

MUTABELLA MIRABILIS GEN. ET SP. NOV., A MIOCENE MICROPERFORATE PLANKTONIC FORAMINIFER WITH AN EXTREME LEVEL OF INTRASPECIFIC VARIABILITY

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ABSTRACT

We describe *Mutabella mirabilis*, a new genus and species of Miocene microperforate planktonic foraminifera. The species is known from several drill sites in the tropical Pacific, Indian and Atlantic Oceans (Deep Sea Drilling Project / Ocean Drilling Program Sites 78, 219, 865, 871, 872, 873, 959, and 960). The taxon shows an unusually high level of intraspecific variability in chamber shape and arrangement, aperture position, and test ornament. Some specimens possess supplementary sutural apertures, which may have bulla-like coverings. Others possess a composite tooth-plate reminiscent of certain Cretaceous species. *Mutabella mirabilis* first evolved in early Miocene Biochron M3, and probably became extinct in middle Miocene Biochron M7. A morphometric study from Site 872 (west Pacific) demonstrates that substantial shape change occurred during its evolution, related to the height of the trochospiral chamber arrangement and degree of involution of the test. A stable isotopic comparison with other coexisting species indicates that *M. mirabilis* occupied a shallow (mixed layer) planktonic habitat. A strong positive correlation between test size and $\delta^{13}\text{C}$ indicates that it probably associated with photosynthetic symbionts. *Mutabella mirabilis* seems to have evolved from the long-ranging species *Globigerinita glutinata*, with which it fully intergrades in morphology near the bottom of its stratigraphic range.

INTRODUCTION

In a biostratigraphic study of pelagic sediments recovered during Ocean Drilling Program (ODP) Leg 144 in the western tropical Pacific, one of us (PNP) recorded an unidentified microperforate planktonic foraminifer taxon as “*Tenuitella* sp.” (Pearson, 1995, p. 53; Plate 1, Figs. 23–24). Individuals belonging to this informal taxon were recorded from lower to middle Miocene sediments of three sites (Sites 871, 872 and 873), all on guyots (flat-topped seamounts) in the Marshall Islands region. The specimens were described as showing considerable morphological variability in their coiling style and chamber shape. It was also noted that some specimens possess supplementary sutural apertures, and most have a prominent umbilical tooth. Because of the unusual extent of variability shown by these forms, even in features that would normally be used to discriminate between genera, it was regarded as possible that more than one previously unknown species might have been included in the provisional taxon (Pearson, 1995, p. 53).

A description and additional photomicrographs of the taxon were subsequently circulated among colleagues. Another of us (RDN) recognized the specimens as similar to some occurring in Miocene sediments from ODP Site 865 (Allison Guyot, Central Pacific). This was confirmed by a direct comparison of the assemblages. Furthermore, subsequent drilling in the tropical Atlantic (ODP Leg 158; Sites 959 and 960) recovered more well-preserved assemblages (Norris, 1998). These observations indicated a wide geographical distribution for the species and confirmed its highly aberrant nature.

Although the species has been omitted from standard taxonomic works on Neogene planktonic foraminifera (e.g., Kennett and Srinivasan, 1983; Bolli and Saunders, 1985), it was in fact briefly described and illustrated as “*Globorotalia* sp. 4” by Jenkins and Orr (1972, p. 1096, Plate 18, Figs 7–12) from Deep Sea Drilling Project (DSDP) Site 78 in the eastern equatorial Pacific, and as “*Tenuitella* sp. 1” by Fleisher (1974, p. 1034, Plate 17, Fig 5) from DSDP Site 219 in the Arabian Sea. Also, in his revision of the *Tenuitella* group, Li Qianyu (1987, p. 311) referred to these descriptions under the name “*Tenuitella* sp.”.

It is clear from these occurrences that *Mutabella mirabilis* was widely distributed in early to middle Miocene tropical oceans. This study reports further investigations conducted with the aim of formally describing the species and investigating its paleobiology and stratigraphic distribution. Morphometric analysis demonstrates that populations throughout the stratigraphical range tend to be unimodal in their morphology, indicating that, as far as can be ascertained, only a single species-lineage is represented. Assignment to the genus *Tenuitella* is now regarded as inappropriate, given the many distinctive features of the test, and the fact that it appears to have evolved from the genus *Globigerinita*, with which it intergrades in the lower part of its stratigraphic range. Consequently, the species is formally described in this study as *Mutabella mirabilis* Gen. et sp. nov.

SYSTEMATIC TAXONOMY

Order FORAMINIFERIDA Eichwald, 1830
Family GLOBIGERINITIDAE Bermudez 1961
Genus *Mutabella*, n. gen.

Type species. Mutabella mirabilis, n. sp.

Description. Test trochospiral, with a tendency for planispiral coiling in the final whorl; chambers globular to ovate; aperture variable, from intraumbilical to extraumbilical or axially symmetric, commonly with umbilical tooth-plate; wall microperforate, pustulose, with pustules situated between the pores. Supplementary sutural and areal apertures sometimes occur. Adult test size: 200–450 μm .

Etymology. From Latin “mutabilis” = changeable.

Stratigraphic Range. Lower to middle Miocene.

Remarks. *Mutabella* has a similar or identical wall texture to the genera *Tenuitella* Fleisher, *Globigerinita* Brönnimann, and *Globiger-*

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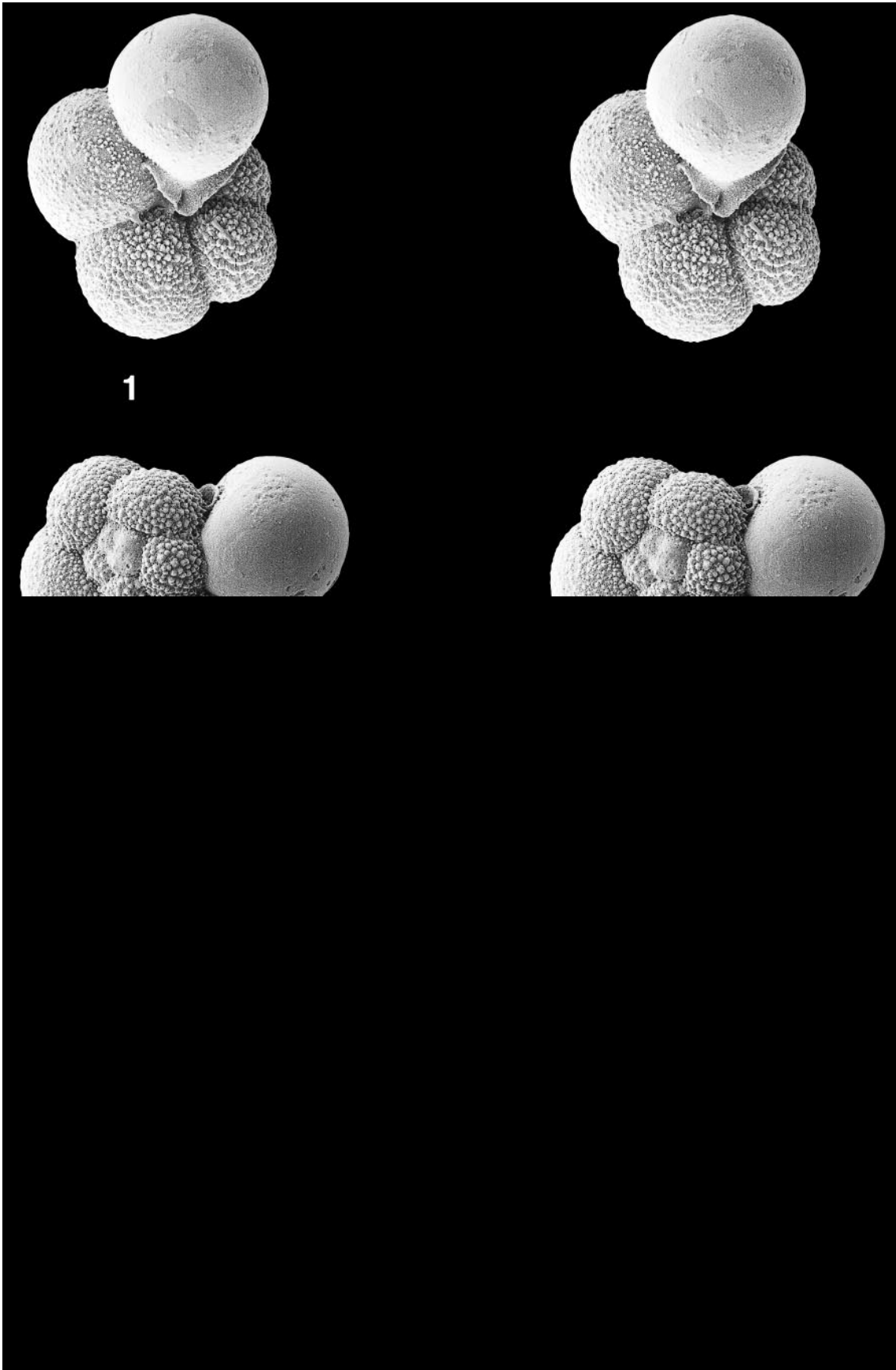


