

PHYLOGENY OF THE LATE CENOMANIAN PLANKTONIC FORAMINIFER *ANATICINELLA MULTILOCOLATA* (MORROW)

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ABSTRACT

Globorotalia? multiloculata Morrow, 1934, has been assigned by some workers to the non-keeled genus *Ticinella*, and by others to the keeled genus *Rotalipora*. Detailed study of assemblages from the Greenhorn Formation shows that it is dominantly non-keeled and hence not referable to *Rotalipora*. However, neither is it a direct descendant of *Ticinella*, which is limited stratigraphically to the Albian and latest Aptian. *Globo-*

rotalia? multiloculata is instead a short-lived, very late Cenomanian descendant of *Rotalipora greenhornensis* (Morrow). The new generic name, *Anaticinella*, is introduced to express its phyletic distinctness. Evidence for its evolutionary origin is both morphologic and biostratigraphic. At present it is known only from the United States, and it may be endemic to this region.

INTRODUCTION

Globorotalia? multiloculata Morrow occurs in the latest Cenomanian portion of the Greenhorn Formation in the western interior of the United States, in strata which also contain the very latest specimens of *Rotalipora greenhornensis* (Morrow) and *R. cushmani* (Morrow). These strata also contain the straight ammonite *Sciponoceras gracile* (Shumard). The Cenomanian-Turonian boundary is now placed at the base of immediately overlying beds containing the first specimens of *Inoceramus labiatus* Schlotheim where Cobban and Reeside (1952) placed it.

In central Kansas where deposition was slow *G.? multiloculata* occurs through a stratigraphic interval of 5 feet. In western South Dakota where deposition was rapid it occurs through a stratigraphic interval of 64 feet. Geographic extent in the western interior has been summarized by Eicher (1969) and detailed stratigraphic occurrences by Eicher and Worstell (1970). It also occurs in beds of the same age in the Britton Formation of northern Texas (J. F. Longoria, personal communication).

Hermes (1968, p. 41-42) has summarized the problem of the affinity of *Globorotalia? multiloculata* Morrow, noting that it has been described both as being keeled and non-keeled, and that the generic identity is in question. The assignment of this species to the non-keeled genus *Ticinella* (Loeblich and Tappan, 1961, p. 292), is enigmatic because *Ticinella* otherwise has a range that extends only from late Aptian to late Albian. Brönnimann and Brown (1955) who first referred it to the genus *Thalmaninella* (now *Rotalipora*) took note of the poorly expressed keel in some specimens and consequently placed it in what is now *Rotalipora ticinensis subticinensis* (Gandolfi, 1957), a transition species in the *Ticinella-Rotalipora* lineage. However, this species likewise does not occur above the late Albian. In summary, *Globorotalia? multiloculata* cannot be a late Cenomanian survivor of true *Ticinella* or of *Ticinella-Rotalipora* transitional species as some workers (e.g. Bandy, 1967, p. 15) have suggested, because no representatives of either of these occurs in the stratigraphic interval between the upper Albian and the uppermost Cenomanian. This

brings up the question of the origin of *Globorotalia? multiloculata*.

The purpose of this paper is to present evidence that *Rotalipora greenhornensis* gave rise to *Globorotalia? multiloculata* in the latest Cenomanian by simply losing its keel. Evidence is found in similarity of morphologic details and also in the coincidence of stratigraphic range. In this interpretation the genus *Rotalipora*, which evolved in the middle Albian from a non-keeled stock, gave rise much later to another short-lived non-keeled form as it rapidly approached extinction.

Globorotalia? multiloculata fits the definition of *Ticinella* in having a non-keeled periphery and supplementary umbilical sutural apertures, but it belongs to a separate and considerably younger lineage. To properly express its unique phyletic identity, it is appropriate that a separate genus be established to contain *Globorotalia? multiloculata* and any other species which may have a similar origin.

