

TAXONOMIC REVISION OF THE LATE CENOMANIAN PLANKTONIC FORAMINIFERA *ROTALIPORA GREENHORNENSIS* (MORROW, 1934)

ATSUSHI ANDO^{1,2,3,4} AND BRIAN T. HUBER¹

ABSTRACT

Rotalipora greenhornensis has long been considered a representative planktonic foraminiferal species of the single-keeled Rotaliporinae of late Cenomanian age. Its taxonomic identity, however, is still ambiguous because this taxon has been distinguished by morphological criteria (numerous, strongly curved chambers, etc.), whereas the other species of *Rotalipora* are distinguished primarily by their apertural and ornamental characters (raised sutures, periumbilical ridges, etc.). The presence of strongly raised sutures throughout the umbilical and spiral sides has also been used to identify *R. greenhornensis*, but this criterion is troublesome as it also applies to its direct ancestor *Rotalipora globotruncanoides*. Reexamination of the holotype and observation of many topotypes and some North Atlantic and Pacific hypotypes reveals that, despite its remarkable morphological variability, *R. greenhornensis* is distinguishable by having umbilical sutures that are not fully raised, with the last several being depressed, and supplementary apertures that are umbilical in position and surrounded by a continuous series of closely-spaced periumbilical ridges. Moreover, reduction of the raised sutures tends to occur simultaneously on both the umbilical and spiral sides. Such apertural and ornamental characters of *R. greenhornensis* serve as its primary distinguishing features, allowing a clear-cut differentiation of this taxon from other species of *Rotalipora*, particularly the closely associated species *R. globotruncanoides* and plano-convex *Rotalipora deeckeii*.

INTRODUCTION

Originally described as *Globorotalia greenhornensis* by Morrow (1934) from the Greenhorn Formation in Kansas, U. S. Western Interior (Pl. 1, fig. 1), *Rotalipora greenhornensis* (Morrow) has been accepted as an important planktonic foraminiferal taxon occurring in the upper Cenomanian at low-to-middle latitudes worldwide. This species constitutes the terminal part of a major phyletic lineage called the *appeninica* group (*sensu* Wonders, 1978) in the single-keeled genus *Rotalipora* (Table 1), and ultimately evolved into non-keeled *Anaticinella multiloculata* (Morrow, 1934) during the latest Cenomanian (Eicher, 1972). The importance of *R. greenhornensis* is further illustrated by the fact that its extinction, along with the other species of *Rotalipora* and *Anaticinella* during the latest Cenomanian, has been linked with paleoenviron-

mental changes associated with Oceanic Anoxic Event 2 (e.g., Leckie, 1985; Jarvis and others, 1988; Huber and others, 1999; Desmares and others, 2003; Keller and Pardo, 2004).

It has long been considered that *R. greenhornensis* is easily distinguished from the other species of *Rotalipora* by its numerous (>8), elongate and strongly curved (i.e., “crescent-shaped”) chambers in the spiral side (e.g., Robaszynski and Caron, 1979; Caron, 1985). Also, the view that *R. greenhornensis* is characterized by its strongly raised sutures throughout the umbilical and spiral sides (e.g., Robaszynski and Caron, 1979; Caron, 1985) has widely been accepted; the strongly curved and raised aspect of umbilical sutures is often expressed as “horseshoe-like.” On the other hand, these morphological and sutural characteristics have been arbitrarily interpreted and used by previous researchers, and the practice resulted in extremely high variability in the hypotypes of *R. greenhornensis*.

González-Donoso and Linares *in* Robaszynski and others (1993) have reintroduced *Rotalipora globotruncanoides* Sigal, 1948 [= senior synonym of the more familiar *Rotalipora brotzeni* (Sigal, 1948; see also Appendix 1 herein)], whose phyletic position is directly ancestral to *R. greenhornensis*. Due to its biostratigraphic importance as an index species defining the base of the Cenomanian Stage (Robaszynski and Caron, 1995; Gale and others, 1996; Kennedy and others, 2004), there has been a significant increase in the use of *R. globotruncanoides* in the recent literature. Nevertheless, there remains uncertainty regarding the taxonomy of *R. globotruncanoides* because its diagnosis states that the umbilical sutures are fully curved and raised, which also applies to *R. greenhornensis* (Table 1). Although it is generally considered that *R. greenhornensis* has “strongly” raised sutures, the criterion that differentiates “strongly” and “normally” raised states of sutures has not been established.

If the taxonomic difference between *R. greenhornensis* and *R. globotruncanoides* is only determined by chamber morphologies, criteria for separating these species are questionable. The genus *Rotalipora* has been shown to have considerable intraspecific variability, and the species level of this taxon seems to be more reasonably assigned based on the positions of supplementary apertures and the presence or absence of ornamental elements (raised sutures, periumbilical ridges, etc.) than by morphological criteria (e.g., González-Donoso and Linares *in* Robaszynski and others, 1993). Thus, it is still difficult to reasonably invalidate the previous considerations that *R. globotruncanoides* should be synonymized under *R. greenhornensis* based on the order of publication date (Loeblich and Tappan, 1961; Pessagno, 1967; Carter and Hart, 1977; Masters, 1977; Leckie, 1984; Caron, 1985).

To establish the taxonomic identity of *R. greenhornensis*, it is necessary that its apertural and ornamental character-

¹Department of Paleobiology, MRC NHB 121, Smithsonian National Museum of Natural History, Washington, D.C. 20013-7912, USA.

²Department of Earth Sciences, Faculty of Science, Chiba University, Chiba 263-8522, Japan.

³Now at Research Institute for Humanity and Nature, Motoyama 457-4, Kamigamo, Kita-ku, Kyoto 603-8047, Japan.

⁴Correspondence author. E-mail: ando@chikyu.ac.jp

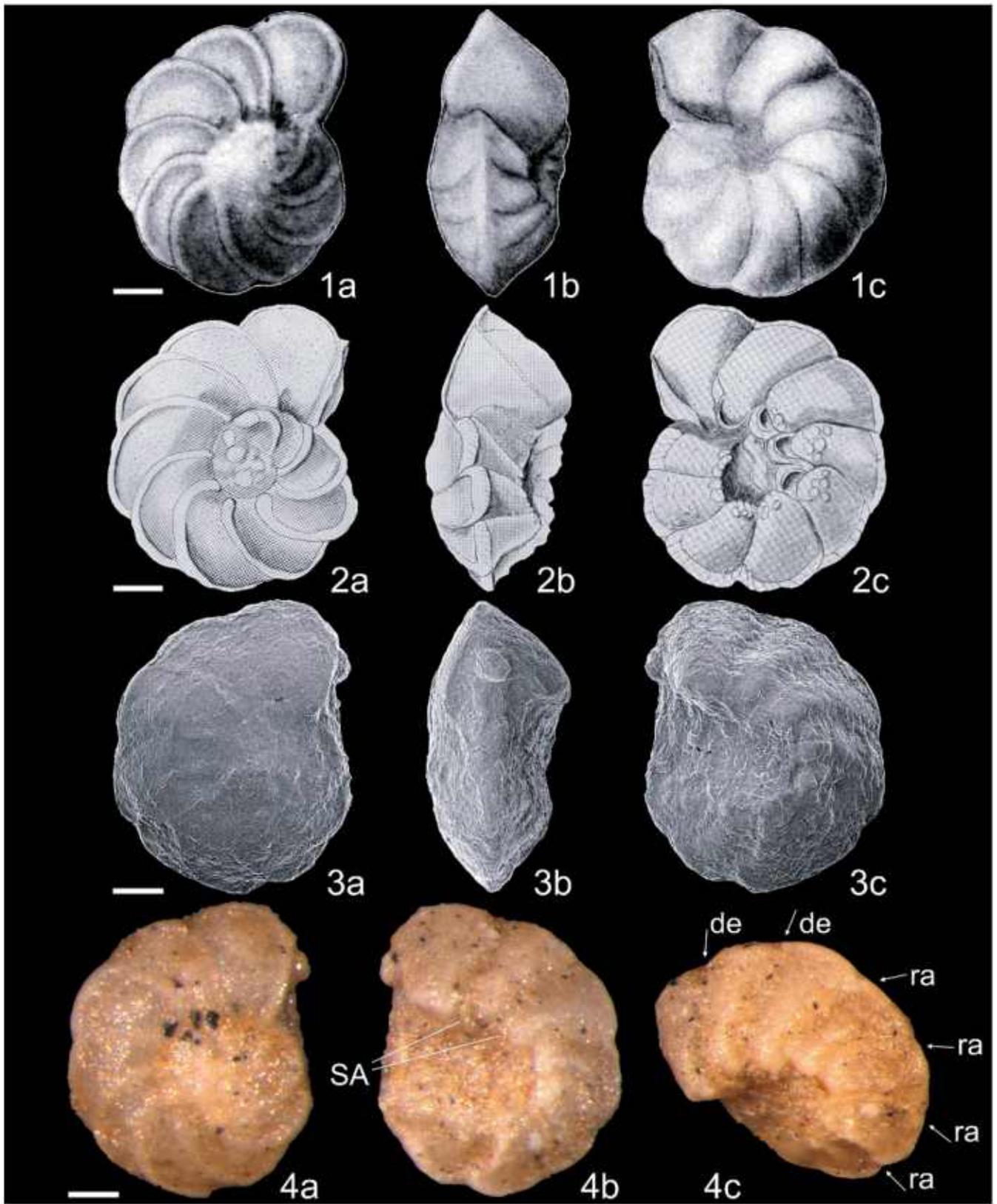


PLATE 1

Holotype of *Rotalipora greenhornensis* (Morrow) (= *Globorotalia greenhornensis* Morrow), USNM 75378. 1 Type figure by Morrow (1934): (a) spiral, (b) edge and (c) umbilical views. 2 Figure redrawn by Brönnimann and Brown (1956): (a) spiral, (b) edge and (c) umbilical views. 3 Uncoated SEM images: (a) spiral, (b) edge and (c) umbilical views. 4 Stereomicroscopic images: (a) spiral, (b) umbilical and (c) inclined rear views; SA = supplementary aperture; de = depressed umbilical suture; ra = raised umbilical suture. Note the presence of periumbilical ridges on all of the chamber surfaces as relatively light-colored and smoothed areas. All scale bars = 100 μ m.

TABLE 1. Interrelationship of rotaliporid species of the major *appenninica* group in terms of the apertural and ornamental characters. Species names are arranged (from left to right) in the order of evolutionary appearance. Note that the traditional species concept of *greenhornensis* does not differentiate it from its direct ancestor *globotruncanoides*.

Apertural/ornamental character	Expression	<i>R. praebalernaensis</i>	<i>R. balernaensis</i>	<i>R. appenninica</i>	<i>R. gandolfii</i>	<i>R. globotruncanoides</i>	<i>R. greenhornensis</i> (traditional)	<i>R. greenhornensis</i> (this study)
Supplementary aperture	Sutural*	×	×	×	×	×	×	
	Fully umbilical							×**
Keel (= equatorial)	In part	×		×	×	×	×	
	In full		×	×	×	×	×	×
Periumbilical ridge	Absent	×	×					
	In part In full			×	×	×	×	×***
Umbilical suture	Fully depressed	×	×	×				
	Partly raised				×			×
	Fully raised					×	×	
Spiral suture	Partly raised	×						×
	Fully raised		×	×	×	×	×	

*Umbilical in position in the early ontogenetic stage, shifts to sutural position in the late ontogenetic stage.

**Highly flexible in position in the late evolutionary stage due to umbilical protrusion of chamber surfaces and/or doubling of supplementary apertures (Eicher, 1972).

