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33. MORPHOLOGY AND AFFINITY OF THE PLANKTONIC FORAMINIFER *CASSIGERINELLOITA AMEKIENSIS* STOLK AND RECLASSIFICATION OF *CASSIGERINELLOITA* STOLK[1]

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ABSTRACT

Cassigerinelloita amekiensis Stolk occurs abundantly in lower middle Eocene samples from the Southern Kerguelen Plateau, drilled during Ocean Drilling Program Leg 120 (Hole 749B). It showed little morphological change during its rather short evolutionary history. Because of its microperforate, pustulate wall and a triserial, pseudoplanispiral coiling mode, *C. amekiensis* appears to be related closely to co-occurring *Guembelitria triseriata* (Terquem). These affinities indicate that the taxa are phylogenetically related and should be classified together in the family Guembelitriidae. The potential paleoceanographic importance of these forms is also discussed.

INTRODUCTION

Stolk (1965) recorded the tiny planktonic foraminifer *Cassigerinelloita amekiensis* from the uppermost lower Eocene to middle Eocene of Nigeria. He believed that this new genus and species were closely related to *Cassigerinella* spp. Pokorny, because these genera were similar in coiling pattern and chamber arrangement. *Cassigerinelloita amekiensis,* however, differs from all known species of *Cassigerinella* in lacking the typical biserial coiling plan and the true umbilicus and in bearing supplementary sutural apertures in the adult stage. Its short range made it a good zonal marker for the ?uppermost lower Eocene to lower middle Eocene of Nigeria.

Despite its importance in biostratigraphy and its ease of identification, as reported in the original description, *C. amekiensis* has never been recorded outside the Niger Delta, and the original description has remained the only source for subsequent attempts for its classification. Loeblich and Tappan (1988), for example, placed this genus in the family Catapsydracidae on the basis of the original descriptions and illustrations, whereas Blow (1979) suggested that it represented "an abortive variant of a ?*Globigerinita* sp."

During our study of planktonic foraminifers from Hole 749B (Southern Kerguelen Plateau, Ocean Drilling Program Leg 120), we found a considerable number of specimens ascribable to *C. amekiensis*. The results from detailed observations are presented in this report.

MATERIAL AND METHODS

Site 749 is located on the western Banzare Bank of the Southern Kerguelen Plateau, at 58°43.03′S, 76°24.45′E; Hole 749B was penetrated to 123.8 m below seafloor (mbsf). Thirty-nine samples spanning Core 120-749B-1H through -13X (119.8 m) were collected as part of a study of Tertiary planktonic foraminifers (see Li et al., this volume).

Samples were washed through a 63-μm sieve and dried; the residues were then examined. Planktonic foraminifers were picked and counted under an optical binocular microscope. Detailed observations and measurements were performed by means of a Hitachi-2500 scanning electron microscope (SEM) on selected specimens, some of which were dissected to observe the morphology of their earlier stages.

Almost all 39 samples yielded beautifully preserved planktonic foraminifers of the middle Eocene to upper Oligocene, characterized by *Globigerina* and *Tenuitella* in Cores 120-749B-1H through -2H, and by *Acarinina* and *Subbotina* in Cores 120-749B-3H through -13X (no recovery in Cores 120-749B-8X and -14X). *Cassigerinelloita amekiensis* occurs in the lowermost 4 samples from Cores 120-749B-11X through -13X, an interval referable to the *A. bullbrooki* Zone in the lower middle Eocene (Schlich, Wise, et al., 1989; Li et al., this volume). This material was compared with two paratype specimens supplied by the Shell Company.

MORPHOLOGICAL CHARACTERS OF *CASSIGERINELLOITA AMEKIENSIS*

Test Size and Chamber Characters

Early *C. amekiensis* has an extremely small test, with an average diameter of 70–80 μm in Sample 120-749B-13X-CC, 0–3 cm. It reached 100–110 μm in breadth in Samples 120-749B-11X-2, 50–53 cm, and -11X-CC, 0–3 cm, along with a rapid increase in abundance in these higher horizons.

All chambers of *C. amekiensis* are spherical or hemispherical, with six to eight rapidly enlarging ones visible on the outside whorl (Plates 1 and 2). Some additional chambers (1–3) may develop in certain large specimens, exhibiting a range of variation within the species.