SYSTEMATICS

Family ROTALIPORIDAE

Subfamily ROTALIPORINAE

Genus *Anaticinella* Eicher, new genus

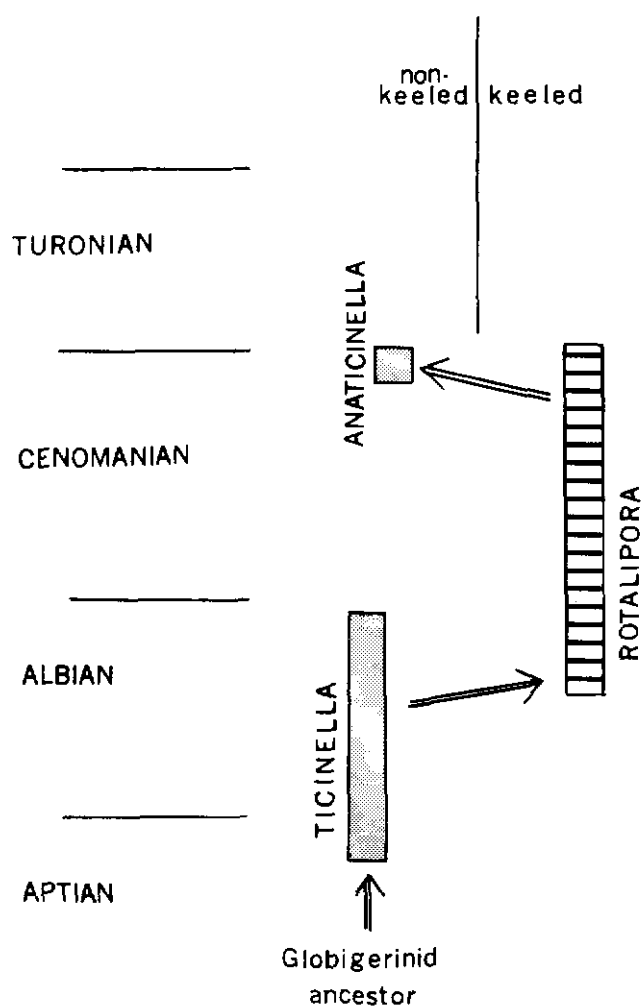
Type Species: Globorotalia? multiloculata Morrow.

Name: From Greek: *ana*, again or return + *Ticinella*.

Gender, feminine.

Diagnosis: Test trochospiral, umbilicate, outline lobate, spire flat to convex; chambers inflated, most lacking keels or poreless margins, some chambers of some specimens with poreless margins or weak keels that are relicts of the *Rotalipora* ancestry; sutures depressed, wall calcareous, perforate, radial in structure, surface smooth; primary aperture interiomarginal, extra-umbilical-umbilical, bordered by a lip that may extend into umbilical plate, secondary sutural apertures on umbilical side, commonly one per suture, rarely two, each bordered by a narrow lip.

Remarks: The genus *Anaticinella* is created for dominantly non-keeled species which are very much like *Ticinella* but which constitute a separate, younger lineage. *Ticinella* is limited to the Aptian and Albian whereas *Anaticinella* occurs in the early Turonian. They are not directly related. *Ticinella* developed a keel and gave rise to the genus *Rotalipora* in the late Albian, and at least one species of *Rotalipora* much later gave rise to a non-keeled *Ticinella*-like form in the late Cenomanian just prior to extinction of the Family Rotaliporinae to which all three genera belong (see text



TEXT FIGURE 1

Phylogeny of the Rotaliporinae.

fig. 1). The rationale for recognizing the new genus is thus largely phyletic. Evidence for its phylogeny is summarized in the following discussion.

Genus *Anaticinella*, new genus

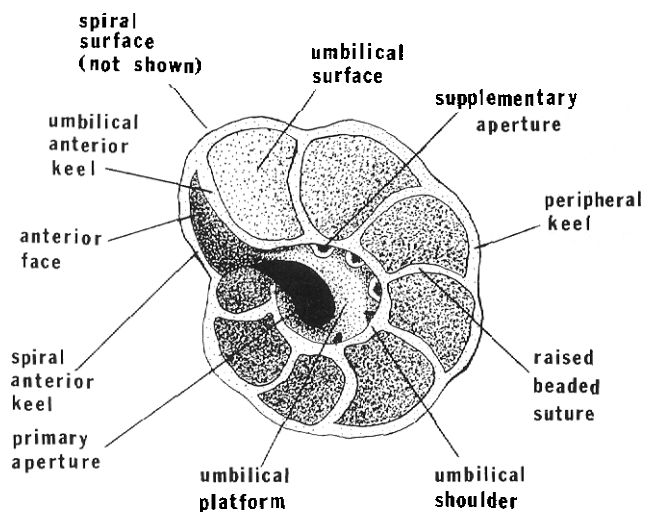
Anaticinella multiloculata (Morrow)