***Poreless periumbilical thickenings in the late evolutionary stage (Eicher, 1972).

istics be uniquely differentiated from those of the other species of *Rotalipora*, particularly its direct ancestor *R. globotruncanoides*. However, such taxonomically important characters have remained uncertain due to a lack of information from the primary type specimen (one holotype only) as is briefly summarized below: (1) Morrow's (1934) type description and figure show that *R. greenhornensis* exhibits fully *depressed* umbilical sutures and smooth umbilical chamber surfaces throughout (Pl. 1, fig. 1); (2) Brönnimann and Brown (1956) provided a more detailed redrawing of the holotype showing fully *depressed* umbilical sutures, periumbilical ridges, and four well-developed supplementary apertures opening in the umbilical area (Pl. 1, fig. 2); (3) Loeblich and Tappan (1961) and Pessagno (1967) made observations on the holotype in their comprehensive taxonomic works and confirmed that Brönnimann and Brown's (1956) redescription is valid; (4) Masters (1977), on the other hand, found that the holotype exhibits only one supplementary aperture and that its umbilical structure is obscured by infilling of debris, implying poor preservation.

In summary, if observations made originally by Morrow (1934) and secondarily by Brönnimann and Brown (1956) are valid, clarification of the *greenhornensis* concept may be possible on the basis of the *depressed* nature of umbilical sutures and/or intraumbilically positioned supplementary apertures. However, as suggested by Masters (1977), inconsistencies in previous observations of the type specimen have led to considerable confusion in what characters should be used for the diagnosis and precise identification of *R. greenhornensis*.

To that end we obtained detailed observations of the holotype of *R. greenhornensis* in order to elucidate its taxonomically important apertural and sutural characters. In addition, numerous topotypes of *R. greenhornensis* were also investigated for the purpose of properly constraining

its intraspecific variability. We further examined some specimens from North Atlantic and Pacific deep-sea sections to constrain the identity of the plano-convex morphotype *Rotalipora deeckeri* with respect to *R. greenhornensis* sensu stricto.

MATERIAL AND METHODS

The holotype of *Rotalipora greenhornensis* (Morrow, 1934) (= *Globorotalia greenhornensis* Morrow) is deposited in the Cushman Collection of the Smithsonian National Museum of Natural History (NMNH) with the collection number of USNM 75378. As this specimen co-occurs with *Rotalipora cushmani* (Morrow, 1934) (= *Globorotalia cushmani* Morrow, 1934), the type level is within the *R. cushmani* Zone. Scanning electron microscopic (SEM) images of this specimen were obtained at the Smithsonian NMNH without applying a conductive coating by using a low-kilovoltage setting on a Leica Stereoscan 440 SEM. This specimen was also examined under an OLYMPUS SZX-12-MD stereomicroscope at the Smithsonian NMNH to illustrate its diagenetically enhanced features. This stereomicroscope enables generation of a totally focused magnified image of a specimen by digitally synthesizing multiple focal-depth images taken from top to bottom (e.g., the plan and edge views in Plate 1 were initially captured as three and seven evenly-spaced layers, respectively).

The topotypes of *R. greenhornensis* examined in this study are also deposited in the Cushman Collection of the Smithsonian NMNH. A total of 20 specimens is mounted on a one-hole microslide that is given the collection number of USNM 479719 in the "Loeblich Collection." In addition, another USNM 371488 specimen that is identical to that figured in Loeblich and Tappan (1961; Pl. 7, fig. 9) was also examined. Information written on both microslides states

that both were collected from Morrow's (1934) type locality (Greenhorn Limestone, Hartland Shale Member, SE 1/4, sec. 31, T. 21 S., R. 22 W., north bank of creek about 1/4 mile west of road, Hodgeman Co., Kansas) by Max Furrer in 1959. This in turn indicates that a suite of USNM 479719 specimens corresponds to those studied in Loeblich and Tappan (1961) as "unfigured topotypes." Uncoated SEM images of the selected specimens were obtained by using a JEOL JSM-6330F field emission SEM at Tohoku University.

We further present several well-preserved specimens of *R. greenhornensis* and plano-convex *Rotalipora deeckei* from the upper Cenomanian of Ocean Drilling Program (ODP) Site 1050 (western North Atlantic Ocean) and Deep Sea Drilling Project (DSDP) Site 463 (central Pacific Ocean) in order to highlight taxonomic differences between the two species. For ODP Site 1050, the samples used are the same as those examined in Huber and others (1999). For DSDP Site 463, the foraminiferal sample was obtained from semi-lithified chalk by applying the glacial acetic acid method (e.g., Tur and others, 2001). Details of the mid-Cretaceous planktonic foraminiferal biostratigraphy for Site 463 will be reported in a forthcoming paper (Ando and Kaiho, unpublished data). These specimens are deposited in the Cushman Collection, Smithsonian NMNH with the collection numbers of USNM 531410–531413.

PRIMARY AND SECONDARY TYPES OF *ROTALIPORA GREENHORNENSIS*

REEXAMINATION OF HOLOTYPE

As shown by the SEM and stereomicroscopic images (Pl. 1, figs. 3, 4), the holotype of *Rotalipora greenhornensis* is poorly preserved and has been subjected to dissolution and/or mineralogical replacement of the original test, but, fortunately, its important taxonomic characters are retained. Our reexamination of the holotype is described below, together with comments on the original description by Morrow (1934; Pl. 1, fig. 1 herein) and subsequent observations by Brönnimann and Brown (1956; Pl. 1, fig. 2 herein) and Masters (1977).

Apertural characteristics

The primary aperture is entirely obscured. The supplementary apertures are hardly recognizable, but two faint ones, whose positions are nearly umbilical, are discernible near the umbilical margin along the last two sutures (Pl. 1, fig. 4b). This observation is consistent with that of Masters (1977), who observed only one supplementary aperture. On the other hand, the depiction of four well-developed supplementary apertures by Brönnimann and Brown (1956) is inaccurate.

Ornamental characteristics

The umbilical sutures are difficult to recognize, but we found that the last two are clearly *depressed*, whereas the others are *raised*. This feature can be faintly seen in the SEM image (Pl. 1, fig. 3c) and is best shown in the inclined rear view of a stereomicroscopic image (Pl. 1, fig. 4c). This

observation is inconsistent with both the original drawing by Morrow (1934) and the secondary drawing by Brönnimann and Brown (1956), respectively, both of whom illustrate fully depressed umbilical sutures. The sutures in the spiral side are fully raised, though not distinctive due to dissolution.

The periumbilical ridges are diagenetically highlighted in the stereomicroscopic view as relatively light-colored and smoothed areas on all of the umbilical chamber surfaces (Pl. 1, fig. 4b). Periumbilical ridges were also depicted by Brönnimann and Brown (1956), although the pustule-like structures shown in their illustration are not recognized here.

The porticus (umbilical cover-plate) is unrecognizable because the umbilical area is obscured by diagenetic replacement and infilling of calcite cement. Our observations contradict Brönnimann and Brown's (1956) redrawing, which shows an empty umbilical area provided with a porticus. By contrast, the observation made by Masters (1977) is appropriate.

Morphological characteristics

Gross morphology and chamber arrangement of the holotype reexamined in this study are similar to those illustrated by Morrow (1934) and Brönnimann and Brown (1956) in that the specimen is 9-chambered with a slightly lobulate periphery and an elliptical peripheral outline. However, some differences exist. The profile is equally biconvex, not asymmetrically biconvex with a more inflated umbilical side (Brönnimann and Brown, 1956). Chambers in the spiral side are initially strongly curved and elongate but become semi-circular in shape, unlike the illustrations by Morrow (1934) and Brönnimann and Brown (1956) that emphasize strongly curved and elongate chambers throughout the final whorl except for the ultimate chamber. The dimension of the umbilicus is about one-third of the maximum test diameter and, as pointed out by Masters (1977), not as small as that illustrated by Morrow (1934).

OBSERVATIONS OF TOPOTYPES

Among 20 topotype specimens mounted in the USNM 479719 microslide, ten fully-adult specimens were selected for SEM imaging (Pls. 2, 3). The rejected specimens are much smaller in size and are not considered here. In addition, SEM images of Loeblich and Tappan's (1961; Pl. 7, fig. 9) topotype specimen (USNM 371488) are included in Plate 3. Preservation of these specimens is moderate to good, sufficient to retain the details of apertural and ornamental characters as well as pores. It is noteworthy that the selection of the USNM 479719 topotypes by Loeblich and Tappan (1961) was randomly made because (1) specimens with various ontogenetic stages are included in the microslide and (2) rotaliporid species from the Greenhorn Limestone recorded by Loeblich and Tappan (1961) are *greenhornensis* and *cushmani* only. Thus, these authors were not selective in preparing the microslide.

Apertural and ornamental characteristics

Among the topotypes examined, three of the USNM 479719 specimens (Pl. 2, figs. 1–3) show depression of the

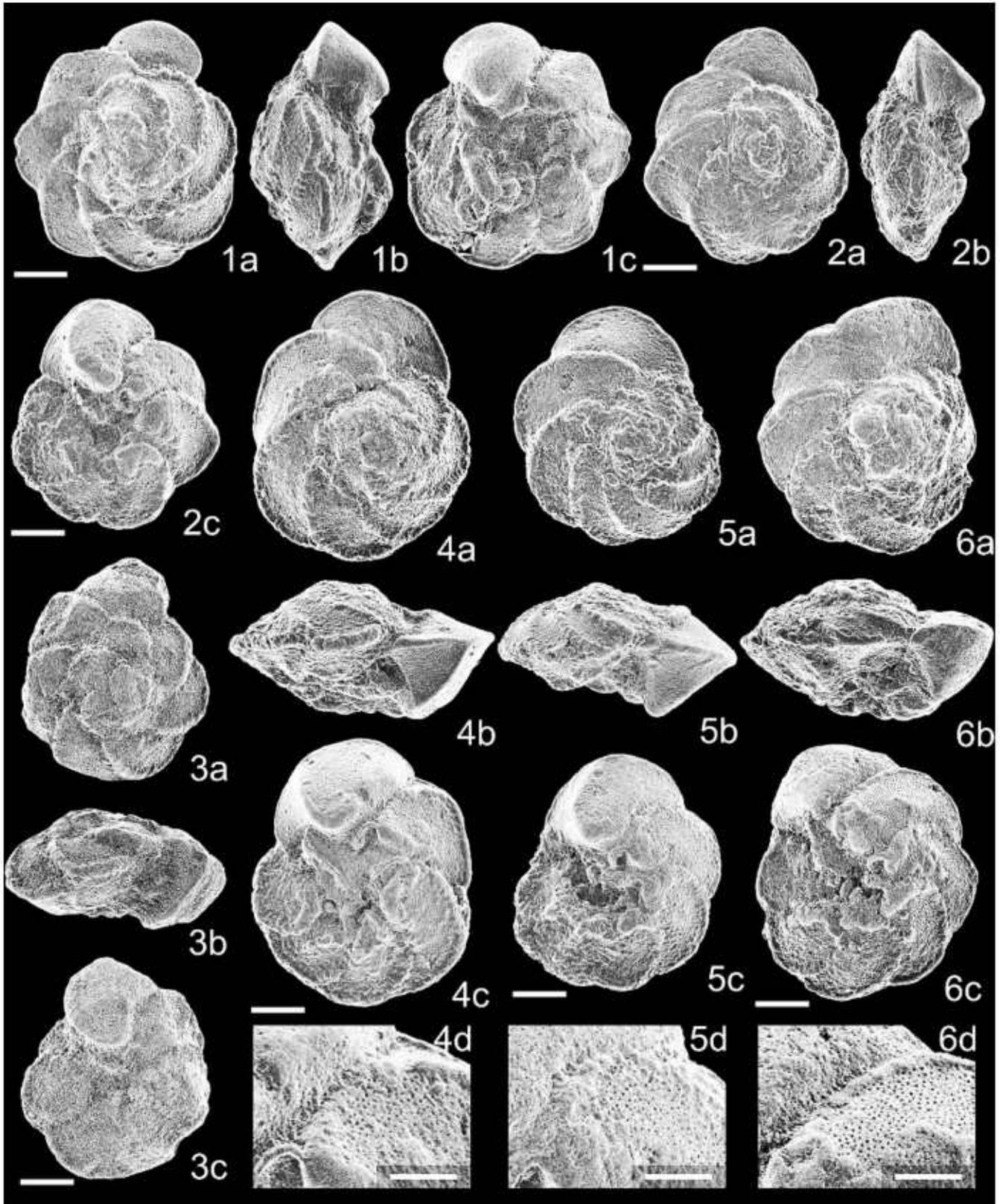


PLATE 2

Selected topotypes of *Rotalipora greenhornensis* (Morrow) from USNM 479719 microslide. 1–3 Specimens with depressed last several (one to four) umbilical sutures: (a) spiral, (b) edge and (c) umbilical views. 4–6 Specimens with diminished (discontinuous and/or penetrated by pores) last umbilical suture: (a) spiral, (b) edge and (c) umbilical views, and (d) enlargement of last umbilical suture. Scale bars: 1–3, 4a–c, 5a–c, 6a–c = 100 μm ; 4d, 5d, 6d = 50 μm .