Wall Texture

The wall is microperforate, with micropores (diameter about 0.5–1 μm) penetrating the wall and small pustules on its surface. On the last one or two chambers, the pustules are generally smaller and weaker, whereas those on the earlier chambers are larger and denser (Plate 1, Figs. 2 and 6). We found no pore pits or pore mounds or surface textures other than pustules, nor did we observe a completely smooth wall.

The thickness of the wall is about 2 μm, but the walls thicken toward the early test, where they may reach 3–4 μm as a result of secondary calcification (Plate 1, Figs. 10 and 11).

The paratypes are similarly microperforate (pores about 1 μm in diameter) and bear well-developed pustules that are almost twice as large as those on our specimens from Hole 749B.

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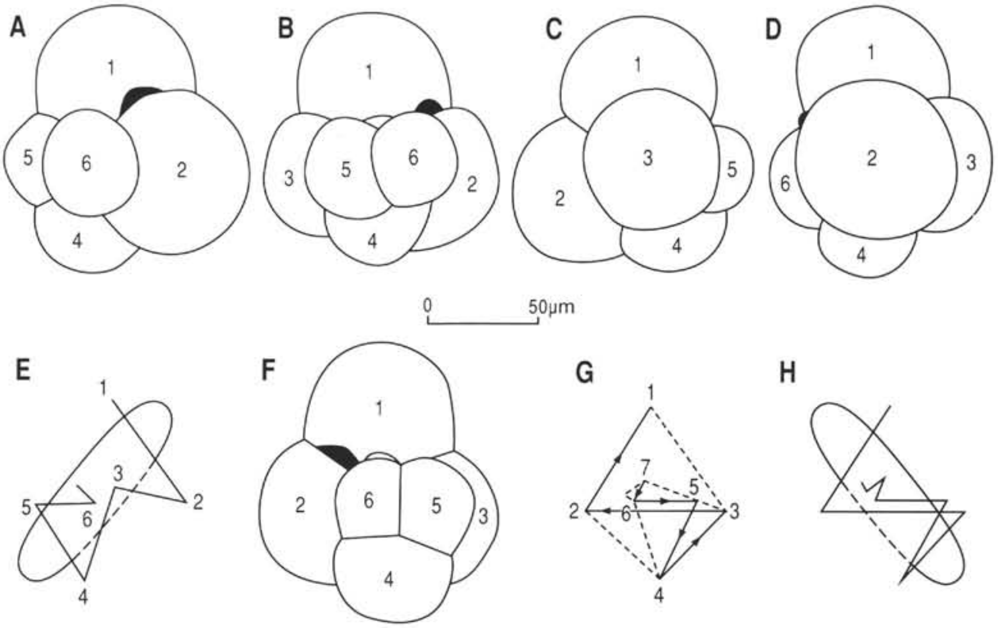

Figure 1. **A–D.** Line drawings based on the holotype figures of *C. amekiensis* in Stolk (1965), with successive numbering of the chambers. **E.** Coiling pattern in holotype (A). **F.** Specimen from Sample 120-749B-11X-CC, 0–3 cm (as in Plate 1, Fig. 1) with chamber centers indicated for coiling reconstruction. **G.** Schematic two-dimensional illustration of triserial chamber arrangement in preceding figure (F). Note that only a single alternation of direction is followed (i.e., the direction of coiling from 6 to 5 is the same as from 4 to 3, and the direction of coiling from 5 to 4 is the same as from 3 to 2). **H.** As in the preceding figure (G), showing triserially pseudoplanispiral coiling.