Plate 1, fig. 5; Plate 2, figs. 2-7

Globorotalia? multiloculata Morrow, 1934, p. 200, pl. 31, figs. 3, 5.

Thalmaninella multiloculata (Morrow). Brönnimann and Brown, 1956, p. 534, pl. 20, figs. 1-3.

Ticinella multiloculata (Morrow). Loeblich and Tappan, 1961, p. 292, pl. 6, fig. 13. Eicher and Worstell, 1970, p. 312, pl. 13, figs. 2, 4.



TEXT FIGURE 2

Terminology of morphologic features of *Rotalipora greenhornensis*.

Anaticinella multiloculata has a strongly lobate outline and a trochoid spire that may be strongly convex or nearly flat. The final whorl contains five to nine strongly inflated chambers that are separated by deeply depressed sutures. The chambers of the final whorl increase gradually or little at all. The final chamber commonly possesses a flat anterior face (see text fig. 2 for terminology) that contains fewer perforations than the spiral or umbilical chamber surfaces. In about a third of the specimens examined one or more of the chambers of the final whorl have a poreless margin

or a peripheral keel, that ranges from faint to prominent. The primary interiomarginal aperture is bordered by a broad lip that is a continuation of a prominent umbilical platform. Supplementary apertures are high arches bordered by a lip at the umbilical margins of the sutures.

Genus *Rotalipora* Brotzen, 1942

Rotalipora greenhornensis (Morrow)

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

Rotalipora greenhornensis (Morrow). Loeblich and Tappan, 1961, p. 299, pl. 7, figs. 5–10. Eicher and Worstell, 1970, p. 312, pl. 12, fig. 2, pl. 13, fig. 3.

Rotalipora greenhornensis typically has a smooth peripheral outline and a thick peripheral keel which bifurcates at the peripheral angle of the final chamber into spiral and umbilical anterior keels (see text fig. 2). The anterior keels border a flat or slightly concave anterior face, and with the addition of successive chambers they become beaded ridges that mark the nearly flush sutures both spirally and umbilically. The six to nine chambers are roughly triangular in cross-section—i.e. the peripheral keel forms the apex and the spiral and umbilical surfaces of individual chambers are only slightly convex (see plate 1, fig. 1). Specimens may be dorsally very convex or nearly flat. Chambers of the final whorl increase gradually in size. The primary aperture is bordered by a broad lip that is a continuation of the umbilical platform. Supplementary apertures are rounded arches at the base of the prominent umbilical shoulder.