last several (one to four) umbilical sutures in the final whorl. An additional three USNM 479719 specimens (Pl. 2, figs. 4–6) exhibit a diminished raised umbilical suture between the ultimate and penultimate chambers, where it is faintly thickened but discontinuous and/or penetrated by pores. These six specimens characteristically have umbilically positioned supplementary apertures, which are surrounded by a continuous series of closely-spaced periumbilical ridges. Such characteristics correspond to those of the holotype, and, therefore, we suggest that this topotype suite represents the *greenhornensis* concept.

In contrast, the other four USNM 479719 topotypes and a Loeblich and Tappan (1961) USNM 371488 topotype, all shown in Plate 3, do not correspond to the holotype in that they have fully raised umbilical sutures. The raised umbilical sutures and periumbilical ridges in the later part of the final whorl are united with the adumbilical ridges parallel to the posterior chamber margin; these ornamental elements, together with keeled periphery, exhibit an overall “fish-hook” shape. In addition, their supplementary apertures tend to be in the base-of-suture position and are inserted within the somewhat enlarged gaps between the periumbilical ridges. Such features indicate that these specimens are more appropriately identified as *R. globotruncanoides* (see also Appendix 1).

Both groups of topotypes have an umbilical cover-plate of variable extent. Some of these specimens (e.g., Pl. 2, fig. 4; Pl. 3, fig. 1) exhibit a large-sized “umbilical platform” (*sensu* Eicher, 1972).

Morphological characteristics

On the whole, the morphological features are highly variable among the *greenhornensis* and *globotruncanoides* groups included in the *greenhornensis* topotype suite examined herein (Pls. 2, 3), although a certain *morphological trend* may exist in that both groups consistently have an equally biconvex profile. The number of chambers varies from 5 to 7-1/2. The shape of chambers viewed on the spiral side is semi-circular to strongly curved; only a few specimens exhibit true elongate, crescentic chambers throughout the final whorl (Pl. 2, fig. 5; Pl. 3, figs. 4, 5), the character that was believed typical of *R. greenhornensis*. The mode of increase in chamber size in the last whorl varies from nearly equidimensional to rapid. The periphery is smooth to lobulate, and the peripheral outline is circular to somewhat elliptical. The umbilicus is narrow to broad (one-third the maximum test diameter) in width.

NOTES ON SPECIES-LEVEL CLASSIFICATION OF THE APPENNINICA GROUP

Despite apparent polyphyletism, Albian–Cenomanian single-keeled taxa of the subfamily Rotaliporinae have been grouped under the genus *Rotalipora*. Wonders (1978) summarized earlier classifications and proposed three phyletic groups in *Rotalipora*: (1) the *ticinensis* group, which evolved from *Ticinella praeticinensis* Sigal, 1966 (Sigal, 1966); (2) the *appenninica* group, which evolved from *Ticinella raynaudi* Sigal, 1966 (Sigal, 1969); and (3) the

cushmani group, the origin of which is uncertain. For these groups, Wonders (1978) designated the genera *Pseudothalmanninella* Wonders, 1977; *Thalmanninella* Sigal, 1948; and *Rotalipora* Brotzen, 1942, respectively. To date, no general agreement has been reached for the usage of these three phyletic groups at the genus or subgenus level. Nonetheless, the validity of such a three-fold grouping for *Rotalipora* has been well accepted.

With respect to the *appenninica* group, to which *R. greenhornensis* belongs, the following species are presently regarded as valid taxa, and are listed in the order of evolutionary appearance (Table 1): (1) *Rotalipora praebalernaensis* Sigal, 1969; (2) *Rotalipora balernaensis* (Gandolfi, 1957); (3) *Rotalipora appenninica* (Renz, 1936); (4) *Rotalipora gandolfii* Luterbacher and Premoli Silva, 1962; (5) *Rotalipora globotruncanoides* Sigal, 1948; and (6) *Rotalipora greenhornensis* (Morrow, 1934). In addition to this major lineage series, the following two species with a distinctive plano-convex to cylindrical morphology have been considered as having evolved from this lineage: *Rotalipora reicheli* (Mornod, 1950) and *Rotalipora deeckeii* (Franke, 1925).

In the early studies of Cretaceous planktonic foraminifera, rotaliporid taxa presently included in the *appenninica* group were typologically classified, drawing attention to evolutionary changes in gross morphologies from thin, spiro-convex forms to thick, umbilico-convex forms (Gandolfi, 1942). Subsequently, Gandolfi (1957) recognized the significance of ornamentation as a distinguishing feature at the (sub)species level, and on this basis he identified differences among *R. balernaensis* [= *Globotruncana* (*Rotalipora*) *appenninica balernaensis*], *R. gandolfii* [= *G. (R.) appenninica appenninica*] and *R. globotruncanoides* [= *G. (R.) appenninica globotruncanoides*]. Gandolfi (1957, p. 62) stated that “a particular evolutionary trend (bioseries) is therefore suggested, i.e. from tests with radial and depressed umbilical sutures to tests with curved and raised umbilical sutures.” Further, Gandolfi (1957) assigned a (sub)species rank to the partly-keeled evolutionary stage for *Rotalipora subticinensis* [= *G. (Thalmanninella) ticinensis subticinensis*] in the *ticinensis* group, and this proposal was followed by Sigal (1969) in the recognition of *R. praebalernaensis*.

In the 1960's and 1970's, several comprehensive taxonomic works were published (Loeblich and Tappan, 1961; Pessagno, 1967; Postuma, 1971; Carter and Hart, 1977; Masters, 1977; Wonders, 1978) in which the major focus of the rotaliporid taxonomy was the generic classification in terms of supplementary apertural positions, i.e., the *Rotalipora* vs. *Thalmanninella* problem. With respect to the species-level classifications adopted therein, there was agreement that species of the *appenninica* group tracked an evolutionary trend from flatter, less-ornamented, fewer-chambered forms to thicker, ornamented, many-chambered forms, and the trend is basically consistent with Gandolfi's (1957) observation. However, the proposed schemes were still morphologically oriented, and significance of the ornamental characters was less emphasized. Accordingly, there clearly was a tendency of accepting *appenninica* and *greenhornensis* as valid taxa in *Rotalipora*, whereas the other species [including *evoluta* (an early Cenomanian evolute-

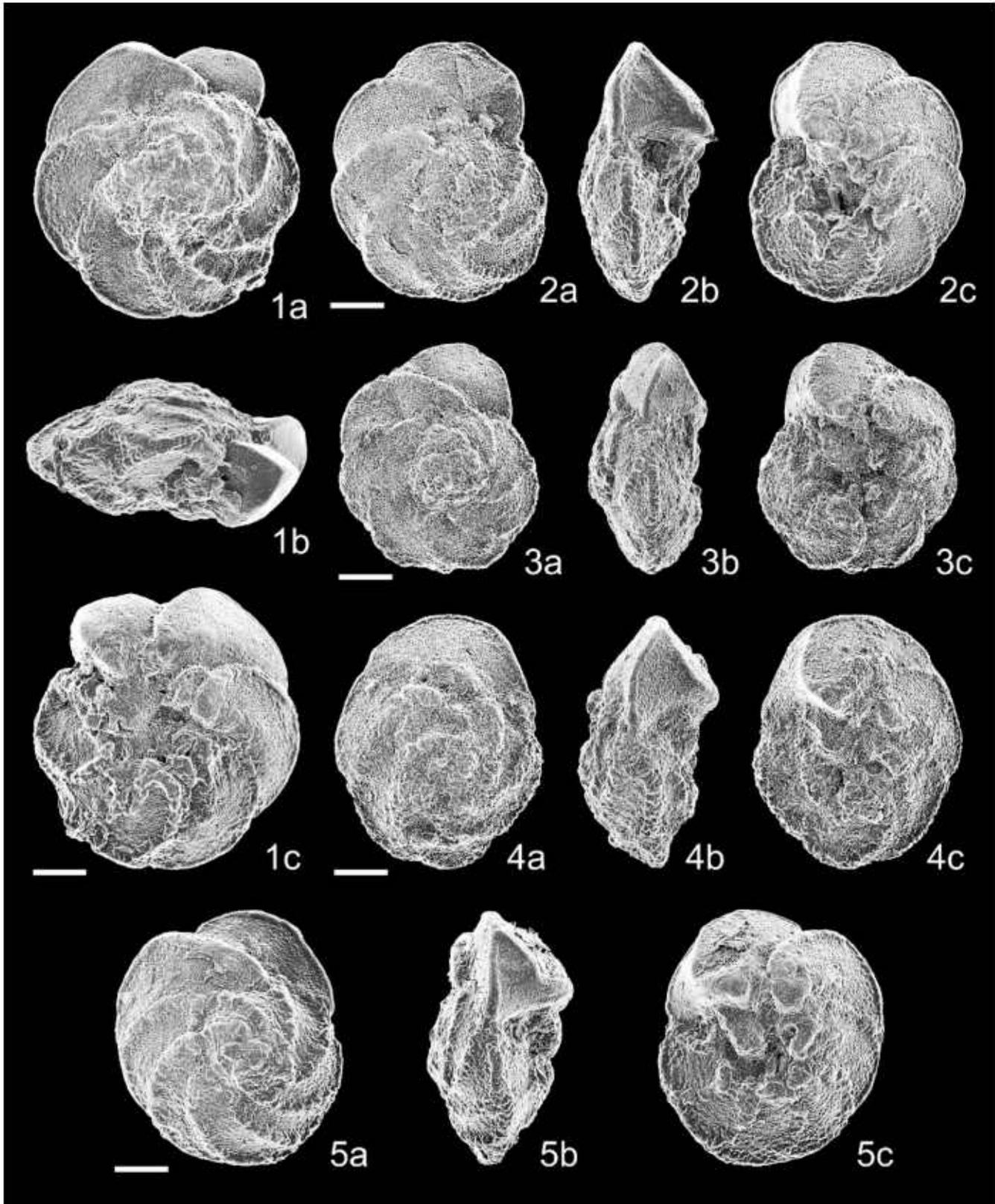


PLATE 3

Rotalipora globotruncanoides Sigal from toptype assemblage of *Rotalipora greenhornensis* (Morrow). 1–4 Selected specimens from USNM 479719 microslide: (a) spiral, (b) edge and (c) umbilical views. 5 Specimen identical to that figured by Loeblich and Tappan (1961; Pl. 7, fig. 9): (a) spiral, (b) edge and (c) umbilical views; USNM 371488. All scale bars = 100 μ m.

form) and *brotzeni*] were more or less treated as synonyms under *appenninica*, *greenhornensis* or others.