PLATE 1.

Mutabella mirabilis Gen. et sp. nov, holotype (USNM 510205), stereographic views. Figure 1, umbilical (ventral) view. Figure 2, spiral (dorsal) view. Figure 3, side (apertural) view. Sample 144-872A-10H-6, 59–61 cm.

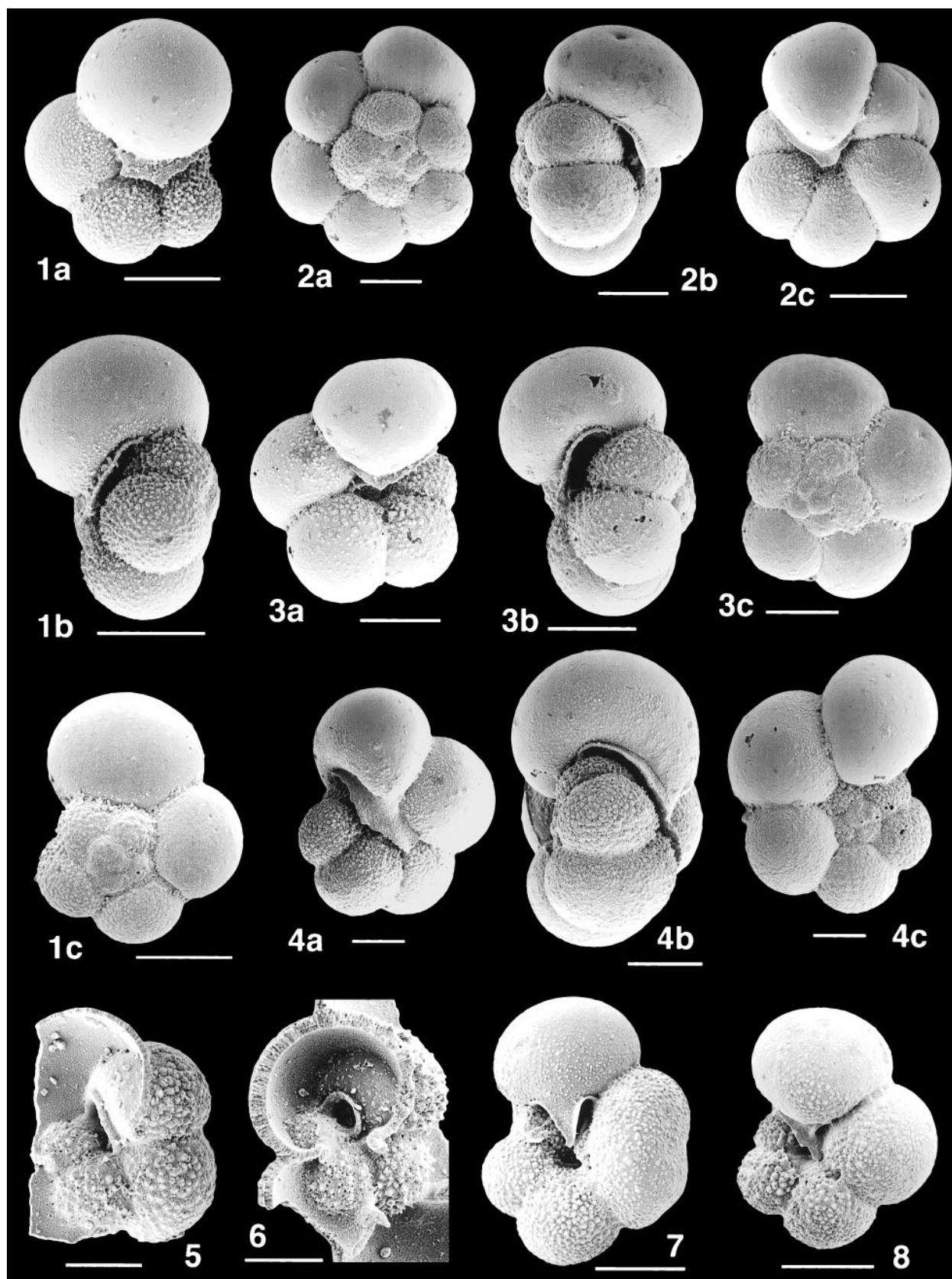


PLATE 2.

Mutabella mirabilis Gen. et. sp. nov. paratypes. Figure 1a-c, USNM 510206 Sample 872C-10H-7, 20–22 cm. Figure 2a-c, USNM 510207, Sample 865B-1H-3, 50–52 cm. Figure 3a-c, USNM 510208, Sample 872C-9H-6, 20–22 cm. Figure 4a-c, USNM 510209, Sample 865B-1H-3, 50–52 cm. Figures 5 (USNM 510210) and 6 (USNM 510211), Sample 865B-1H-3, 50–52 cm. Figure 7, USNM 510212, Sample 959A-21-2, 57–59 cm. Figure 8, USNM 510213, Sample 959A-22-3, 56–58 cm.

inatella Cushman and Stainforth, all of which also occur in the lower Miocene. It is distinguished from *Tenuitella* principally by its larger size, the frequent development of an umbilical tooth-plate, and the presence of supplementary sutural or areal apertures on some specimens. It differs from *Globigerinita* principally by the larger number of chambers per whorl, the frequent presence of an umbilical tooth-plate, and the apertural position, which is usually asymmetrical. It differs from *Globigerinatella* by having a lower trochospiral chamber arrangement, a less globular morphology, and an umbilical tooth-plate in some specimens, and by lacking multiple superimposed chamber-like bullae.

Mutabella mirabilis Pearson, Norris, and Empson, new species
Pl. 1, Figs 1-3 (holotype); Pl. 2, Figs. 1-8; Pl. 3, Figs 1-7, Pl. 4, Figs. 1-4.

Globorotalia sp. 4 Jenkins and Orr, 1972, p. 1096, Pl. 18: Figs. 7-12.