PLATE 1

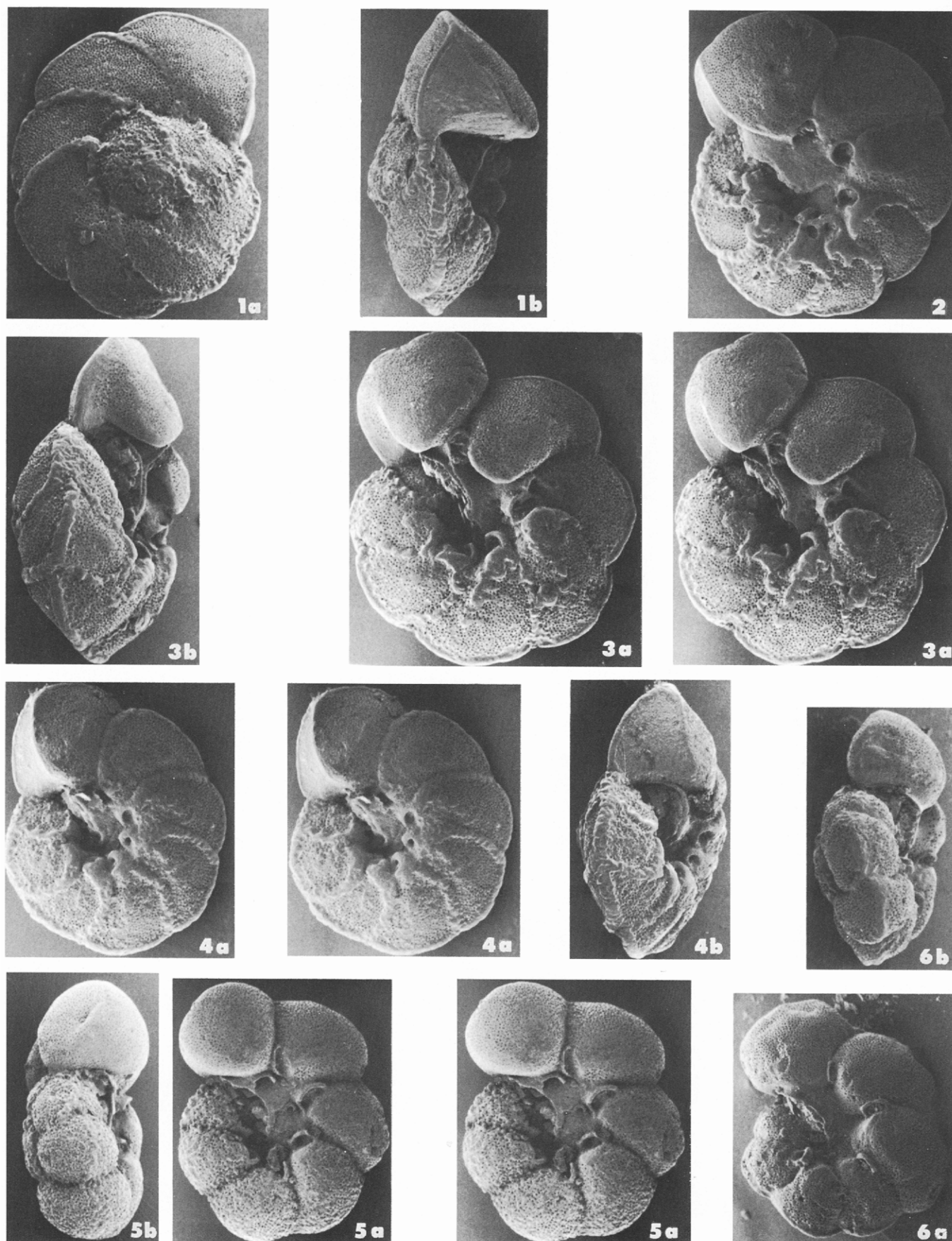
All figures $\times 100$

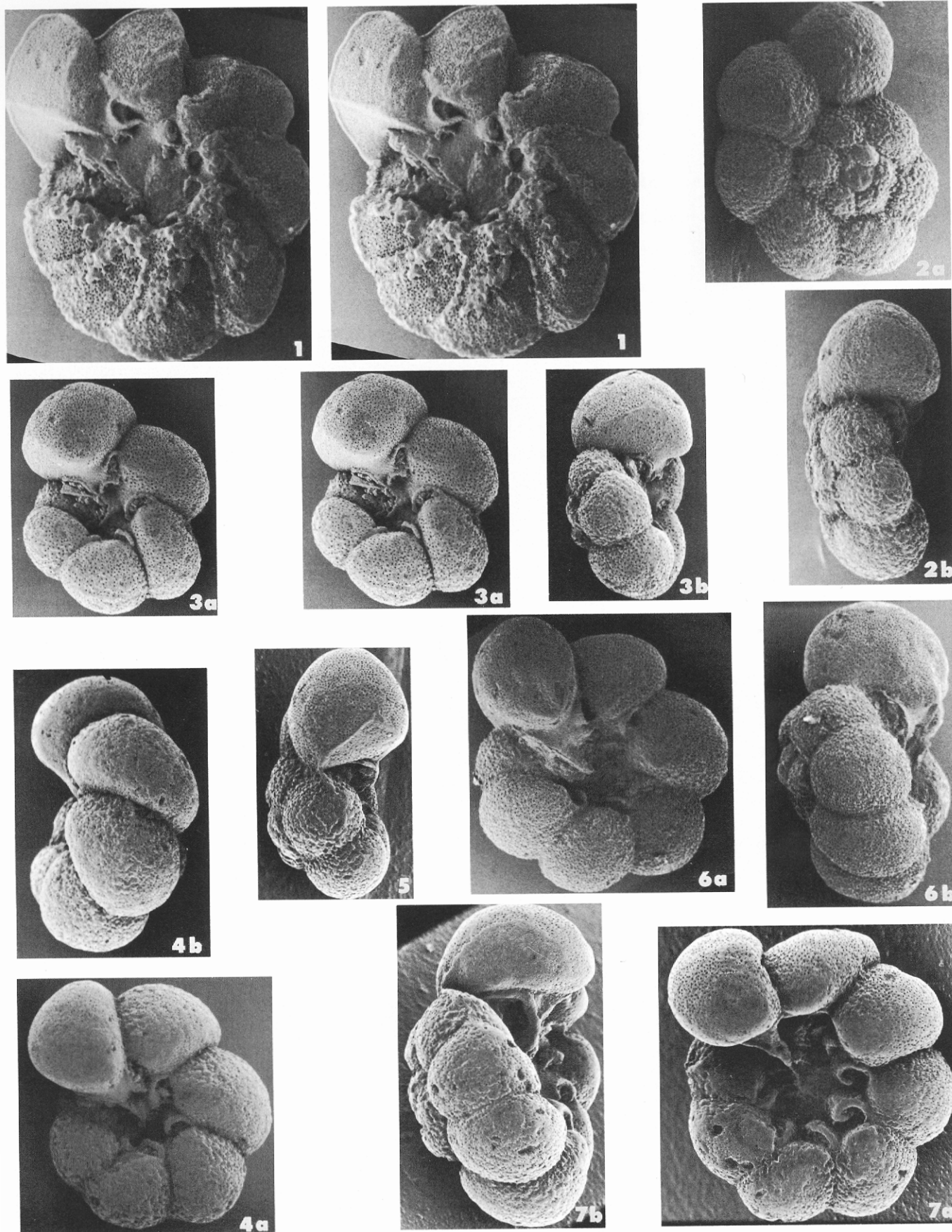
1–4, 6 *Rotalipora greenhornensis*

- 1 a, spiral and b, edge views of a specimen with raised sutures throughout and a very high umbilical shoulder on the final chamber. UCM 28445; locality 2.
- 2 Umbilical view of a specimen with a double supplementary aperture on the final chamber, a wide umbilicus with a large umbilical platform, and a fairly low anterior face on the final chamber. UCM 28444; locality 2.
- 3 a, umbilical stereopair and b, edge views of a specimen with diminished anterior keels, deeply depressed late sutures which breach the umbilical shoulder, and pro-

nounced umbilical protrusion of late chambers. UCM 28446; locality 2.

- 4 a, umbilical stereopair and b, edge views of a typical specimen with raised sutures throughout, a narrow umbilicus, and a small but well developed umbilical platform. UCM 28443; locality 2.
- 6 a, umbilical and b, edge views of a specimen that has lost the anterior keels and raised sutures throughout. UCM 28447; locality 2.
- 5 *Anaticinella multiloculata*: a, umbilical stereopair and b, edge views of a specimen with a distinct peripheral band throughout the test and a prominent double supplementary aperture on the last two chambers. UCM 28448; locality 2.