In their major monographs, Robaszynski and Caron (1979) and Caron (1985) recognized the evolutionary sequence of *appenninica*–*gandolfii*–*brotzeni* in terms of the step-wise acquisition of periumbilical ridges and raised sutures. However, no particular explanation was given for the inclusion of *brotzeni* or exclusion of some potentially valid species. The work by González-Donoso and Linares in Robaszynski and others (1993) was the first comprehensive treatment of all of the potentially valid taxa in the *appenninica* group, and used the sequence of evolutionary changes in the ornamental characters rather than morphological features.

This study basically concurs with the species-level classification of the major *appenninica* group by González-Donoso and Linares in Robaszynski and others (1993), which recognizes the priority of ornamental characters over morphological features. This seems reasonable for *Rotalipora*, which has empirically been known by its high-intraspecific morphological variability. Moreover, with the exception of *greenhornensis*, each species in the major *appenninica* group recognized therein conforms to its primary type.

As a rule, taxonomic characters employed in the species-level classification of Cretaceous planktonic foraminifera include the sizes and arrangement of chambers as well as ornamentation (cf., Huber, 1994), and, in the case of *Rotalipora*, position of supplementary apertures. These characters are basically treated as equal in taxonomic value, and hence it is difficult to logically demonstrate the priority of ornamental characters over morphological features at the species level. In the evolution of *Rotalipora*, however, the apparent irreversibility of changes in the ornamental characters implies that there was a genetic basis to the pattern. This is supported by our own observations from North Atlantic and Pacific deep-sea sections. On the other hand, though not verified by rigorous morphometric analysis, remarks on the high-morphological variability in *Rotalipora* are found elsewhere in the literature. In particular, González-Donoso and Linares in Robaszynski and others (1993, p. 433) have shown that a total of 32 morphotypes can be recognized if the classification of the *appenninica* group is based solely on morphologies. Thus, morphological features are too variable to be adopted as the primary distinguishing features for the species-level classification. It is our contention that, despite the presence of an overall morphological trend from flat, spirally convex to thick, biconvex forms, the rotaliporid taxonomy should be based on the apertural and ornamental characters that are apparently of unidirectional evolutionary significance (Table 1).

It should be emphasized that all presently valid taxa of the *ticinensis* group (*R. subticinensis*, *R. ticinensis* and *R. tehamaensis*) and the *cushmani* group (*R. montsalvensis* and *R. cushmani*) are distinguished primarily by apertural and ornamental characters as well. Thus, identification of *R. greenhornensis* by these non-morphological characters would be favorable from the viewpoint of retaining taxonomic coherence among the rotaliporid species.

TAXONOMIC CLARIFICATION OF *ROTALIPORA GREENHORNENSIS*

By accepting the significance of the apertural and ornamental characters as the first-order distinguishing features in the species-level classification of the genus *Rotalipora*, it is possible to clarify the concept of *Rotalipora greenhornensis*. Recognition of the partly raised nature of the umbilical sutures in the holotype is considered essential (Pl. 1). This character is common in many of the topotypes examined (Pl. 2). This finding reasonably rules out the previous view (e.g., Robaszynski and Caron, 1979; Caron, 1985) that *R. greenhornensis* is typified by having “strongly” raised sutures throughout the umbilical and spiral sides (Table 1). Observations of the topotypes further show that the depression of raised umbilical sutures begins with the last one and then progresses backward.

It is proposed that the onset of reduction of raised umbilical sutures (i.e., with at least one umbilical suture discontinuous and/or penetrated by pores) defines the evolutionary appearance of *R. greenhornensis* from *Rotalipora globotruncanoides*. This proposition conforms to criteria currently employed in the taxonomy of Cretaceous planktonic foraminifera. Under the current scheme, one means of designating species rank is to identify the non-acquisition, partly acquired, or fully acquired state of a given taxonomic character. For example, in the case of the evolutionary sequence of *appenninica*–*gandolfii*–*globotruncanoides*, *R. appenninica* is typified by its *fully depressed* umbilical sutures (= non-acquisition state) and *R. globotruncanoides* by its *fully raised* umbilical sutures (= fully acquired state). The intermediate state with *partly raised* umbilical sutures is attributed to *Rotalipora gandolfii*, wherein the number of raised sutures is not considered, i.e., if at least one suture in the final whorl is raised, the species rank of *gandolfii* is given. Our proposed concept of *R. greenhornensis* is validated by analogy with this case, such that *R. greenhornensis* is accepted principally as the state with *partly raised* umbilical sutures that constitutes an evolutionarily transition from *R. globotruncanoides* (sutures *fully raised*) to *R. greenhornensis* and then *Anaticinella multiloculata* (periphery partly keeled and rounded, sutures *fully depressed*). Hence, if reduction of at least one raised umbilical suture is recognized, the species rank of *greenhornensis* should be assigned (this is not simply a return to the state of *R. gandolfii*; see later discussion).

Though supplementary apertures of the holotype are only faintly recognized due to poor preservation, observations of the *greenhornensis* topotypes in Plate 2, where the partly depressed nature of umbilical sutures is identical to that of the holotype, allow characterization of the supplementary apertural feature. They are nearly umbilical in position, being surrounded by a continuous series of closely-spaced periumbilical ridges. It seems that the shift of supplementary apertures into the umbilical area is almost simultaneous with the onset of depression of umbilical sutures.

In summary, partly raised umbilical sutures, umbilically positioned supplementary apertures, and closely-spaced periumbilical ridges are taken as the diagnostic features of *R. greenhornensis*. This allows for decisive differentiation of

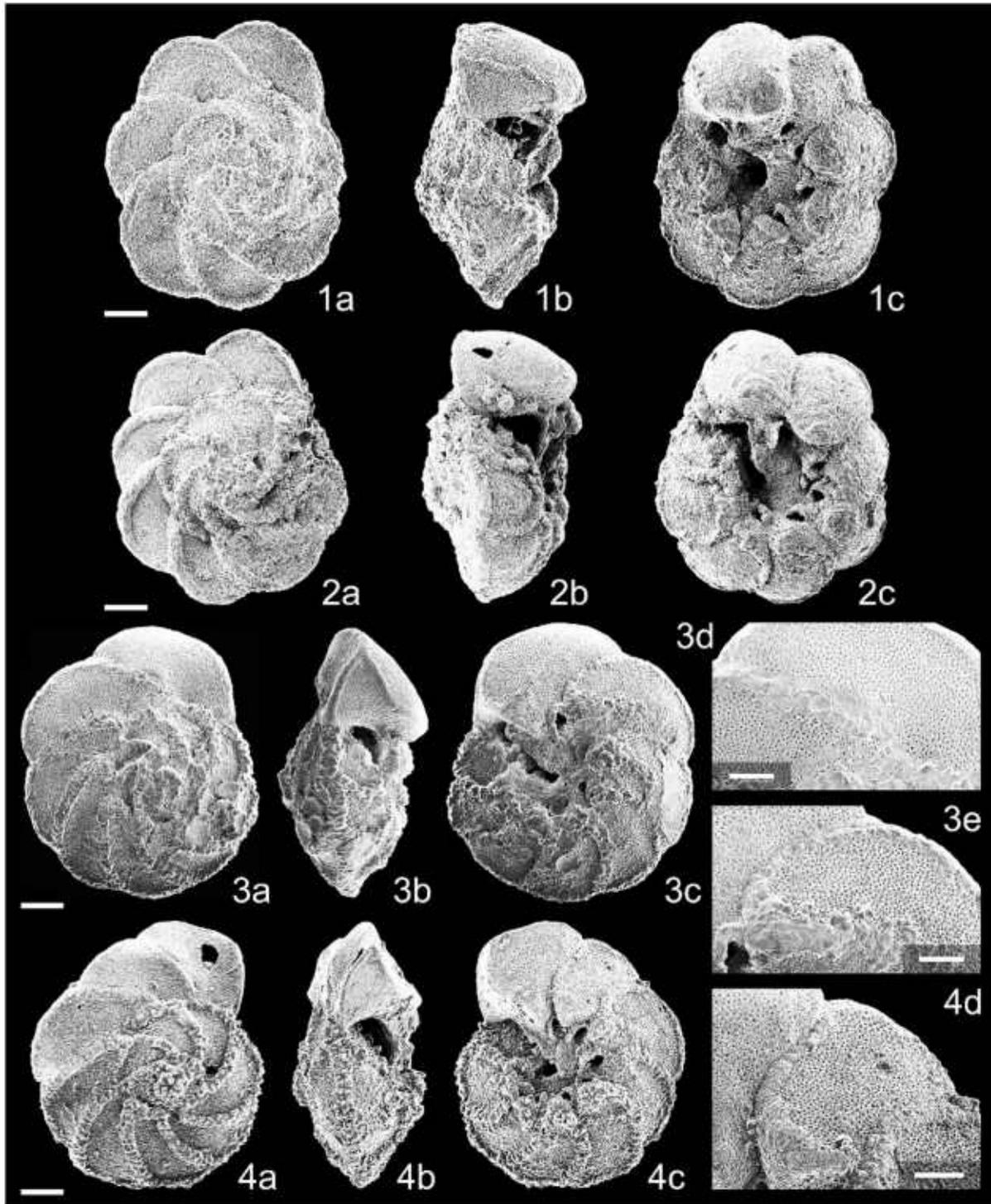


PLATE 4

Comparison between *Rotalipora deeckei* (Franke) and *Rotalipora greenhornensis* (Morrow). **1** *Rotalipora deeckei* (Franke): (a) spiral, (b) edge and (c) umbilical views; USNM 531410; ODP Sample 1050C-21R-1, 135–136 cm; *Rotalipora cushmani* Zone. **2** *Rotalipora deeckei* (Franke): (a) spiral, (b) edge and (c) umbilical views; USNM 531411; ODP Sample 1050C-21R-1, 135–136 cm; *R. cushmani* Zone. **3** *Rotalipora greenhornensis* (Morrow): (a) spiral, (b) edge and (c) umbilical views, and (d, e) enlargement of diminished last suture on the spiral and umbilical sides, respectively; USNM 531412; ODP Sample 1050C-21R-7, 105–108 cm; *R. cushmani* Zone. Note that the last suture on the spiral side is faintly raised but markedly weaker than the others, and it is penetrated by pores at a part meeting the inner whorl. **4** *Rotalipora greenhornensis* (Morrow): (a) spiral, (b) edge and (c) umbilical views, and (d) enlargement of last umbilical suture; USNM 531413; DSDP Sample 463-37-cc, 3–5 cm; co-occurrence with *Whiteinella archaeocretacea* Pessagno. Note that, the last suture on the spiral side is only faintly rimmed and that on the umbilical side is weakly raised but penetrated by pores at both the umbilical and peripheral ends. Scale bars: 1–2, 3a–c, 4a–c = 100 μ m; 3d–e, 4d = 50 μ m.

this taxon from its direct ancestor *R. globotruncanoides* (Table 1). It is noteworthy that these criteria also apply to another topotype figured by Robaszynski and Caron (1979; Pl. 12, fig. 1), and also Caron (1985; Fig. 32, fig. 2). Wonders (1978, p. 134) noted that "the sutures between the last chambers may be depressed and bordered by weak sutural bands, if at all," on the basis of observations of Tunisian specimens.