Tenuitella sp. 1 Fleisher, 1974, p. 1034, Pl. 17, Fig. 5.

Tenuitella sp. Pearson, 1995, p. 53, Pl. 1, Figs. 23-24.

Tenuitella sp. Norris, 1998, p. 455, Pl. 3, Figs. 7, 11-13, 19-20.

Description of holotype. The maximum diameter is 260 μm ; the minimum diameter is 195 μm . The test is comprised of 12 or 13 chambers arranged in a low sinistral trochospiral with about $4\frac{1}{2}$ chambers in the last whorl. Chambers are subglobular and slightly radially compressed except for the last chamber, which is almost spherical. Chambers expand fairly rapidly in size, such that the final chamber is about twice as wide as the first full chamber in the final whorl. Sutures on both sides of the test are depressed and radial with a slight degree of curvature. The aperture is a low, broad asymmetrical arch, situated in an intra-extraumbilical position. It is covered by an irregular tooth-plate, which is a composite structure formed by the fusion of the apertural lips of the final and penultimate chambers. The wall texture is microperforate and pustulose, and appears slightly translucent under the light microscope. Pustules are about 2-5 μm in diameter at their base and tend to be conical or tetrahedral. They are more prominent on the earlier chambers of the final whorl, becoming progressively smaller and less angular on later chambers. The final chamber lacks distinct pustules except in proximity to the apertural tooth-plate. The proloculus and first two or three chambers are obscured by smooth superficial calcification. Pores are distributed irregularly, but not strictly randomly, between the pustules. A single circular perforation, with a diameter of about 10 μm is present at the base of the final suture on the spiral side, and may represent a minute supplementary aperture.

Type Sample. Ocean Drilling Program (ODP) Sample 144-872A-10H-6, 59-61 cm; Biozone M3/4 (=N6/7).

Type Locality. ODP Hole 872A, Lo-En Guyot, Marshall Islands region, west Pacific Ocean (10°05.850'N, 162°51.960'E).

Etymology. Latin "mirabilis" = wonderful or strange.

Deposition. The type specimens are deposited in the United States National Museum, Washington, D.C. Holotype USNM 510205 and paratypes 510206-510223.

Morphological variability. The extraordinary feature of *M. mirabilis* is the high level of intraspecific variation. The holotype is a relatively "conservative" specimen. Some aspects of the morphological variability are examined in the morphometric study reported below. Other aspects are best explained with reference to the illustrated paratype specimens on Plates 2-4.

The specimen illustrated on Plate 2, Figs 2a-c has 5 $\frac{1}{2}$ chambers in the final whorl and a much lower rate of chamber expansion than the holotype. The chamber shape is also noticeably different, with chambers appearing a little more radially compressed on the spiral side, but radially extended on the umbilical side, tapering toward the umbilicus.

The specimen illustrated on Plate 2, Figs 3a-c is similar to the holotype in its overall shape. However, the tooth-plate is less well developed and has only a single point, directed toward the antepenultimate suture, and the aperture is higher and more arched.

The specimen on Plate 2, Figs 4a-c has a lower trochospiral than the holotype. The chambers of the final whorl are dorsally inflated, such that the proloculus is situated in a dorsal "umbilical" rather than near the apex of the test as in the holotype. The aperture extends past the periphery and slightly onto the spiral side. The tooth-plate is correspondingly elongate and irregular.

The specimens on Plate 2, Figs. 5 and 6 have been deliberately broken to reveal the morphology of the earlier chambers. Each has

four chambers in the early whorl and an extraumbilical foramen with a pronounced flaring lip. The chamber shape and arrangement are similar to the supposed ancestor, *Globigerinita glutinata* (see below), but the aperture is more extraumbilical than is typical for that taxon.

The specimen on Plate 2, Fig. 7 shows a very pronounced triangular tooth bordered by a thin lip and an irregular penultimate chamber. Those on Plate 2, Fig. 8 and Plate 3, figs. 1-4 illustrate a feature that is commonly encountered in this species, namely a composite tooth-plate. This is a complex structure, having been formed by the superimposition of the tooth of the final chamber onto the tooth of the penultimate chamber. The final tooth-plate is not in contact with the preceding tooth-plate along its entire length, but arches on to it, leaving an aperture on the posterior side, which connects directly with the primary aperture. The structure thus formed is similar to that seen in some species of the unrelated Cretaceous genera *Ticinella* and *Rotalipora*.

The specimens on Plate 3, Figs 1-4 also further illustrate the variation in test shape and apertural modification in the species. Some of them have small circular pits of unknown origin on the test surface. The specimen on Plate 3, Fig 4a-c shows a series of beaded calcite deposits on the sutures, which probably cover small supplementary apertures similar to the bullae sometimes seen in *Globigerinatella insueta* (see, for example, Pearson, 1995, Plate 2, Fig. 8). This specimen also has a curious long slit-like supplementary aperture on the spiral side beneath the final chamber, with an irregular tooth-plate like covering. This structure is clearly allied to the primary aperture and tooth-plate, but does not visibly connect on the outside of the test. The double-aperture is similar to the structure seen occasionally in various planispiral planktonic foraminifera, such as Eocene *Pseudohastigerina*, and has been observed on a number of specimens of *Mutabella*. A further spiral aperture which has a more rounded shape occurs beneath the penultimate chamber.

Many of the specimens discussed above have a tendency towards a more planispiral coiling mode, at least with respect to the final whorl. Some specimens are almost axially symmetric and biumbilicate in appearance, such as that shown on Plate 3, Fig. 5. In specimens such as this, the tooth-plate tends to be much reduced, constituting a more regular apertural lip. Note also the supplementary sutural apertures of this specimen.

The specimen on Plate 3, Fig. 6 shows an enlargement of the apertures on another, peeled specimen showing that when well-formed, they tend to be circular and bordered by a regular lip, as seen in *Globigerinatella insueta*.