METHODS OF STUDY

Anaticinella multiloculata and *Rotalipora greenhornensis* appear superficially so different (compare for example plate 1, fig. 4 with plate 2, fig. 7) that a close genetic affinity does not immediately suggest itself. Because of the apparent lack of antecedents I had earlier considered the appearance of *A. multiloculata* in the Greenhorn Formation a probable result of its development elsewhere and its immigration into the western interior (Eicher, 1969, p. 173). However, subsequent studies have caused me to change this opinion. Samples that are rich in well preserved specimens of *A. multiloculata* also contain abundant very late representatives of *R. greenhornensis* that are unusual in their great variability. On photographs taken with the scanning electron microscope most of the very distinctive features of *A. multiloculata* were found to have nearly identical counterparts in coexisting representatives of *R. greenhornensis*. Features in common include prominent loop-like supplementary apertures, occasional doubling of supplementary apertures on one or more of the final chambers, a prominent umbilical platform, late chambers that protrude umbilically. In addition approximately one out of every three specimens of *A. multiloculata* has faint keels or peripheral bands on one or more chambers. These common structural features suggest that *R. greenhornensis* gave rise to *A. multiloculata* by the simple loss of its keel.

For a measure of the extent to which the two species share common characteristics 213 large (0.44–0.77 mm) well-preserved specimens of *A. multiloculata* and 167 large (0.39–0.79 mm) well-preserved specimens of *R. greenhornensis* were picked from two samples from the *A. multiloculata* range zone and were examined

with care. These specimens plus an additional 788 specimens from the same samples were counted for coiling directions. The sample localities are:

1. Black Gap: NW¼ Sec. 16, T 1 S, R 8 E, Pennington County, South Dakota; Greenhorn Formation, 61–71 feet below the top.
2. Bunker Hill: Sec. 18, T 13 S, R 12 W, Russell County, Kansas; Greenhorn Formation, 22.8–27.7 feet above the base.

R. greenhornensis in these samples varies greatly. It has a greater size, width of umbilicus, extent of umbilical platform, and much greater variation in test and chamber shapes, in depression of sutures, and in number of chambers in the final whorl than it has in the lower portion of its range zone. Coexisting specimens of *A. multiloculata* show strikingly similar structural details, coiling ratios and limits of variation.

In addition to the similarities of features, the selected samples yielded specimens showing all gradations between typical specimens of *R. greenhornensis* and wholly unkeeled specimens of *A. multiloculata*. The specimens illustrated on plates 1 and 2, show a series of structural changes involving the loss of the *R. greenhornensis* keel, and these suggest themselves as a model for the evolutionary change.

SIMILARITY OF FEATURES

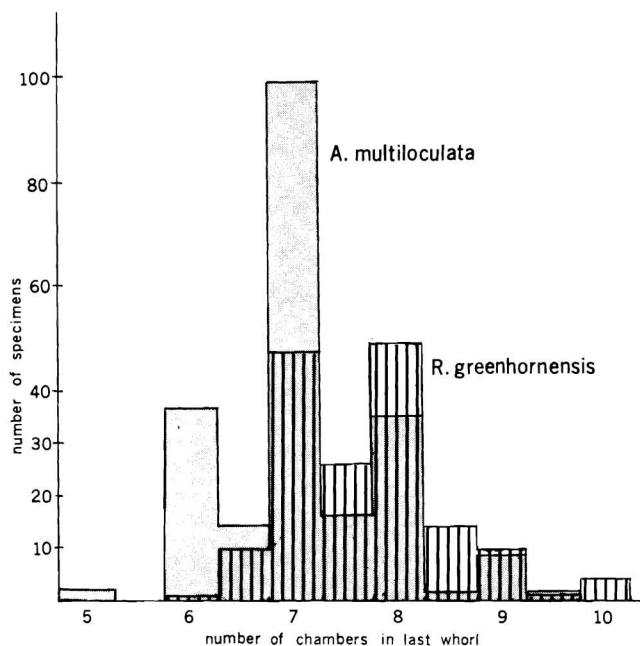
COILING RATIOS

Of 817 specimens of *A. multiloculata* examined for coiling direction 741 or 90.7 percent are dextral, and of 351 specimens of *R. greenhornensis* 311 or 88.6 percent are dextral. This close agreement may be taken as evidence of genetic affinity.