Coiling Mode

Chambers in *C. amekiensis* are arranged triserially in a very low trochospire (= pseudoplanispire) to form a polygonal, subspherical test without a true umbilicus or distinct periphery. The successive triserial whorls are themselves coiled, so that the test (like that of *Cassigerinella*) has two simultaneous but distinct axes of coiling (Fig. 1). Viewed from their outer margin, or from the side opposite to the apertures, any three successive chambers always constitute a unique trigonal pattern, with the last-formed chamber situated across the suture of the previous two, in the shape of an isosceles triangle (Plate 1, Figs. 3, 5, and 6; Plate 2, Figs. 2, 3, and 5). Furthermore, in tests where the early whorls are invisible, an alternate coiling direction in the chambers suggests pseudoplanispirality. For every three consecutive chambers, only a single alternation of coiling direction occurs through ontogeny, even in specimens with the final chamber in a different position (cf. Plate 1, Figs. 1 and 10 with Plate 2, Figs. 7 and 1, respectively). This pseudoplanispirality produces a false appearance of the chambers being coiled in pairs like that in *Cassigerinella,* that is, the odd-numbered chambers are located on one side and the even ones on the other (Fig. 1). Biserially planispiral *Cassigerinella* spp., however, always possess laterally flattened tests with pseudoumbilici and a distinct periphery, to which the aperture is directed (Saito and Biscaye, 1977; Li, 1986). Three successive chambers in these flattened *Cassigerinella* never constitute an isosceles triangle, a basic unit in the polygonal test of *C. amekiensis*. The term "triserial pseudoplanispiral coiling" is here introduced to define the peculiar mode that characterizes *C. amekiensis,* the first record of its type among the planktonic foraminifers.

Apertural Features

A semicircular or low-arched aperture, with or without a thin lip, is clearly visible in most individuals of *C. amekiensis* and is always located across the suture between the last and penultimate chambers and the early chambers in the outer whorl. Our specimens did not have an apertural face as subspherical as in the holotype (see Fig. 1); it remains inflated as part of the spherical chamber (Plate 1, Figs. 1, 2, 4, and 9; Plate 2, Figs. 1, 4, and 9). No toothplates were observed in dissected specimens.

Some individuals may have an additional sutural aperture on the side of the chamber opposite to the primary one; in this case, several additional chambers ("bullae" of Stolk, 1965, but not of Bolli et al., 1957) may also develop on these apertures to form a test marked by chamber proliferation (Plate 1, Figs. 9, 12, and 13).

AFFINITY AND PHYLOGENY

The diagnostic morphological characters of *Cassigerinelloita amekiensis,* as described above, include the microperforate, pustulate wall and triserial, pseudoplanispiral coiling. Therefore, forms with these or similar characters should be considered as closely related phylogenetically. In our material, the only form with similar morphology and occurring together with *C. amekiensis* is *Guembelitria triseriata* (Terquem) (Plate 2, Figs. 10–12). This species, as considered here, includes all known Eocene triserial taxa, such as *G. columbiana* Howe (1939) and *G. stavensis* Bandy (1949), because all these morphotypes coexist in our samples and further division seems unjustified (see also McGowran and Beecroft, 1985). *Guembelitria samwelli* Jenkins (1978) is another similar form, but it occurs only in the middle Oligocene in southern oceans.