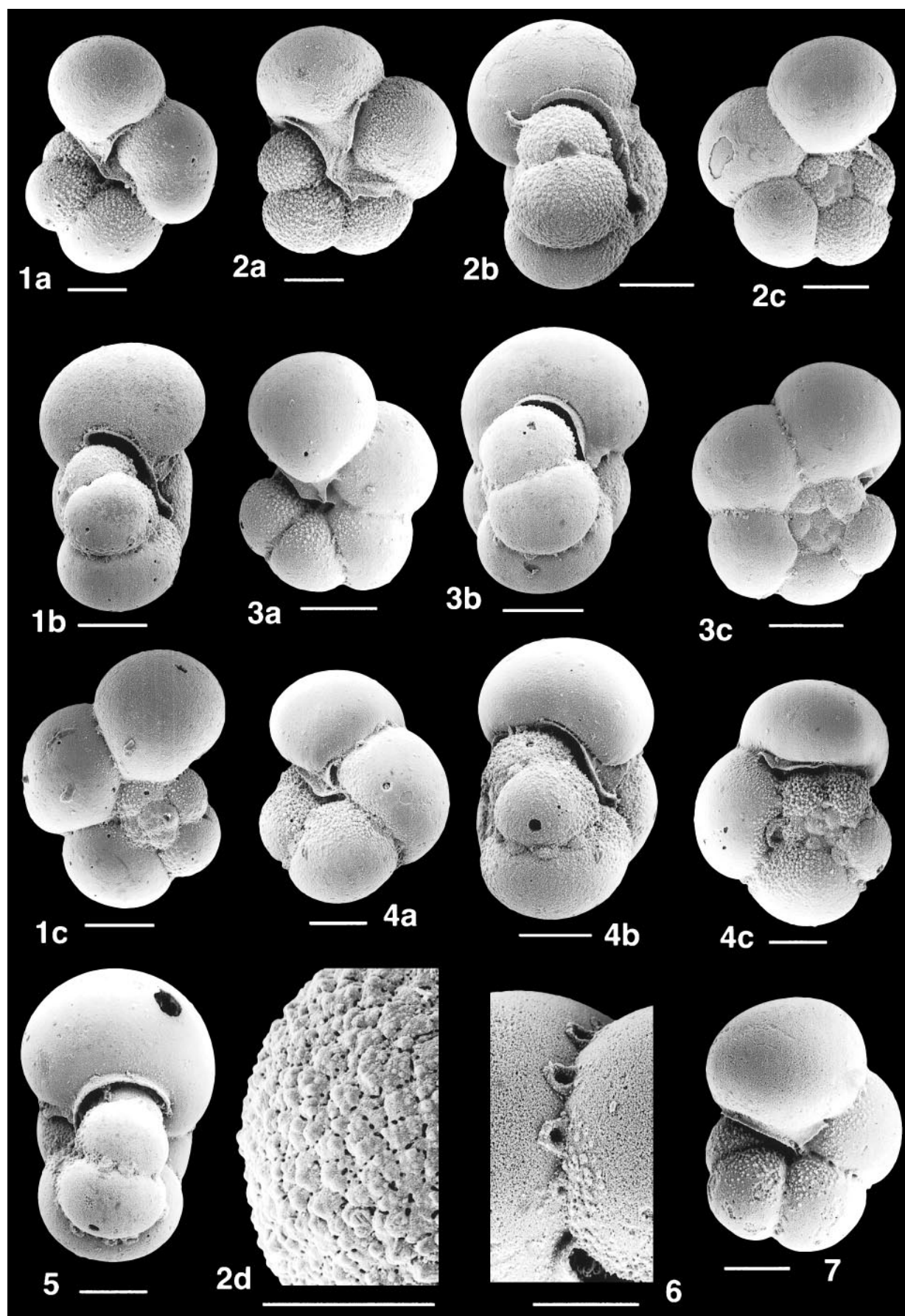
Further specimens are shown on Plate 4, Figs. 1-4. The specimen on Plate 4, Fig. 3 shows an areal aperture with a pronounced lip on the final chamber. This is a rare but not unique feature of *M. mirabilis*. Other specimens on the plate show an approach in morphology to *Globigerinita glutinata* (specimens of which are shown in Plate 4, Figs 8-10) in the early part of the stratigraphical range of *M. mirabilis*.

Stratigraphic Range. Probably from Zone M3 (lower Miocene) to Zone M7 (middle Miocene) (see discussion below).

KNOWN OCCURRENCES OF *MUTABELLA MIRABILIS*

SITE 78, EASTERN EQUATORIAL PACIFIC

Jenkins and Orr (1972, p. 1096) recorded specimens of *M. mirabilis* as "*Globorotalia* sp. 4" from a single sample from the top of Core 3, Section 3 of Site 78, tropical Pacific (07°57.37'N, 127°21.39'W). Also recorded in this sample was *Praeorbulina circularis*, which indicates Zone M5b. They described the species as "unkeeled *Globorotalia* with distinct umbilical teeth". The specimens illustrated on their Plate 18, Figs. 7-12 clearly show the microperforate wall texture and other features typical of the taxon, as described in this study. The specimens in their Figs. 7 and 10 show the composite umbilical tooth-plate that is often observed in *M. mirabilis*, and the specimen in their Fig. 11 shows an approach to planispiral coiling in the final whorl.



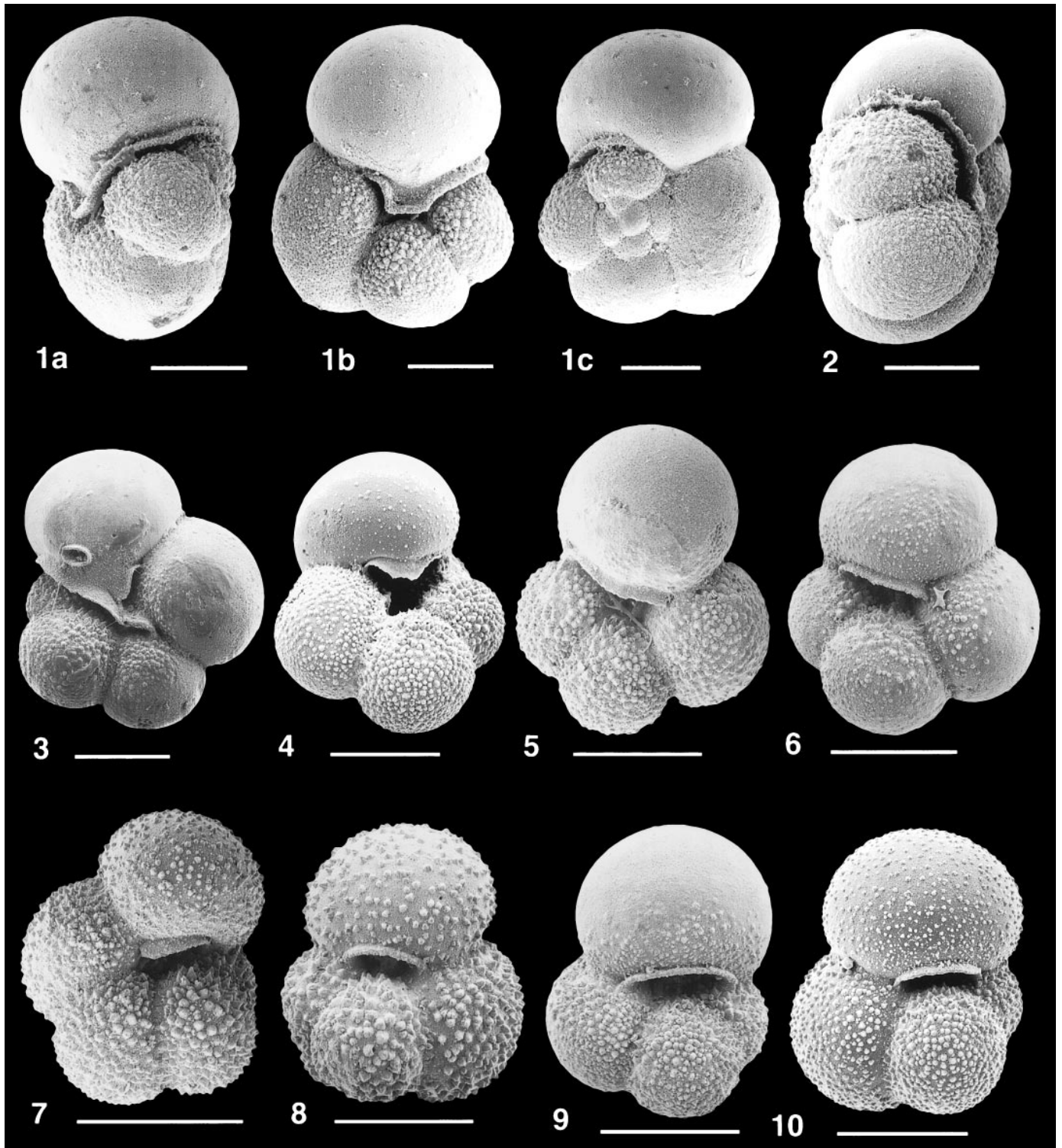


PLATE 4.