PLATE 2

All figures $\times 100$

- 1 *Rotalipora greenhornensis*: Umbilical stereopair of a specimen with depressed sutures and lobate outline in the last half of the final whorl and with a double supplementary aperture on the final two chambers; locality 2.
- 2–7 *Anaticinella multiloculata*
 - 2 a, spiral and b, edge views of a specimen with a slender profile, a slight umbilical protrusion of the final chamber, and a flat spiral surface. UCM 28451; locality 1.
 - 3 a, umbilical stereopair and b, edge views of a specimen showing umbilically protruding late chambers, a remnant of anterior face and a double supplementary aperture on the final chamber. UCM 28450; locality 1.
 - 4 a, umbilical and b, rear edge views of a specimen showing lack of peripheral imperforate band but pronounced umbilical protrusion of late chambers. UCM 28449; locality 1.
 - 5 Edge view of a specimen lacking peripheral keel but with vestigial anterior keels. UCM 28033; locality 2.
 - 6 a, umbilical and b, edge views of a specimen with a thick profile and a convex spiral surface. UCM 28452; locality 2.
 - 7 a, umbilical and b, edge views of a specimen with a wide umbilicus, a very large umbilical platform and a prominent anterior face. UCM 28034; locality 2.



TEXT FIGURE 3

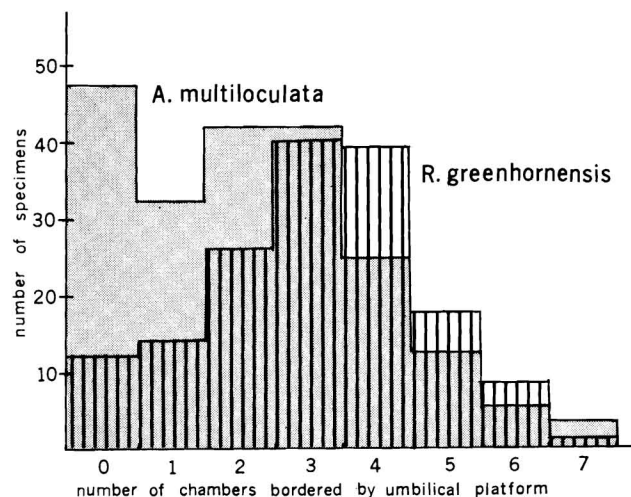
Number of chambers in final whorl of *Anaticinella multiloculata* and *Rotalipora greenhornensis*.

NUMBER OF CHAMBERS

The number of chambers in the final whorl was determined to the nearest half chamber, and the results are tabulated in text fig. 3. The range of variation for the two species is similar.

SUPPLEMENTARY APERTURES

The supplementary apertures of *A. multiloculata* are large rounded arches bordered by a lip, and they resemble the prominent supplementary apertures of coexisting specimens of *R. greenhornensis* much more than they do the typically subdued apertures of the Albian species of *Ticinella*. Eight of 167 specimens of *R. greenhornensis* (5 percent) and 41 of 213 specimens of *A. multiloculata* (19 percent) examined in detail have two supplementary apertures on one or more of the late chambers. The significance of double supplementary apertures is unknown. Double supplementary apertures have also been observed in occasional coexisting specimens of *Rotalipora cushmani*. Hence, the presence in both *A. multiloculata* and *R. greenhornensis* of double supplementary apertures is not as indicative of close affinity as is the similarity of shape of supplementary apertures.



TEXT FIGURE 4

Extent of umbilical platforms in *Anaticinella multiloculata* and *Rotalipora greenhornensis*.

UMBILICAL PLATFORM

The umbilical platform is a distinctive structure that is present on the vast majority of specimens of both *R. greenhornensis* and *A. multiloculata* that were examined in detail. Umbilical platforms vary greatly in size, as the specimens figured on plates 1 and 2 show. In the specimens studied a measure of the extent of the umbilical platform was provided by the number of chambers it borders. The designation "1" indicates that it borders only the final chamber (and is hence little more than a large apertural flap), a "3" indicates that it borders the final three chambers, a "0", that no umbilical platform is present. Results are tabulated in text fig. 4 which shows that extents of umbilical platforms in the two species are similar except that a comparatively large number of *A. multiloculata* specimens (22 percent) lack them entirely. The significant fact is that a large proportion of both species share this somewhat unusual feature, and this is considered supporting evidence for their genetic affinity.