As emphasized above, morphological features such as numerous chambers (>8; holotype 9-chambered) in the final whorl, strongly curved and elongate (i.e., crescent-shaped) chambers in the spiral side, and/or smooth and circular peripheral outline have long been considered the keys to identification of *R. greenhornensis*. Though such morphologies certainly exist, previous studies seem to have overemphasized these morphological features. Observations of a suite of the topotypes (Pl. 2) reveal that the chambers in the final whorl are six to eight on average, and their shape on the spiral side is not strictly crescentic, but in many cases semi-circular. Morphological features, such as crescentic chambers or a circular peripheral outline, are not inherent to *R. greenhornensis* but apply to the highly evolved forms of *R. globotruncanoides* (Pl. 3, figs. 4, 5).

Among previous studies dealing with *R. greenhornensis*, it was only Eicher (1972) that presented detailed observations of its intraspecific variation using large numbers of hypotypes. On the basis of materials from the U. S. Western Interior, Eicher (1972) recognized that the *greenhornensis* concept encompasses a series of evolutionary changes in taxonomic characters, and is expressed in considerable morphological variability. It is first manifested by the loss and/or depression of raised umbilical sutures, which begins with the last ones and progresses backwards, with an accompanying inflation of chamber surfaces both umbilically and spirally. This manifestation is followed by the loss of a peripheral keel (at least in part) and rounding of the equatorial periphery, giving rise to *Anaticinella multiloculata* (Morrow, 1934). Our observation of the manner of reduction of raised umbilical sutures agrees with that of Eicher (1972). However, Eicher (1972) made no mention regarding how *R. greenhornensis* is differentiated from *R. globotruncanoides*, because *globotruncanoides* (or *brotzeni*) was not considered a valid taxon. In our opinion, some of the hypotypes identified as *R. greenhornensis* by Eicher (1972; Pl. 1, figs. 1, 4) are more appropriately assigned to *R. globotruncanoides* as judged from their fully raised sutures (see Emended Description).

NOTES ON SO-CALLED *ROTALIPORA DEECKEI*

Rotalipora deeckei (Franke, 1925) is another potentially valid species of the *appenninica* group that occurs in the *Rotalipora cushmani* Zone of late Cenomanian age. Identification of *R. deeckei* has been morphological, depending on its plano-convex to cylindrical profile, and hence its phyletic position has not yet been established on the basis of the apertural and ornamental characteristics. Such taxonomically important characters are uncertain due to the inadequate understanding of the primary types. The holotype was originally poorly illustrated and, as noted by Dalbiez (1957), it has been lost. Moreover, one paratype is

of questionable identity, as it was obtained from an undefined horizon of a completely different locality (Dalbiez, 1957). If differentiation between *Rotalipora greenhornensis* and *R. deeckei* is solely based on dorsal/ventral convexity, then they should be considered synonymous (Pessagno, 1967; Carter and Hart, 1977).

We found a plano-convex rotaliporid species from the *Rotalipora cushmani* Zone of ODP Site 1050 (North Atlantic Ocean) that we confidently identify as *R. deeckei* (Pl. 4, figs. 1, 2). It conforms well to the figured hypotypes by Dalbiez (1957, Text-figs. 1–4), Douglas (1969; Pl. 1, fig. 3), Wonders (1978; Pl. 3, fig. 3) and Robaszynski and Caron (1979; Pl. 9, figs. 1, 2) in terms of external morphology as well as apertural and sutural characteristics (not comparable to González-Donoso and Linares in Robaszynski and others, 1993; Pl. XIX, fig. 6). Our Site 1050 specimens are well preserved and allow further discussion of the apertural and sutural details of *R. deeckei*. For comparison, two representative specimens of the early evolutionary stage of *R. greenhornensis* from ODP Site 1050 and DSDP Site 463 (central Pacific Ocean) are also presented (Pl. 4, figs. 3, 4).

The two *R. deeckei* specimens from the North Atlantic Ocean exhibit partly raised umbilical sutures. Each of these specimens has four radial, depressed umbilical sutures in the later part of the final whorl, whereas the earlier sutures are curved and raised. Their supplementary apertures are umbilical in position, bordered by periumbilical ridges and/or thickenings that are tightly packed and somewhat umbilically overhanging. These features closely resemble those of *R. greenhornensis*.

Despite close affinity in taxonomic characters on the umbilical side, the fundamental difference between *R. deeckei* and *R. greenhornensis* can be discriminated on the basis of the sutural characters on their spiral sides. In the case of *R. deeckei*, development of the raised spiral sutures is remarkable throughout the final whorl (Pl. 4, figs. 1, 2). On the other hand, there apparently exists a tendency where the spiral sutures of *R. greenhornensis* are not fully raised and the last one is diminished, in concert with those on the umbilical side (Pl. 4, figs. 3, 4). The simultaneous loss of raised sutures on both the spiral and umbilical sides is also recognizable on the topotypes examined in this study (Pl. 2) and by Robaszynski and Caron (1979; Pl. 12, fig. 1). It is also well illustrated on the American and Tunisian hypotypes of Pessagno (1967; Pl. 51, figs. 15–17, 19–21), Eicher and Worstell (1970; Pl. 12, fig. 2) and Wonders (1978; Pl. 3, fig. 2). Notably, a particularly good example of the relationship between *R. deeckei* and *R. greenhornensis* considered herein is presented by Wonders (1978; compare Pl. 3, figs. 2, 3). Recognition of such sutural characteristics in our central Pacific specimen (Pl. 4, fig. 4) clearly indicates that the presence of depressed spiral and umbilical sutures is not regionally expressed but universal and fundamental to *R. greenhornensis*. Hence, this character is here proposed as an additional criterion for identification of *R. greenhornensis*. It stands to reason that the transition from *R. globotruncanoides* to *R. greenhornensis* was not simply a return to the state of *Rotalipora gandolfii*, but was a unidirectional process attaining a new evolutionary state.

CONCLUDING REMARKS

Detailed observations of the holotype, many topotypes and some North Atlantic and Pacific hypotypes lead us to conclude that apertural and ornamental characters rather than morphological features provide a stable basis for the taxonomy of the late Cenomanian planktonic foraminifera *Rotalipora greenhornensis*. Given the reasonable assumption that apertural and ornamental characters take precedence over morphological features for the species-level classification of *Rotalipora*, the partly raised sutures on both the umbilical and spiral sides, umbilically positioned supplementary apertures, and closely-spaced periumbilical ridges are essential for identification of *R. greenhornensis*. From an evolutionary viewpoint, *R. greenhornensis* represents a transitional state from *Rotalipora globotruncanoides* (sutures fully raised and curved, supplementary apertures base-of-suture in position) to *Anaticinella multiloculata* (not entirely keeled, sutures fully depressed, chambers strongly inflated and smooth) via loss of the ornamental elements. Intraspecific variation observed from the topotypes and hypotypes suggests that the previously well-accepted morphological terms for *R. greenhornensis*, such as numerous (>8), strongly curved and elongate (i.e., crescent-shaped) chambers, have overemphasized one aspect of its variability.

This study provides evidence for unraveling one longstanding problem in the taxonomy of *Rotalipora*, an important group of mid-Cretaceous planktonic foraminiferal biostratigraphy and paleoenvironmental reconstruction. Extinction of *R. greenhornensis* and/or *R. deecke* has been a subject of wide interest in terms of latest Cenomanian paleoceanographic changes. On the other hand, it seems that difficulty in recognizing their entries led previous micropaleontologists to consider that the evolutionary appearances of *R. greenhornensis* and/or *R. deecke* have neither biostratigraphic nor paleoenvironmental significance. Taxonomic clarification of these rotaliporid species may facilitate planktonic foraminiferal biostratigraphic, paleoceanographic and biodiversity studies of the middle to late Cenomanian.

EMENDED DESCRIPTION

Family ROTALIPORIDAE Sigal, 1958
Subfamily ROTALIPORINAE Sigal, 1958
Genus *Rotalipora* Brotzen, 1942

[Type species: *Rotalipora turonica* Brotzen, 1942 = *Rotalipora cushmani* (Morrow, 1934)]

***Rotalipora greenhornensis* (Morrow, 1934)**

Pl. 1, figs. 3, 4 (holotype); Pl. 2, figs. 1–6 (topotypes); Pl. 4, figs. 3, 4

Globorotalia greenhornensis Morrow in Morrow, 1934, p. 199–200, pl. 31, fig. 1.

Thalmanninella greenhornensis (Morrow) in Brönnimann and Brown, 1956, p. 535–536, pl. XX, figs. 7–9 (= holotype).

Rotalipora greenhornensis (Morrow) in Pessagno, 1967, p. 295–297, pl. 51, figs. 13–21 [? pl. 50, fig. 3].

Rotalipora greenhornensis (Morrow) in Eicher and Worstell, 1970, p. 312, pl. 12, fig. 2; pl. 13, fig. 3.

Rotalipora greenhornensis (Morrow) in Barr, 1972, p. 16, pl. 3, fig. 3 [non pl. 3, fig. 4].

Rotalipora greenhornensis (Morrow) in Eicher, 1972, p. 186, pl. 1, figs. 2, 3, 6; pl. 2, fig. 1 [? pl. 1, fig. 1; non pl. 1, fig. 4].

Rotalipora greenhornensis (Morrow) in Dailey, 1973, p. 85, pl. 19, fig. 1.

Rotalipora greenhornensis (Morrow) in Carter and Hart, 1977, p. 44–46, pl. 4, figs. 10, 12 [? pl. 4, fig. 11].

Rotalipora greenhornensis (Morrow) in Ujiie and Randrianasolo, 1977, p. 191, pl. 7, fig. 4; pl. 8, fig. 2.

Thalmanninella greenhornensis (Morrow) in Wonders, 1978, p. 133–134, pl. 3, fig. 2 [non pl. 3, fig. 1].

Rotalipora greenhornensis (Morrow) in Robaszynski and Caron, 1979, p. 85–90, pl. 3, fig. 1; pl. 12, fig. 1 (= topotype); pl. 13, fig. 1 [non pl. 12, fig. 2 (= topotype)]; pl. 13, fig. 2].

Rotalipora greenhornensis (Morrow) in Caron, 1985, p. 69, Fig. 32, figs. 1 (= holotype), 2 (= topotype).

Rotalipora greenhornensis (Morrow) in Leckie, 1985, p. 143, pl. 4, figs. 9, 10 [non pl. 4, figs. 13, 14].

Rotalipora greenhornensis (Morrow) in Jarvis and others, 1988, Fig. 12, fig. d.

Rotalipora greenhornensis (Morrow) in Premoli Silva and Sliter, 1986, pl. 3, figs. 1–3, 5–7, 10.

Rotalipora greenhornensis (Morrow) in Huber and others, 1999, p. 417, pl. 3, fig. 16 [non pl. 3, fig. 18].

Rotalipora greenhornensis (Morrow) in Desmares and others, 2003, Fig. 2, fig. 1c.

Rotalipora deecke (Franke) in Keller and Pardo, 2004, pl. 1, figs. 8, 12, non *Rotalipora greenhornensis* (Morrow) in Loeblich and Tappan, 1961, p. 299–301, pl. 7, figs. 5–8, 9 (= topotype), 10.

non *Rotalipora greenhornensis* (Morrow) in Douglas, 1969, p. 174, pl. 1, fig. 3.

non *Rotalipora greenhornensis* (Morrow) in Porthault, 1969, p. 533, pl. 1, fig. 7.

non *Rotalipora greenhornensis* (Morrow) in Postuma, 1971, p. 80–81.