Mutabella mirabilis Gen. et. sp. nov. paratype. Figure 1a-c, USNM 510220, Sample 865B-1H-6, 50–52 cm. Figure 2, USNM 510221, Sample 865B-1H-6, 50–52 cm. Figure 3, USNM 510222, Sample 872A-10H-6, 59–61 cm. Figure 4, USNM 510223, Sample 959A, 21–2, 57–59 cm. *Globigerinita glutinata* sensu lato. Figure 5, Sample 872A-11H-3, 20–22 cm. Figure 6, Sample 872A-11H-3, 20–22 cm. Figures 7–9, Sample 872A-11H-3, 20–22 cm. Figure 10, Sample 959A-21–2, 57–59 cm.

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PLATE 3.

Mutabella mirabilis Gen. et. sp. nov. paratypes. Figure 1a-c, USNM 510214, Sample 865B-1H-3, 50–52 cm. Figure 2a-d, USNM 510215, Sample 865B-1H-3, 50–52 cm. Figure 3a-c, USNM 510216, Sample 865B-1H-3, 50–52 cm. Figure 4a-c, USNM 510217, Sample 865B-1H-6, 50–52 cm. Figure 5, USNM 510218, Sample 865B-1H-6, 50–52 cm. Figure 6–7, USNM 510219, Sample 865B-1H-3, 50–52 cm (figure 6 is detail of same specimen as figure 7).

SITE 219, ARABIAN SEA

Fleisher (1974, p. 1034) recorded specimens of *M. mirabilis* as “*Tenuitella* sp. 1”, which was found as a rare component of a single sample from Core 13, Section 1 of Site 219 (9°01.75'N, 72°52.67'E). The stratigraphic level of this sample is Zone M7. Fleisher referred to the anomalously large size of the taxon relative to other species that he included in the new genus *Tenuitella*, and drew attention to the “persistent umbilical flap”. A single specimen was illustrated, which clearly belongs to the species.

SITE 865, ALLISON GUYOT, MID-PACIFIC

A comprehensive planktonic foraminifer biostratigraphy of ODP Site 865, Allison Guyot (18°26.410'N, 179°33.339'W), has yet to be published. Preliminary investigations indicate that *M. mirabilis* is present throughout Core 143-865B-1H. Samples from this core are assigned to Zone M5 (Norris and Nishi, unpublished data), but the stratigraphical range is truncated above and below by unconformities.

SITE 871, LIMALOK GUYOT, WEST PACIFIC

Pearson (1995, p. 53) described the presence of *M. mirabilis* (recorded as “*Tenuitella* sp.”) from ODP Site 871 (Limalok Guyot; 5°33.432'N, 172°20.658'E). The species is very rare at this site, and consequently did not appear on the published range-chart, which includes only selected samples. Additional study has confirmed the presence of occasional specimens of *M. mirabilis* from Sample 144-871A-10H-1, 59-61 cm (Zone M3/4) to Sample 144-871A-8H-1, 125-127 cm (Zone M5b). The rarity of the species in this site in comparison with its relative abundance in Sites 872 and 873 (see below) is curious, considering all three sites have similarly well-preserved assemblages. Possibly the species peaked in abundance in Pacific sub-tropical latitudes and was rare in more equatorial waters. Alternatively, the species may have been ecologically opportunistic and its presence was not favoured by the hydrographic conditions prevailing above Limalok Guyot.

SITE 872, LO-EN GUYOT, WEST PACIFIC

Pearson (1995, Table 4) recorded *M. mirabilis* (as “*Tenuitella* sp.”) from a number of samples from ODP Site 872 (Lo-En Guyot, 10°05.850'N, 162°51.960'E). The lowermost specimens are found in Sample 872C-11H-2, 20-22 cm (Zone M3/4) and the species occurs from there continuously up to Sample 872C-9H-3, 20-22 cm (Zone M7). Additional study has revealed very rare specimens up to Sample 144-872C-8H-4, 78-80 cm (Zone M8). It should be noted that low-level reworking is also a consistent feature of these guyot-top environments, and occasionally reworking is severe (see Pearson, 1995, p. 39-43). Hence, rare specimens cannot be used to confidently identify the last occurrence datum. Note that the morphometric and isotopic studies reported below were conducted on specimens from Holes 872A and 872C.

SITE 873, WODEJEBATO GUYOT, WEST PACIFIC

Pearson (1995, Table 7) recorded *M. mirabilis* (as “*Tenuitella* sp.”) from various samples from Site 873 (11°53.796'N, 16°55.188'E), ranging from the bottom of the pelagic section, Sample 144-873B-6H-CC (Zone M4) up to Sample 144-873B-4H-5, 36-38 cm (Zone M9). All of these samples come from a severely reworked interval of the pelagic cap, and hence the last occurrence can not be used to establish the true stratigraphical range.

SITE 959

Norris (1998, p. 455) recorded *M. mirabilis* (as “*Tenuitella* sp.”) from Site 959 (3°37.656'N, 2°44.49'W), ranging from Sample 158-959A-23X-3, 60-64 cm (Zone M4) to Sample 158-959A-21X-5, 54-57 cm (Zone M5). The lowest occurrence at this site is in poorly preserved material. The topmost occurrence appears to be at a lower level than occurs in the Pacific and Indian Oceans, and possibly at neighboring Site 960 (see below).

SITE 960

Norris (1998, p. 455) recorded *M. mirabilis* (as “*Tenuitella* sp.”) from Site 960 (3°35.025'N, 2°44.149'W), ranging from Sample 158-960C-13H-3, 34-36 cm (Zone M3) to Sample 158-960C-11H-2, 34-36 cm. This topmost sample also contains the zone fossil *Orbulina suturalis*, and may therefore be assigned to Zone M6 or higher, but alternatively, specimens of *Orbulina* might have been introduced into the sample by down-hole contamination.

STRATIGRAPHICAL RANGE OF *MUTABELLA MIRABILIS*

None of the sites from which *M. mirabilis* have so far been recovered allows the stratigraphic range to be established unambiguously. The first occurrence appears to be in Zone M3, because it co-occurs with *Catapsydrax unicus* at Site 960. Unfortunately, *Catapsydrax* is very rare in the west Pacific sites. At Site 872, a complete intergradation of *Mutabella mirabilis* with *G. glutinata* is observed, indicating the true level of its origin between the first occurrences of *Globigerinatella* sp. (forms without areal apertures) and *Globigerinatella insueta* s. str. (forms possessing areal apertures). This can be considered to be within the lower part of Zone M3 (see Pearson, 1995, p. for a discussion of that Zone [= Zone N6]). The upper part of the stratigraphical range is probably within Zone M7. *Mutabella mirabilis* co-occurs with *Orbulina* at Sites 217, 872, 873, and questionably at Site 960. It co-occurs with *Fohsella peripheroacuta* at Sites 872 and 873, indicating Zone M7. Higher occurrences at these sites are probably due to reworking.

MORPHOMETRIC STUDY OF *MUTABELLA MIRABILIS*

Initial investigations of *M. mirabilis* suggested that the morphology of the species changed significantly through its stratigraphic range. We undertook a morphometric study to investigate this variation. The site with the most complete stratigraphical record is Site 872 (Lo-En Guyot), where the

TABLE 1. Sample numbers, depths, and biozone assignments for the samples used in the morphometric analysis.