MORPHOLOGIC INTERGRADATIONS

Morphologic intergradations between *R. greenhornensis* and *A. multiloculata* constitute additional evidence for their genetic affinity and suggest the probable scheme of evolution. In the Greenhorn Formation these two species intergrade in the following way:

In many specimens of *R. greenhornensis* the normally high anterior face (measured from the periphery of the previous whorl to the periphery of the final chamber), like that on the specimens shown in plate 1, figs. 1 and 4, becomes considerably lower in the late chambers (see plate 1, fig. 2). As the lower anterior face appears in successively earlier chambers of the final whorl a strongly lobate outline develops (see plate 2, fig. 1). Simultaneously the late chambers tend to lose their anterior keels which in turn results, as new chambers are added, in loss of the beaded raised sutures. Sutures then become depressed. These developments tend to precede loss of the peripheral keel in the evolutionary sequence. The specimen shown in plate 1, fig. 6 illustrates the completion of this process. Although this specimen has a strong peripheral keel, it has no anterior keels and beaded raised sutures are missing throughout. All sutures are depressed and umbilical and spiral surfaces of chambers have become quite convex. The changes documented here begin with the latest chambers and work progressively backwards so that the inferred evolutionary development can be seen in many individual specimens.

In the specimens shown in plate 1, figs. 3 and 6, and plate 2, fig. 1, as the umbilical shoulder is breached by depression of the sutures, the inner margins of the umbilical sides of the late chambers are left with protrusions that are relicts of the umbilical shoulder. In some specimens (see plate 1, fig. 3) the protrusions tend slightly to overhang the umbilicus. These characteristic protrusions of the umbilical sides of chambers can be traced through many intermediate specimens into typical specimens of *A. multiloculata* where they manifest themselves as axially elongated chambers (see particularly plate 2, figs. 3, 4, 6 and 7).

Even after the anterior keels are lost the flattened anterior face commonly remains prominent. This face typically has fewer pores than the umbilical or spiral surfaces of the chamber and this helps to identify it in specimens of *A. multiloculata*, particularly in SEM photographs (see plate 2, figs. 3 and 7).

All gradations can be observed from specimens like that in plate 1, fig. 6 with inflated chambers and depressed sutures and yet with a peripheral keel throughout (hence a *Rotalipora*) to specimens with an imperforate peripheral band, and finally to completely keeless specimens of *A. multiloculata*. For example, the specimen shown in plate 1, fig. 5, has a smoothly rounded periphery on most chambers (and is hence placed in *A. multiloculata*) and yet, the early chambers of the final whorl possess a distinct peripheral

band. In the specimen shown in plate 2, fig. 2 early chambers of the final whorl show only a faint peripheral alignment of surface pustules. Progressing farther, the *A. multiloculata* specimens in plate 2, figs. 3–7 show little or no evidence of an imperforate peripheral band. The specimen shown in fig. 5, however, has distinct relict anterior keels, which clearly reflects its ancestry.

SUMMARY

The wide variations introduced into assemblages of *Rotalipora greenhornensis* in the western interior of the United States shortly before it became extinct in latest Cenomanian time were probably responses to environmental pressures, the nature of which is unknown. One of the genetic changes produced at this time caused loss of the pronounced peripheral keel. The resultant forms, here referred to *Anaticinella*, are very much like the *Rotalipora* from which they evolved except for the absence of the keel, and they do appear superficially much different.

Biostratigraphic evidence supports the evidence obtained from the detailed morphologic studies. Species of *Ticinella* can be ruled out as direct ancestors of *Anaticinella* because none occurs in the lower and middle portion of the Cenomanian Stage. Very shortly after it was produced, *A. multiloculata*, as well as its parent, *R. greenhornensis*, and the coexisting *Rotalipora cushmani*, became extinct. Thus ended a distinctive group of planktonic foraminifera, the Rotaliporinae which, in one sense, had come full circle. The group had diversified following the rise of the keeled genus *Rotalipora* from a non-keeled *Ticinella* ancestor in the Albian, and morphologic variations that evolved immediately prior to its disappearance included a return to the *Ticinella* form. *Anaticinella multiloculata* apparently left no descendants and it has not yet been found outside the interior Cretaceous seaway in the United States. It may be endemic to the interior seaway.

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