? *Rotalipora greenhornensis* (Morrow) in Masters, 1977, p. 508–511, pl. 31, figs. 5, 6 (= topotype).

non *Rotalipora greenhornensis* (Morrow) in Petters, 1977, pl. 4, figs. 3–5.

non *Rotalipora greenhornensis* (Morrow) in Leckie, 1984, p. 601, pl. 15, figs. 1–4; pl. 16, figs. 7–12.

non *Rotalipora greenhornensis* (Morrow) in Hart and others, 1989, p. 360, pl. 7.23, figs. 1–3.

non *Rotalipora* (*Thalmanninella*) *greenhornensis* (Morrow) in González-Donoso and Linares in Robaszynski and others, 1993, p. 431, pl. XIX, figs. 7, 8, 10.

non *Rotalipora greenhornensis* (Morrow) in Lipson-Benitah, 1994, p. 85, pl. 1, fig. 7.

non *Rotalipora greenhornensis* (Morrow) in Sliter, 1995, pl. 1, figs. 6–8.

non *Rotalipora greenhornensis* (Morrow) in Lamolda and others, 1997, Fig. 6, figs. a–c.

? *Rotalipora greenhornensis* (Morrow) in Lipson-Benitah and others, 1997, p. 487, Fig. 12, fig. 3.

non *Rotalipora greenhornensis* (Morrow) in Hasegawa, 1999, p. 188, Fig. 9, fig. 5.

non *Rotalipora greenhornensis* (Morrow) in Keller and Pardo, 2004, pl. 1, figs. 1–3.

Diagnosis. *R. greenhornensis* differs principally from the other species in this single-keeled genus in having sutures not fully raised but partly (at least one or more) depressed or diminished (i.e., discontinuous and/or penetrated by pores) on both the umbilical and spiral sides. Supplementary apertures are umbilical in position throughout, surrounded by closely-spaced periumbilical ridges (or thickenings) forming a continuous series. Specifically, onset of diminishment of raised umbilical sutures is proposed as defining the appearance of this taxon.

Emended description. Wall smooth, macroperforate. Test large, trochospiral, equally biconvex, moderate to high in spiral and ventral sides. From 6 to 8, rarely 9, chambers in the final whorl, equidimensional or increasing gradually to somewhat rapidly in size as added, semi-circular to curved in shape on the umbilical side, semi-circular to strongly curved and elongate (i.e., crescentic) in shape on the spiral side. Equatorial periphery smooth to lobulate, circular to slightly elliptical in outline, angular in edge view surrounded entirely by one

keel. Umbilicus deep, narrow to broad (one-third of maximum test diameter), accompanied by an umbilical cover-plate of variable size, sometimes having a large-sized "umbilical platform." Umbilical shoulder provided throughout with periumbilical ridges (or thickenings) that are closely spaced and comprising a continuous series. Umbilical sutures curved, raised and beaded in the earlier part of the last whorl, later becoming smoothly limbate, and, ultimately, depressed or diminished (i.e., discontinuous and/or penetrated by pores) at least in part (i.e., one or more). Likewise, spiral sutures curved, raised and beaded in the earlier part, becoming smoothly limbate and then depressed or diminished in the later part. Primary aperture umbilical-extraumbilical, bordered by a lip extended from an umbilical cover-plate. Supplementary apertures nearly umbilical in position (but still opening directly into chamber), each bordered by a lip.

Distinguishing features. *R. greenhornensis* differs from its direct ancestor *Rotalipora globotruncanoides* in having not entirely raised but partly depressed umbilical and spiral sutures, supplementary apertures that are nearly umbilical in position, and closely-spaced periumbilical ridges. *R. globotruncanoides* (particularly in its highly evolved stage) is morphologically indistinguishable, but distinctive by having curved, fully raised sutures and supplementary apertures whose positions are base-of-suture. In particular, *R. globotruncanoides* has diagnostic "fish-hook" ornamentation on the umbilical face, which is characterized by a combination of keeled periphery, raised umbilical suture, periumbilical ridge, and adumbilical ridge parallel to the posterior chamber margin. Loss of these characters in *R. greenhornensis* appears to be relevant to more tightly packed chambers, inhibiting the development of supplementary apertures within the sutural gap and of adumbilical ridges along the posterior chamber margin.

Rotalipora greenhornensis differs from its direct descendent *Anaticinella multiloculata* in that the former has partly raised sutures and an acute, entirely keeled equatorial periphery, whereas the latter has a smooth, rounded equatorial periphery (though it still has, in part, a keel or poreless margin) and fully depressed sutures due to the strong inflation of chambers (Eicher, 1972). Though not encountered in this study, *R. greenhornensis* in its latest evolutionary stage is significantly variable in taxonomic characters (Eicher, 1972). An intermediate morphotype characterized by having fully depressed sutures, but entirely keeled margin is known to exist (Eicher and Worstell, 1970, pl. 13, fig. 3; Eicher, 1972, pl. 1, fig. 6; Leckie, 1985, pl. 4, figs. 9, 10) and has been identified as *R. greenhornensis*.

Plano-convex *Rotalipora deeckeii* resembles *R. greenhornensis* in having partly depressed umbilical sutures in the later part of the final whorl and umbilically positioned supplementary apertures. However, sutures on the spiral side of *R. deeckeii* are markedly raised throughout, whereas those of *R. greenhornensis* are partly depressed or diminished. Similarly, *Rotalipora gandolfii* superficially resembles *R. greenhornensis* by its morphology and partly depressed umbilical sutures, but it differs in having sutural supplementary apertures and it lacks the partly depressed spiral sutures.

Rotalipora greenhornensis is morphologically highly variable, but it consistently has an equally biconvex, moderate to thick profile. It never presents a compressed profile as thin as *Rotalipora praebalernaensis*, *Rotalipora balernaensis* and *Rotalipora appenninica*.

Type material. Holotype: collection number USNM 75378; Cushman Collection, Smithsonian National Museum of Natural History, Washington, D.C. Type locality: Greenhorn Limestone, Hartland Shale Member, SE 1/4, sec. 31, T. 21 S., R. 22 W., north bank of creek about 1/4 mile west of road, Hodgeman Co., Kansas (Morrow, 1934).

Dimensions. Maximum diameter: holotype = 0.60 mm; topotypes = 0.41–0.51 mm. Maximum thickness: holotype = 0.29 mm; topotypes = 0.23–0.27 mm.

Stratigraphic range. *Rotalipora cushmani* Zone, upper Cenomanian.

Biogeographic distribution. Cosmopolitan, low to middle latitudes. Available records of occurrence with accurate illustration (listed above): U. S. Western Interior; U. S. Gulf Coast; California; western

North Atlantic Ocean; United Kingdom; Tunisia; Libya; Madagascar; central Pacific Ocean.

Discussion. Despite general consensus that *R. greenhornensis* is easily identified by its morphological characters, such as numerous (>8), strongly curved and elongate (i.e., crescentic) chambers or strongly raised and curved sutures throughout the umbilical and spiral sides, our detailed reexamination of the primary and secondary types does not support any of the previously well-accepted characterizations. For detailed discussion of the primary type (one holotype), inherent taxonomic characters, and intraspecific variation of *R. greenhornensis* as well as notes on plano-convex *R. deeckeii*, see text and emended description.

As a result of the taxonomic revision of this study, nearly all of above-listed hypotypes with "non" are reinterpreted as *R. globotruncanoides* or, to a lesser extent, *R. gandolfii* and *R. deeckeii*. We note that the illustration of the spiral view only (specimens with "?" in the above list) cannot be taken as evidence for the presence of *R. greenhornensis*.

González-Donoso and Linares in Robaszynski and others (1993) identified some unusual Tunisian specimens of *Rotalipora* of middle Cenomanian age, and assigned them to *R. greenhornensis* on the grounds that they have fully depressed umbilical sutures that are conformable with the holotype illustrations by Morrow (1934) and Brönnimann and Brown (1956). This approach seems reasonable but it is invalidated due to the fact that the fully depressed nature of the umbilical sutures is not represented by the holotype. Besides, the Tunisian specimens differ from *R. greenhornensis* sensu stricto in lacking any evidence for depression of raised sutures on the spiral side and in possessing different supplementary apertural features.

There certainly exists an intermediate morphology between *R. globotruncanoides* and *R. greenhornensis* in the literature, including Eicher (1972; pl. 1, fig. 4), Leckie (1985; pl. 4, figs. 13, 14), and Lipson-Benitah (1994; pl. 1, fig. 7). These are here regarded as *R. globotruncanoides* because they have curved and fully raised sutures, although this form differs from *R. globotruncanoides* sensu stricto and is close to *R. greenhornensis* in having umbilically shifted supplementary apertures and in lacking true fish-hook shaped ornamentation on the umbilical chamber surfaces. Two of our figured specimens of *R. globotruncanoides* (Pl. 3, figs. 2, 5) are similar to this state. Further, it probably corresponds to one of the paratypes of *Thalmanninella brotzeni* illustrated by J. Sigal (Sigal, 1948; pl. II, fig. 7). If this form constitutes a sufficiently separate biostratigraphic range with respect to *R. greenhornensis* within the evolutionary sequence from *R. globotruncanoides* to *R. greenhornensis*, it may be worth establishing a new species as it is distinctive on the basis of one of the most important species-level taxonomic characters. This is likely, as our preliminary results from DSDP Site 463 and ODP Site 1050 show that this morphotype occurs commonly prior to the evolutionary appearance of *R. greenhornensis* sensu stricto.

Currently, *Rotalipora brotzeni* (= *Thalmanninella brotzeni*) is considered a junior synonym of *R. globotruncanoides*. However, *R. brotzeni* is reminiscent of *R. greenhornensis* as judged from its type figure (Sigal, 1948; pl. 1, fig. 5) showing a weakly developed last umbilical suture as well as umbilically positioned supplementary apertures; the latter feature was originally considered the diagnosis of the genus *Thalmanninella*. This interpretation may be equivocal, because another illustration of *R. brotzeni* presented later by the same author (Sigal, 1952; Fig. 25) exhibits development of fully raised umbilical sutures, which in turn suggests that this taxon may be attributed to the above-mentioned *R. globotruncanoides*–*R. greenhornensis* transitional state or to a pre-adult individual of *R. globotruncanoides*.

ACKNOWLEDGMENTS

The authors wish to thank Scott Whittaker (SEM Lab, Smithsonian NMNH) and Motoyoshi Oda and Kentaro Hatakeda (both at Tohoku University) for their help with microscopic work. Critical reviews by Michèle Caron (Université de Fribourg), Antoine A. H. Wonders (Strata-Data Ltd.) and Isabella Premoli Silva (Università di Milano), and editorial handling by the Editor Charlotte A. Brunner (University of Southern Mississippi) are

acknowledged. This study was supported by a Grant-in-Aid for Research Fellow of the Japan Society for the Promotion of Science for Young Scientists to A.A.

