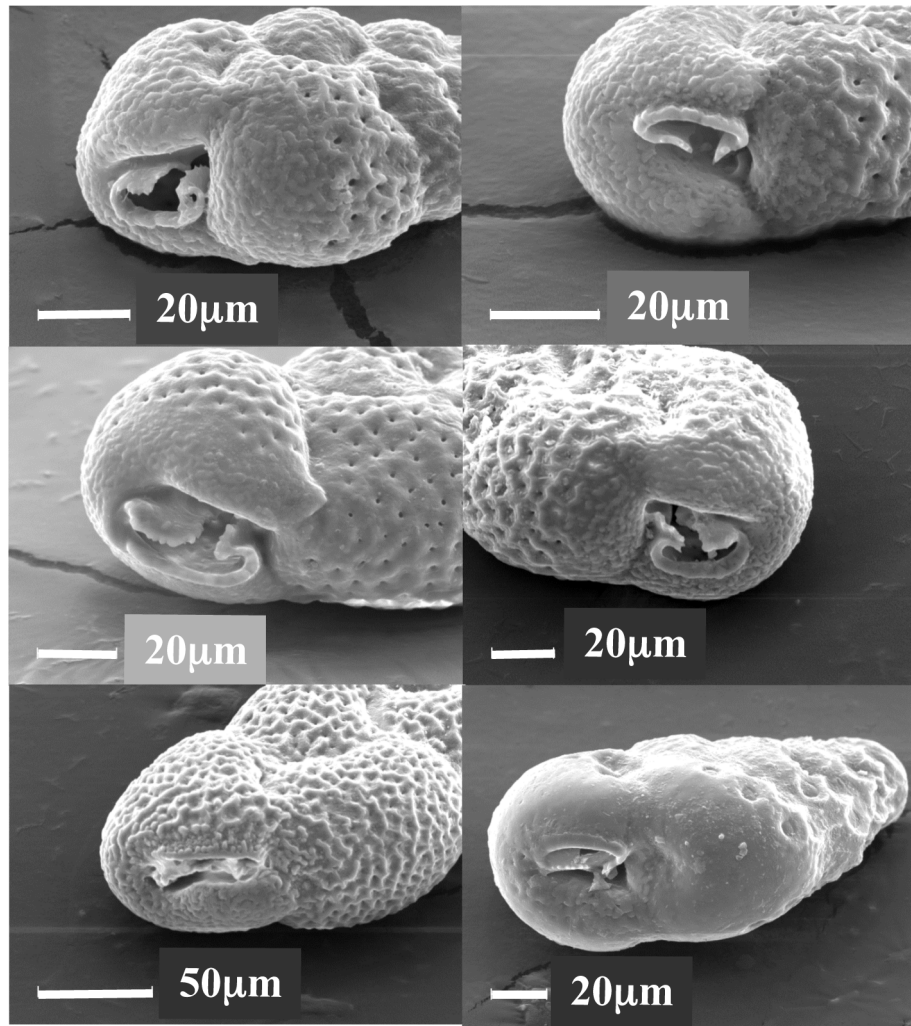


Fig. S2. Details of the variability in apertural structure (including tooth plate) and wall structure in *S. globigerus* collected in the Indian Ocean.

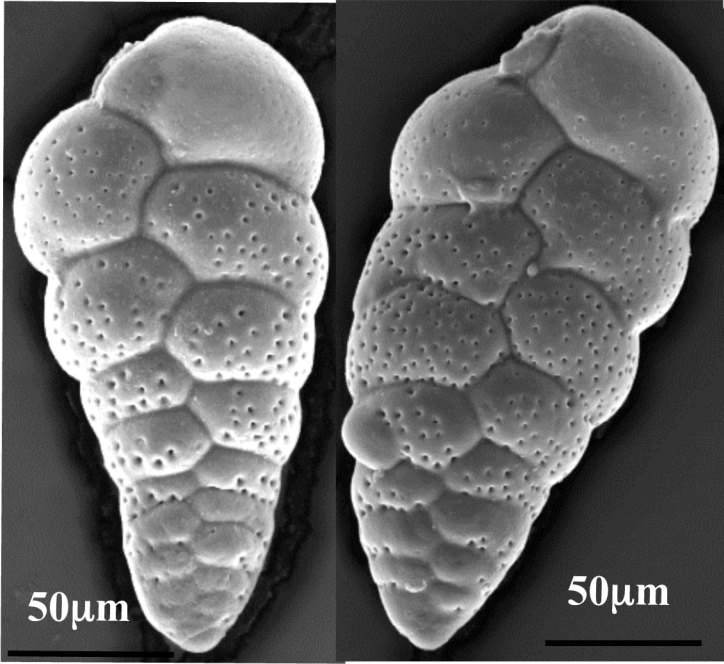
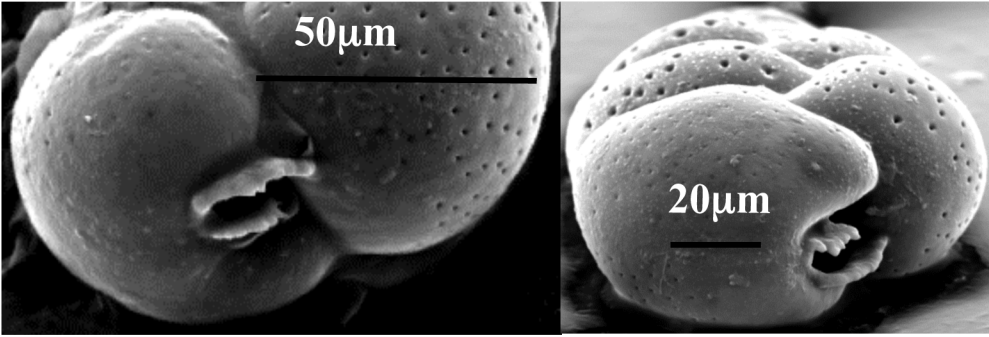


Fig. S3. Morphology of specimens of *S. globulosus* collected in the Indian Ocean. Note the smooth wall (in contrast to the cancellate wall of *S. globigerus*) but the similarity in aperture and tooth plate.