Sample	Depth	Biozone
144-872A-9H-2, 59–61 cm	77.6 mbsf.*	M7
144-872A-9H-5, 59–61 cm	82.1 mbsf.	M5b
144-872A-10H-2, 59–61 cm	88.6 mbsf.	M5a
144-872A-10H-6, 59–61 cm	93.1 mbsf.	M5a
144-872A-11H-4, 59–61 cm	99.6 mbsf.	M3/4

* meters below sea floor.

species is present from Zone M3/4 through to Zone M7. Unfortunately, there is a short hiatus at this site (Zone M6 is missing) and reworking is commonly encountered. For this reason, a high-resolution study was not attempted.

We measured specimens from five freshly washed samples from Hole 872A, sieved at 150 μ m. Samples identification numbers, depths, and their biozones are given in Table 1. From each sample, 50 specimens were mounted on assemblage slides with the dorsal side upward and the coiling axis as vertical as could be judged. They were viewed using a Hamamatsu C3077 CCD image capture digitiser on a Macintosh Quadra with NIH Image 1.44 software. The coiling direction, maximum diameter, total number of chambers, number of chambers in the final whorl, and the height and inter-sutural length (ISL) of the last five chambers were measured for each specimen (Fig. 1). A further 150 specimens were picked from each sample and only their coiling direction determined.

Results of the morphometric study are shown in Fig. 2. The Chamber Expansion Index (CEI) is a measure of the average areal increase in chamber size in the last whorl, calculated according to the following equation:

$$\text{CEI} = \text{Cube root}[(\text{ISL}_{T-1} \times H_{T-1}) - (\text{ISL}_{T-4} \times H_{T-4})] \quad (1)$$

Note that the final chamber is often aberrant in size and shape, and can be smaller than the preceding chamber (kummerform), so it was not used in this index.

The Dorsal Chamber View Index (DCVI) was calculated as follows:

$$\text{DCVI} = \text{ISL}_{T-1}/H_{T-1} \quad (2)$$

This index effectively measures the degree of elongation of the penultimate chamber as visible from the spiral side. This is partly a function of chamber shape and partly a function of the degree of trochospirality. More trochospiral specimens are more involute and have less of the full height of the chambers of the final whorl visible from the spiral side; hence they have a greater DCVI.

All samples tend to be unimodal, so that there is no evidence for more than one biospecies in any of the samples. The CEI and coiling ratio are effectively constant, as far as can be judged with the present data. The coiling ratio is close to 50%. In total, 1000 specimens were measured, of which 468 were dextral (46.8%). The 95% confidence interval for this ratio extends to 49.89%, indicating that the real coiling ratio may be truly random.

Significant morphological changes occur through the core (Fig. 2; Table 2). Changes in the maximum diameter and

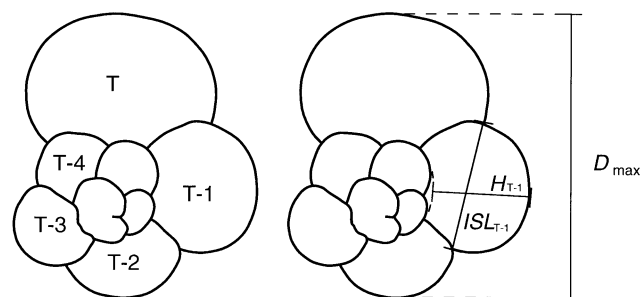


FIGURE 1. Morphometric measurements taken on the dorsal side of *Mutabella mirabilis*. A: Chambers were numbered from the terminal chamber (T) backwards because it was sometimes difficult to establish the precise number of chambers in the inner whorl. B: The height (H) and inter-sutural length (ISL) were recorded for the last final chambers, as well as the maximum diameter, the coiling direction (in this case, sinistral) and the number of chambers in the final whorl (in this case, 4.5).

the number of chambers in the final whorl appear to be positively correlated, but negatively correlated with DCVI. Considering the fact that no significant changes in the total number of chambers or CEI were detected, this covariation is explained by the fact that the initial population was more trochospiral and more involute than later populations. As the height of the spire was reduced, space restrictions necessitated an increase in the number of chambers in the final whorl and a more evolute coil. Because a greater proportion of the chamber height is visible from the spiral side on such specimens, the DCVI decreased. In the later part of the stratigraphical range, these morphological changes were reversed to some extent, but not completely.

Individuals in the lowermost population analyzed (Sample 144-872A-11H-4, 59-61 cm) show a complete intergradation with another species, *Globigerinita glutinata*. That species has a higher trochospiral than typical *M. mirabilis*, fewer chambers per whorl, and a more umbilically centred aperture. A somewhat arbitrary criterion, namely the presence of an irregular tooth-like structure, was used to assign specimens to *M. mirabilis*. It is possible that the real biological population at this level included forms that are effectively indistinguishable from *Globigerinita glutinata*, and thus the morphological range in this sample implied by Figure 2 may be more pronounced than is indicated.

ISOTOPIC STUDY OF *MUTABELLA MIRABILIS*

Originally, it was thought that the various unusual aspects of *M. mirabilis* might be explicable if it had secondarily become benthic in its life habitat. The sedimentary and trophic conditions on guyot tops appear to have been especially disadvantageous for most benthic foraminifer species (Pearson, 1995, p. 22), leaving a potential niche for specialized plankton-derived species to occupy. The “benthic” hypothesis for *Mutabella* would have explained 1) its unusual range of morphological variation, if it were evolving into a largely vacant benthic niche, 2) the fact that it had rarely been discovered in non-guyot sediments, and 3) the fact that it is abundant on some guyots, but extremely rare on others. We conducted a stable isotope study to investigate this possibility.

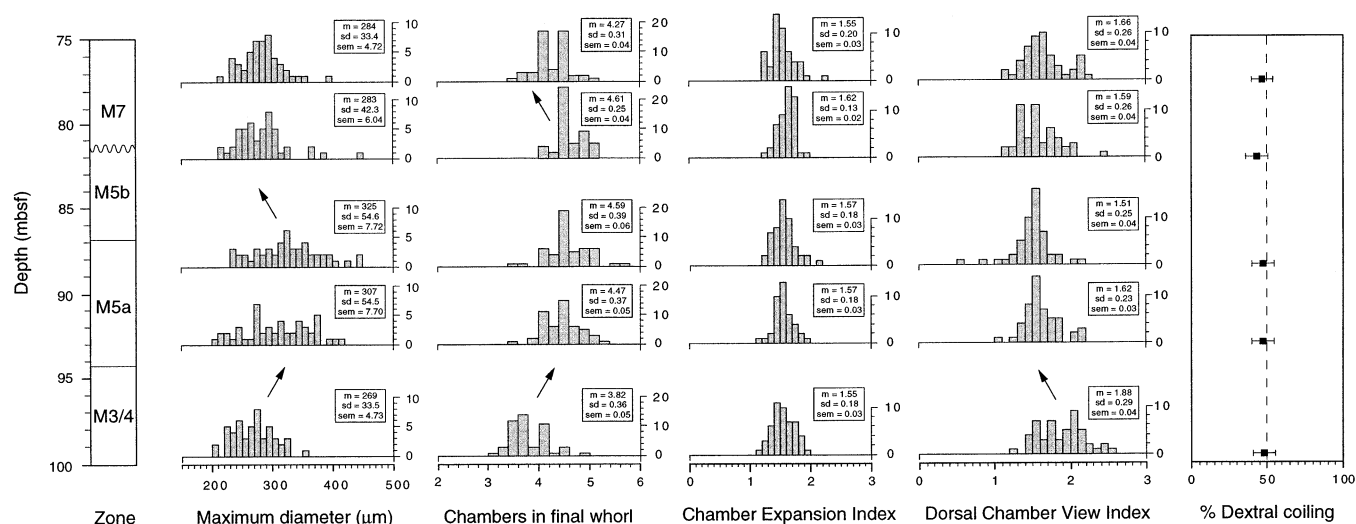


FIGURE 2. Morphometric data for five samples of *Mutabella mirabilis* from Hole 872A (samples as in Table 1). For the coiling ratio data, error bars correspond to 95% confidence intervals.