REFERENCES

- BARR, F. T., 1972, Cretaceous biostratigraphy and planktonic foraminifera of Libya: *Micropaleontology*, v. 18, p. 1–46.
- BOLLI, H. M., 1957, The genera *Praeglobotruncana*, *Rotalipora*, *Globotruncana*, and *Abathomphalus* in the Upper Cretaceous of Trinidad, B. W. I., in Loeblich, A. R., Jr., *Studies in Foraminifera: United States National Museum Bulletin*, no. 215, p. 51–60.
- BRÖNNIMANN, P., and BROWN, N. K., JR., 1956, Taxonomy of the Globotruncanidae: *Eclogae Geologicae Helvetiae*, v. 48, p. 503–561.
- BROTZEN, F., 1942, Die Foraminiferengattung *Gavelinella* nov. gen. und die Systematik der Rotaliiformes: *Sveriges Geologiska Undersökning, série C*, no. 451 (Årsbok 36, no. 8), p. 1–60.
- CARON, M., 1985, 4. Cretaceous planktonic foraminifera, in Bolli, H., Saunders, J. B., and Perch-Nielsen, K. (eds.), *Plankton Stratigraphy*: Cambridge University Press, Cambridge, p. 17–86.
- CARTER, D. J., and HART, M. B., 1977, Aspects of mid-Cretaceous stratigraphical micropaleontology: *Bulletin of the British Museum of Natural History (Geology)*, v. 29, p. 1–135.
- DAILEY, D. H., 1973, Early Cretaceous foraminifera from the Budden Canyon Formation, northwestern Sacramento Valley, California: *University of California Publications in Geological Sciences*, v. 106, 111 p.
- DALBIEZ, F., 1957, The generic position of *Rotalia deeckeii* Franke, 1925: *Micropaleontology*, v. 3, p. 187–188.
- DESMARES, D., GROSHENY, D., and BEAUDOIN, B., 2003, Hétérochronies du développement *sensu* Gould chez les foraminifères planctoniques cénomaniens: exemple de néoténie dans le bassin du Western Interior américain: *Comptes Rendus Paleovol*, v. 2, p. 587–595.
- DOUGLAS, R. G., 1969, Upper Cretaceous planktonic foraminifera in northern California: Part 1—Systematics: *Micropaleontology*, v. 15, p. 151–209.
- EICHER, D. L., 1972, Phylogeny of the late Cenomanian planktonic foraminifer *Anaticinella multiloculata* (Morrow): *Journal of Foraminiferal Research*, v. 2, p. 184–190.
- , and WORSTELL, P., 1970, Cenomanian and Turonian foraminifera from the Great Plains, United States: *Micropaleontology*, v. 16, p. 269–324.
- FRANKE, A., 1925, Die Foraminiferen der pommerschen Kreide: *Abhandlungen aus dem Geologisch-Palaeontologischen Institut der Universität Greifswald*, v. 6, p. 1–96.
- GALE, A. S., KENNEDY, W. J., BURNETT, J. A., CARON, M., and KIDD, B. E., 1996, The Late Albian to Early Cenomanian succession at Mont Risou near Rosans (Drôme, SE France): an integrated study (ammonites, inoceramids, planktonic foraminifera, nanofossils, oxygen and carbon isotopes): *Cretaceous Research*, v. 17, p. 515–606.
- GANDOLFI, R., 1942, Ricerche micropaleontologiche e stratigrafiche sulla Scaglia e sul flysch cretaci dei Dintorni di Balerna (Canton Ticino): *Rivista Italiana di Paleontologia*, v. 48, p. 1–160.
- , 1957, Notes on some species of *Globotruncana*: *Contributions from the Cushman Foundation for Foraminiferal Research*, v. 8, p. 59–65.
- HART, M. B., BAILEY, H. W., CRITTENDEN, S., FLETCHER, B. N., PRICE, R. J., and SWIECICKI, A., 1989, 7. Cretaceous, in Jenkins, D. G., and Murray, J. W. (eds.), *Stratigraphical Atlas of Fossil Foraminifera*, Second Edition: Ellis Horwood Limited, Chichester, p. 273–371.
- HASEGAWA, T., 1999, Planktonic foraminifera and biochronology of the Cenomanian–Turonian (Cretaceous) sequence in the Oyubari area, Hokkaido, Japan: *Paleontological Research*, v. 3, p. 173–192.
- HUBER, B. T., 1994, Ontogenetic morphometrics of some Late Cretaceous trochospiral planktonic foraminifera from the Austral Realm: *Smithsonian Contributions to Paleobiology*, no. 77, 85 p.
- , LECKIE, R. M., NORRIS, R. D., BRALOWER, T. J., and COBABE, E., 1999, Foraminiferal assemblage and stable isotopic change across the Cenomanian–Turonian boundary in the subtropical North Atlantic: *Journal of Foraminiferal Research*, v. 29, p. 392–417.
- JARVIS, I., CARSON, G. A., COOPER, M. K. E., HART, M. B., LEARY, P. N., TOCHER, B. A., HORNE, D., and ROSENFELD, A., 1988, Microfossil Assemblages and the Cenomanian–Turonian (late Cretaceous) Oceanic Anoxic Event: *Cretaceous Research*, v. 9, p. 3–103.
- KELLER, G., and PARDO, A., 2004, Age and paleoenvironment of the Cenomanian–Turonian global stratotype section and point at Pueblo, Colorado: *Marine Micropaleontology*, v. 51, p. 95–128.
- KENNEDY, W. J., GALE, A. S., LEES, J. A., and CARON, M., 2004, The Global Boundary Stratotype Section and Point (GSSP) for the base of the Cenomanian Stage, Mont Risou, Hautes-Alpes, France: *Episodes*, v. 27, p. 21–32.
- LAMOLDA, M. A., GOROSTIDI, A., MARTINEZ, R., LÓPEZ, G., and PERYT, D., 1997, Fossil occurrences in the Upper Cenomanian–Lower Turonian at Ganuza, northern Spain: an approach to Cenomanian/Turonian boundary chronostratigraphy: *Cretaceous Research*, v. 18, p. 331–353.
- LECKIE, R. M., 1984, Mid-Cretaceous planktonic foraminiferal biostratigraphy off central Morocco, Deep Sea Drilling Project Leg 79, Sites 545 and 547, in Hinz, K., Winterer, E. L., and others. (eds.), *Initial Reports of the Deep Sea Drilling Project*, v. 62: U. S. Government Printing Office, Washington, D. C., p. 579–620.
- , 1985, Foraminifera of the Cenomanian–Turonian boundary interval, Greenhorn Formation, Rock Canyon Anticline, Pueblo, Colorado, in Pratt, L., Kauffman, E. G., and Zelt, F. B. (eds.), *Fine-grained Deposits and Biofacies of the Cretaceous Western Interior Seaway: Evidence of Cyclic Sedimentary Processes*. Society of Economic Paleontologists and Mineralogists, Field Trip Guidebook No. 4, p. 139–149.
- LIPSON-BENITAH, S., 1994, Cenomanian stratigraphical micropaleontology of shelf deposits-Israel: *Revista Española de Micropaleontología*, v. XXVI, p. 83–100.
- , ALMOGI-LABIN, A., and SASS, E., 1997, Cenomanian biostratigraphy and palaeoenvironments in the northwest Carmel region, northern Israel: *Cretaceous Research*, v. 18, p. 469–491.
- LOEBLICH, A. R., JR., and TAPPAN, H., 1961, Cretaceous planktonic foraminifera: Part I—Cenomanian: *Micropaleontology*, v. 7, p. 257–304.
- , ———, 1964, Sarcodina, Chiefly “Thecamoebians” and Foraminiferida, in Moore, R. C. (ed.), *Treatise on Invertebrate Paleontology*, Part C. Protista 2, v. 1–2: The Geological Society of America and the University of Kansas Press, Lawrence, Kansas, 900 p.
- LONGORIA, J. F., and GAMPER, M. A., 1975, The classification and evolution of Cretaceous planktonic foraminifera. Part I: The superfamily Hedbergelloidea: *Revista Española de Micropaleontología*, Número Especial, enero 1975, p. 61–96.
- LUTERBACHER, H. P., and PREMOLI SILVA, I., 1962, Note preliminaire sur une revision du profil de Gubbio: *Rivista Italiana di Paleontologia*, v. 68, p. 253–288.
- MASTERS, B. A., 1977, Mesozoic planktonic foraminifera: A worldwide review and analysis, in Ramsay, A. T. S. (ed.), *Oceanic Micropaleontology*, v. 1: Academic Press, London, p. 301–731.
- MORNOD, L., 1950, Les Globorotalidés du Crétacé supérieur du Montsalvens (Préalpes fribourgeoises): *Eclogae Geologicae Helvetiae*, v. 42, p. 573–596.
- MORROW, A. L., 1934, Foraminifera and ostracoda from the Upper Cretaceous of Kansas: *Journal of Paleontology*, v. 8, p. 186–205.
- PESSAGNO, E. A., JR., 1967, Upper Cretaceous planktonic foraminifera from the western Gulf Coastal Plain: *Palaeontographica Americana*, v. 5, p. 245–445.
- PETTERS, S. W., 1977, Upper Cretaceous planktonic foraminifera from the subsurface of the Atlantic Coastal Plain of New Jersey: *Journal of Foraminiferal Research*, v. 7, p. 165–187.
- PORTHAULT, B., 1969, Foraminifères planctoniques et biostratigraphie du Cénomanien dans le sud-est de la France, in Brönnimann, P., and Renz, H. H. (eds.), *Proceedings of the First International Conference on Planktonic Microfossils*, Geneva, 1967, v. 2: E. J. Brill, Leiden, p. 526–546.
- POSTUMA, J. A., 1971, *Manual of Planktonic Foraminifera*: Elsevier Publishing Company, Amsterdam, 422 p.

- PREMOLI SILVA, I., and SLITER, W. V., 1986, Late Aptian and Cenomanian-Turonian planktonic foraminifers from Deep Sea Drilling Project Site 585, Leg 89, East Mariana Basin, in Moberly, R., Schlanger, S. O., and others (eds.), Initial Reports of the Deep Sea Drilling Project, v. 89: U. S. Government Printing Office, Washington, D. C., p. 297–309.
- REICHEL, M., 1949, Observations sur les Globotruncana du gisement de la Breggia (Tessin): *Eclogae Geologicae Helvetiae*, v. 42, p. 596–617.
- RENZ, O., 1936, Stratigraphie und mikropalaeontologische Untersuchung der Scaglia (Obere Kreide-Tertiär) im zentralen Apennin: *Eclogae Geologicae Helvetiae*, v. 29, p. 1–149.
- , LUTERBACHER, H. P., and SCHNEIDER, A., 1963, Stratigraphisch-palaeontologische Untersuchungen im Albien und Cénomanien der Neuenburger Jura: *Eclogae Geologicae Helvetiae*, v. 56, p. 1073–1116.
- ROBASZYNSKI, F., and CARON, M. (COORDINATORS), 1979, Atlas de foraminifères planctoniques du Crétacé moyen (mer Boréale et Téthys): *Cahiers de Micropaléontologie*, no. 1, 185 p.
- , 1995, Foraminifères planctoniques du Crétacé: commentarie de la zonation Europe-Méditerranée: *Bulletin de la Société Géologique de France*, v. 166, p. 681–692.
- , AMÉDRO, F., DUPUIS, C., HARDENBOL, J., GONZÁLEZ DONOSO, J. M., LINARES, D., and GARTNER, S., 1993, Le Cénomanien de la région de Kalaat Senan (Tunisie centrale): litho-biostratigraphie et interprétation séquentielle: *Revue de Paléobiologie*, v. 12, p. 351–505.
- SIGAL, J., 1948, Notes sur les genres de Foraminifères *Rotalipora Brotzen* 1942 et *Thalmaninella*: Famille des *Globorotaliidae*: *Revue de l'Institut Français du Pétrole*, v. 3, p. 95–103.
- , 1952, Aperçu stratigraphique sur la micropaléontologie du Crétacé: XIX Congrès Géologique International, Monographies Régionales, Ire Série: Algérie, no. 26: Alger. 47 p.
- , 1958, La classification actuelle des familles de Foraminifères planctoniques du Crétacé: *Compte Rendu Sommaire des Séances de la Société Géologique de France*, v. 11–12, p. 262–265.
- , 1966, Contribution à une monographie des Rosalines 1. Le genre *Ticinella* Reichel, souche des Rotalipores: *Eclogae Geologicae Helvetiae*, v. 59, p. 187–217.
- , 1969, Contribution à une monographie des Rosalines. 2. L'espèce *Rotalipora appenninica* (O. Renz, 1936), origine phylétique et taxinomie, in Brönnimann, P., and Renz, H. H. (eds.), Proceedings of the First International Conference on Planktonic Microfossils, Geneva, 1967, v. 2: E. J. Brill, Leiden, p. 622–639.
- SLITER, W. V., 1995, Cretaceous planktonic foraminifers from Sites 865, 866, and 869: A synthesis of Cretaceous pelagic sedimentation in the central Pacific Ocean Basin, in Winterer, E. L., Sager, W. W., Firth, J. V., and Sinton, J. M. (eds.), Proceedings of the Ocean Drilling Program, Scientific Results, v. 143: Ocean Drilling Program, College Station, TX, p. 15–30.
- TUR, N. A., SMIRNOV, J. P., and HUBER, B. T., 2001, Late Albian–Coniacian planktic foraminifera and biostratigraphy of the northeastern Caucasus: *Cretaceous Research*, v. 22, p. 719–734.
- UJIIÉ, H., and RANDRIANASOLO, A., 1977, Cenomanian planktonic foraminifera from Diégo-Suarez, northern Madagascar: *Bulletin of the National Science Museum, Series C (Geology & Paleontology)*, v. 3, p. 183–194.
- WONDERS, A. A. H., 1978, Phylogeny, classification and biostratigraphic distribution of keeled Rotaliporinae: Proceedings of the Koninklijke Nederlandse Akademie van Wetenschappen, series B: palaeontology, geology, physics, chemistry, v. 81, p. 113–144.

Received 13 April 2006
Accepted 17 November 2006

APPENDIX 1

USNM Metatypes of *Rotalipora globotruncanoides* and *Thalmaninella brotzeni*

After submission of this paper, type materials of J. Sigal were found at le Muséum national d'Histoire naturelle, Paris by M. Caron and I. Premoli Silva. The collection includes the primary types of *Rotalipora globotruncanoides* Sigal (one holotype and three paratypes) and *Thalmaninella brotzeni* Sigal [= *Rotalipora brotzeni* (Sigal); one holotype and one paratype]. According to reexamination of these primary types by Caron and Premoli Silva (written communication, 2006; unpublished report given at the Mesozoic Planktonic Foraminiferal Working Group meeting in FORAMS 2006, Natal, Brazil), *R. globotruncanoides* and *R. brotzeni* are considered to be separate taxa as judged from their differences in growth rate, chamber morphology, position of supplementary apertures, and other characters. Furthermore, they suggested that the umbilical sutures of *R. globotruncanoides* are not entirely raised. These observations urge reconsideration of the *globotruncanoides* concept adopted in this study (Table 1).

Because stability in the species concept of *R. globotruncanoides* is essential to successful taxonomic revision of *R. greenhornensis*, new information from Sigal's primary types is of considerable significance. At least at present, however, it is not reasonable to follow the ongoing revisory work of Caron and Premoli Silva (written communication, 2006) in light of Articles 7 to 9 of the International Code of Zoological Nomenclature. It should be noted that clarification of the species concepts of *R. globotruncanoides* and *R. brotzeni* will be hampered by the fact that Sigal (1948) erected each species based on the holotype from Sidi-Aïssa, Algeria and the paratype(s) from Morocco. In earlier foraminiferal classification, there were cases in which specimens from different localities were combined to constitute the primary type suite. This practice for designating primary types is no longer acceptable, leaving the status of paratype(s) from different localities in question. Do they retain a status equivalent to that of the primary or secondary types from the type locality? Meanwhile, SEM images of these holotypes are unavailable due to a curatorial policy of le Muséum

national d'Histoire naturelle, Paris (Caron and Premoli Silva, written communication, 2006).

In anticipation of decisive taxonomic clarification for *R. globotruncanoides* and *R. brotzeni* in the near future, we present further evidence that improves upon their equivocal species concepts. Plate A1 presents SEM images of the topotypes of *R. globotruncanoides* and *T. brotzeni*, both of which are deposited in the Cushman Collection, Smithsonian NMNH. The former (Pl. A1, fig. 1; collection number: USNM 387929), to our knowledge, has not been figured elsewhere. The latter (Pl. A1, fig. 2; collection number: USNM P3930) is identical to a specimen illustrated by Bolli (1957; Pl. 9, fig. 7) [the same figure also reprinted in Loeblich and Tappan (1961; Pl. 7, fig. 10) and Loeblich and Tappan (1964; Fig. 528, fig. 3)]. Information written on both microslides states that they were both obtained from the type locality, "Middle Cenomanian: Sidi-Aïssa, Algeria" and were "received from J. Sigal." Thus, each specimen can also be called a "metatype" (the topotype identified by the original author at a date subsequent to publication of the original description), which is deemed to have important status; it is apparently more important than the Moroccan paratypes.

The key taxonomic characters of *R. globotruncanoides* listed in the text and Table 1 are excellently expressed in the USNM 387929 metatype. In our opinion, *R. globotruncanoides* diagnostically exhibits "fish-hook" ornamentation (newly proposed descriptive term) on the umbilical chamber surfaces in the later part of the last whorl, where it is illustrated by a combination of keeled periphery, raised umbilical suture, periumbilical ridge, and adumbilical (= toward umbilicus) ridge parallel to the posterior chamber margin. These lines of additional information reinforce the fidelity of our *globotruncanoides* concept and help validate our taxonomic revision for *R. greenhornensis*.

The metatype of *T. brotzeni*, though not as well preserved, is comparable to *R. globotruncanoides* in having entirely raised umbilical sutures and the fish-hook ornamentation on the ultimate chamber. The *globotruncanoides* and *brotzeni* metatypes, on the other hand, may be separable based on their apertural and morphological features, in which the former exhibits sutural supplementary apertures, a faster

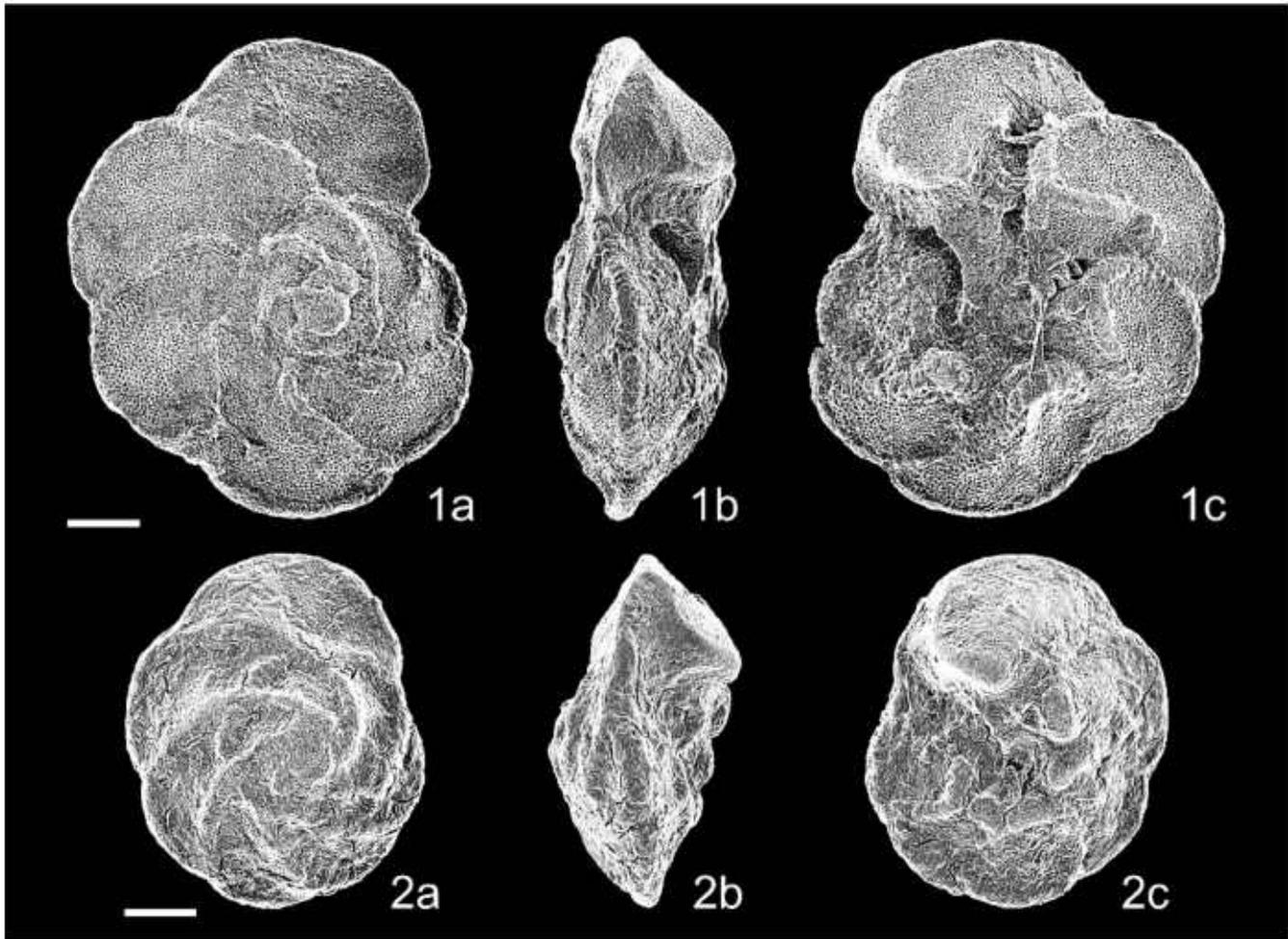


PLATE A1

USNM metatypes of *Rotalipora globotruncanoides* Sigal and *Thalmanninella brotzeni* Sigal. **1** *Rotalipora globotruncanoides* Sigal: (a) spiral, (b) edge and (c) umbilical views; USNM 387929; maximum diameter = 0.66 mm; maximum thickness = 0.26 mm. **2** *Thalmanninella brotzeni* Sigal [= *Rotalipora brotzeni* (Sigal)]: (a) spiral, (b) edge and (c) umbilical views; USNM P3930; maximum diameter = 0.49 mm; maximum thickness = 0.27 mm. Uncoated SEM images obtained by using a JEOL JSM-6330F field emission SEM at Tohoku University. Note that both specimens are arranged at a common magnification. All scale bars = 100 μ m.

growth rate, and an umbilically more convex profile, whereas the latter exhibits umbilically positioned supplementary apertures (only one recognized at the umbilical margin along the last umbilical suture), a slower growth rate, and an equally biconvex profile. This is consistent with the observations of the two holotypes by Caron and Premoli Silva (written communication, 2006). Nevertheless, given their size difference, we cannot rule out the possibility that they represent different ontogenetic stages of the same species, i.e., *R. globotruncanoides* is

a fully adult individual, whereas *T. brotzeni* may be a pre-adult form. In light of significant intraspecific variability in the morphological characteristics of *Rotalipora*, a survey of the entire population is necessary to determine if these two species can be consistently identified in a population. Even if they can be separated morphologically, it is our contention that criteria based on ornamental and apertural characters should be of primary consideration for the species level classification in *Rotalipora*.