A total of 20 samples, each consisting of approximately 30 individuals of typical adult size for the species in question, were picked from Sample 144-872C-10H-2, 78–80 cm (Zone M5a). Seventeen of these samples were of known species of planktonic foraminifer, having a variety of preferred depth habitats. One sample was of mixed species of benthic foraminifera (which are very rare in this sediment). The remaining two samples were both of *Mutabella mirabilis*, the first consisting of regular trochospiral specimens with 4–5 chambers in the final whorl (“Morph 1”), and the second of more planispiral specimens with 5–6 chambers in the final whorl (“Morph 2”). In this way, it was possible to investigate whether the extreme end-member morphs of the taxon yielded different isotopic ratios, as would be expected if they were different species, or different ecotypes of the same species.

Isotopic data ($\delta^{13}\text{C}$ vs $\delta^{18}\text{O}$) are given in Table 3 and plotted in Figure 3. Note that the scale for oxygen isotopic ratios on the x-axis is reversed. The diagram is interpreted according to the model of Pearson et al. (1993, p. 130). The “J” shape on the graph formed by the isotopic ratios is the expected shape for an open ocean site with a stable thermocline (see also Spero and Williams, 1989; Pearson, 1998). Species that plot towards the top-right hand end of the graph are interpreted as having calcified in relatively

warm surface waters. Species that plot in and below the inflection of the “J” are interpreted as having calcified in deeper thermocline environments. One of the species on this plot, *Dentoglobigerina altispira*, has previously been identified as “suspect” in its carbon and oxygen isotopic ratios, which may have been affected by a substantial vital effect (Pearson and Shackleton, 1995, p. 403).

All the known species of planktonic foraminifera plot in approximately the positions on Figure 3 that are expected from other studies of Miocene species (see Pearson and Shackleton, 1995, for a discussion of the isotopic characteristics of many of these species from neighboring Site 871, and references therein). The two *Mutabella* samples plot very close to one another, indicating that there was no significant difference in the calcification temperature of the two morphs. The relatively light $\delta^{18}\text{O}$ suggests that the species was almost certainly planktonic and probably inhabited the surface mixed layer. The relatively positive $\delta^{13}\text{C}$ supports this view and is weak evidence for an association with photosynthesizing symbionts. The closest species to *Mutabella* on Figure 3 are forms belonging to the *Globigerinoides trilobus*-*Praeorbulina* group. The modern descendants of these species (*Globigerinoides sacculifer* and *Orbulina universa*) are known to be relatively shallow-dwelling species that are associated with symbionts. Pearson et al. (1997)

TABLE 2. Results of Student’s *t*-test (two tailed, unpaired) for stratigraphically adjacent samples as shown in Figure 2. Numbers for *t* given in bold are significant at the $P < 0.01$ significance level.

Sample	Dmax	CFW	CEI	DCVI
77.6 mbsf* vs. 82.1 mbsf	0.14 ($P = 0.444$)	5.86 ($P = 0.6 \times 10^{-7}$)	2.08 ($P = 0.041$)	1.30 ($P = 0.195$)
82.1 mbsf vs. 88.6 mbsf	4.26 ($P = 0.00005$)	0.21 ($P = 0.830$)	1.56 ($P = 0.122$)	1.57 ($P = 0.118$)
88.6 mbsf vs. 93.1 mbsf	1.68 ($P = 0.097$)	1.58 ($P = 0.116$)	0.12 ($P = 0.903$)	2.41 ($P = 0.018$)
99.6 mbsf vs. 93.1 mbsf	4.21 ($P = 0.00006$)	8.89 ($P = 0.1 \times 10^{-13}$)	0.34 ($P = 0.736$)	4.81 ($P = 0.5 \times 10^{-5}$)

* meters below sea floor.

TABLE 3. Stable isotope data for multiple species of foraminifera from Sample 144-872C-10H-2, 78–80 cm.

	$\delta^{18}\text{O}$	$\delta^{13}\text{C}$
<i>Benthic species</i>		
Mixed benthic spp. (benthic)	+0.92	1.15
<i>Previously known planktonic species</i>		
<i>Dentoglobigerina altispira</i>	-1.82	3.79
<i>Fohsella peripheroronda</i>	-1.38	1.98
<i>Globigerinatella insueta</i>	-1.78	2.79
<i>Globigerinella praesiphonifera</i>	-1.49	1.93
<i>Globigerinita glutinata</i> (without bulla)	-1.79	2.79
<i>Globigerinita glutinata</i> (with bulla)	-1.45	2.41
<i>Globigerinoides bisphericus</i>	-1.81	3.07
<i>Globigerinoides mitra</i>	-1.78	3.07
<i>Globigerinoides obliquus</i>	-1.75	2.53
<i>Globigerinoides ruber</i>	-1.98	2.70
<i>Globigerinoides trilobus</i>	-1.80	3.16
<i>Globoquadrina dehiscens</i>	-1.51	2.77
<i>Globoquadrina venezuelana</i>	-0.02	1.93
<i>Globorotalia praescitula</i>	-0.71	1.68
<i>Globorotaloides hexagonus</i>	-0.41	2.33
<i>Paragloborotalia mayeri</i>	-1.54	2.20
<i>Praeorbulina sicana</i>	-1.76	3.11
<i>Mutabella mirabilis</i>		
Morph 1 (4–5 chambers)	-1.62	3.07
Morph 2 (5–6 chambers)	-1.65	3.11

have investigated the isotopic characteristic of this lineage in detail for Site 871 and concluded that representatives of these lineages maintained a constant life habitat since the early Miocene, including the time interval represented by the sample analyzed in Figure 3.

To further investigate the hypothesis that *Mutabella* associated with photosynthesizing symbionts, we investigated the range of carbon isotope ratio with size fraction. A strong positive correlation between size and $\delta^{13}\text{C}$ in a species is regarded as evidence of a possible photosymbiotic association in life (Pearson et al., 1993; Norris, 1998; Pearson,

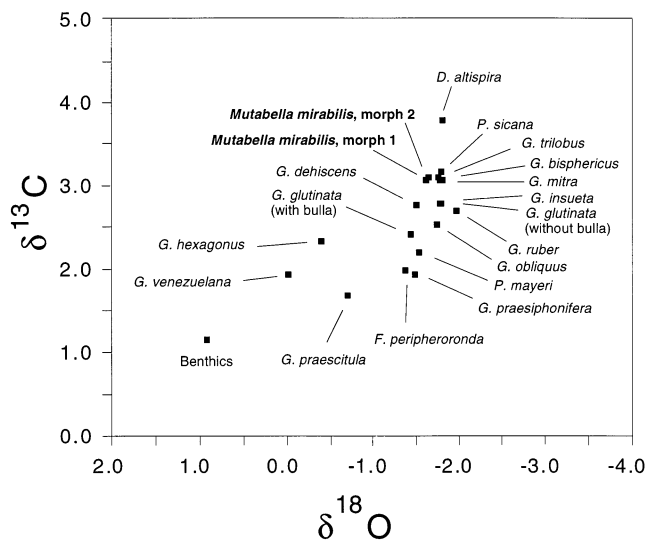
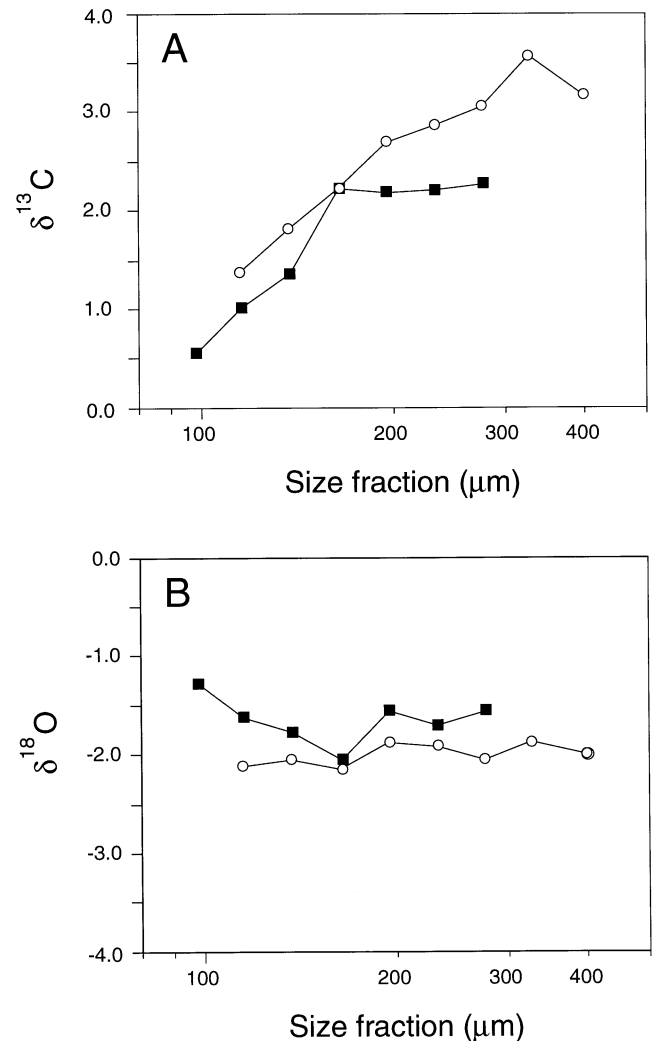


FIGURE 3. Oxygen vs. carbon isotopic plot of multiple species of planktonic foraminifera from Sample 144-872C-10H-2, 78–80 cm (Zone M5a).

TABLE 4. Stable isotope data for different size fractions of *Mutabella mirabilis*.

Size range (μm)	$\delta^{18}\text{O}$	$\delta^{13}\text{C}$
<i>Sample 144-872C-9H-1, 20–22 cm</i>		
106–125	-2.12	1.37
125–150	-2.05	1.81
150–180	-2.15	2.21
180–212	-1.88	2.69
212–255	-1.91	2.86
255–300	-2.05	3.05
300–355	-1.88	3.57
>355	-2.01	3.17
<i>Sample 144-872C-11H-4, 20–22 cm</i>		
90–106	-1.28	0.55
106–125	-1.62	1.02
125–150	-1.78	1.35
150–180	-2.04	2.23
180–212	-1.55	2.19
212–255	-1.70	2.21
255–300	-1.55	2.28

FIGURE 4. Isotopic ratios of *Mutabella mirabilis* as a function of size fraction. Closed squares: Sample 144-872C-11H-4, 20–22 cm (Zone M3/4). Open circles: Sample 144-872C-9H-1, 20–22 cm (Zone M7). A: Carbon isotopes. B: Oxygen isotopes.

count of its wall texture, general shape and apertural position (see also Fleisher, 1974; Li Qianyu, 1987). However, the species is much larger than any member of that genus, and no morphological convergence toward any known species of *Tenuitella* has been observed. As discussed above, a complete intergradation with *Globigerinita glutinata* was found at the base of its stratigraphical range. Dissected specimens also show that the juveniles display a greater similarity to *G. glutinata* than to any species of *Tenuitella*. The general resemblance to *Tenuitella* is now regarded as being due to evolutionary convergence.

Another lineage that bears some similarities to *Mutabella* is *Globigerinatella*. This genus has traditionally been regarded as monospecific (e.g. Bolli and Saunders, 1985), but Pearson (1995, p. 46-47) distinguished forms without areal apertures (*Globigerinatella* sp.) from forms with areal apertures (*G. insueta*). Forms without areal apertures appear first in the stratigraphical record (see also Chaisson and Leckie, 1993; Pearson and Chaisson, 1997). Like *Mutabella*, such forms show a complete intergradation with *Globigerinita glutinata*, but at slightly lower stratigraphical levels than the first appearance of *M. mirabilis*. However, since juveniles of *Globigerinatella* sp. are closely similar to *Globigerinita glutinata*, and are difficult to reliably distinguish, it must also be considered possible that *Mutabella* arose from *Globigerinatella*. Interestingly, *Globigerinatella* sp. commonly possesses supplementary sutural apertures as occur occasionally in *M. mirabilis*. These surround the multiple chamber-like bullae that are used as diagnostic of the genus *Globigerinatella*. The question arises as to whether the supplementary apertures sometimes seen in *Mutabella* are homologous with those in *Globigerinatella*. This would imply that the final few (at least) chambers of *Mutabella* are not genuine chambers but swollen bullae, as in *Globigerinatella*. However, we do not believe that this is likely, because no distinction is generally observed between the earlier and later chambers of the test in *M. mirabilis*.

In summary, *Mutabella* is regarded as having evolved in the early Miocene from *Globigerinita glutinata* (Figure 5), reversing some of the morphological changes associated with the evolution of that species from *Tenuitella* in the late Oligocene. Its evolution shows some parallels with *Globigerinatella*, which is also a descendant of *Globigerinita*.

WHY SO VARIABLE?

From a paleontological perspective, it is interesting that what is apparently a single species should be so variable in its morphology, especially considering that its supposed ancestor, *Globigerinita glutinata*, is quite conservative in form. One possible explanation for this plasticity would be if the later "chambers" of *M. mirabilis* were in fact bullae which are conceivably subject to different and less stringent morphogenetic constraints than true chambers. As discussed above, we have found no evidence for this. Another explanation for the variability might be if the species was evolving into empty ecospace. This, for example, is believed to have occurred among several planktonic foraminiferal species (e.g. *Parvularugoglobigerina eugubina*) after the Cretaceous/Paleogene boundary mass extinction (Olsson et al., 1999, p. 84). However, there is no evidence from the iso-

topic study that the habitat of *Mutabella mirabilis* was in any way different from other species of planktonic foraminifer with which it coexisted. A third possibility is that planktonic foraminifera, in general, tend to have rigid genetic controls on test construction, but in *M. mirabilis* these controls were relaxed (see Möller and Swaddle, 1997, for a review of developmental stability and evolution). Until more is known about the genetics of test construction in foraminifera, this speculation is difficult to test. But whatever the cause of the extreme level of intraspecific variation in *M. mirabilis*, it is interesting that the species survived for several millions of years, which is a typical duration for a planktonic foraminifer species. The morphological variants were not rapidly "weeded out" by natural selection, and the species-lineage does not show an anomalously rapid rate of anagenetic evolution in comparison to other planktonic foraminifera.

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