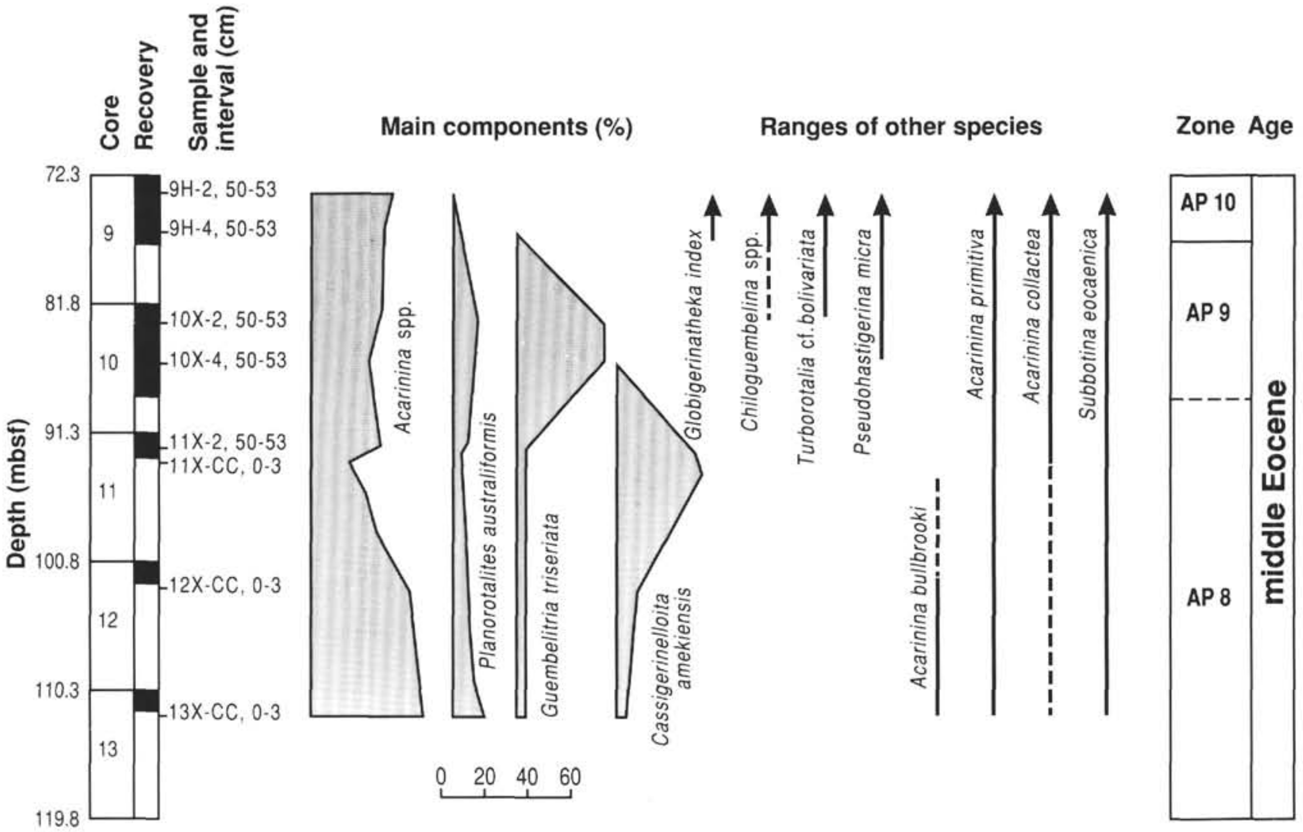

Figure 2. Composition of planktonic foraminifers in Cores 120-749B-9H through -13X. Note that *C. amekiensis* occurs in the *Acarinina bullbrooki* Zone (AP8 of Stott and Kennett, in press), an interval equivalent to upper Zone PlO of Blow (1979) and Berggren and Miller (1988). See also Li et al. (this volume).

Guembelitria triseriata has an almost equally small but elongate test constructed of spherical chambers in a triserial coil (i.e., three in a whorl; see Plate 2, Figs. 10–12). The wall is microperforate and pustulate, with heavier pustules and maximum wall thickness in the early chambers. The aperture, bordered with a distinct lip, is semicircular or low-arched and open to the umbilicus. All these features, except the umbilicus and the test shape, have been found in *C. amekiensis*. In *G. triseriata,* the coiling mode is unidirectional and triserial, producing an elongate test; in *C. amekiensis* triserial coiling is combined with pseudoplanispiral coiling to form a subglobular test shape. Possibly, *C. amekiensis* originated from variants of *G. triseriata* through a change of coiling mode from triserial and highly trochospiral to triserial and pseudoplanispiral.

With this change, the aperture became slightly modified in its location, and the lip thinner to adjust to pseudoplanispirality, producing the unusual reconfiguration of the chambers in *C. amekiensis*. The combined relative abundance of *C. amekiensis* and *G. triseriata* in the fossil fauna further suggests such a relationship. In the lowermost available Sample 120-749B-13X-CC, 0–3 cm, *G. triseriata* and *C. amekiensis* each constituted only 5% of the fauna, and their relative proportions gradually changed to 2%:10% (in Sample 120-749B-12X-CC, 0–3 cm) and 1%:40%–35% (in Samples 120-749B-11X-CC, 0–3 cm, and -11X-2, 50–53 cm). Only after the extinction of C. *amekiensis* in Sample 120-749B-10X-4, 50–53 cm, did *G. triseriata* begin to dominate the fauna (Fig. 2).

After establishing itself in the fauna, *C. amekiensis* gradually increased in test size (from 70 μm in Sample 120-749B-13X-CC, 0–3 cm, to 120 μm in Sample 120-749B-11X-2, 50–54 cm) and achieved a rapid increase in relative abundance. Just before the species became extinct, a few supplementary apertures and bulla-like additional chambers developed on some tests (Plate 1, Figures 9, 12, and 13).

Thus, *Cassigerinelloita amekiensis* appears to be a direct descendant of *G. triseriata* despite the absence of intermediate forms linking the two species at Hole 749B, probably as a result of inadequate sample collection because of nonrecovery of the lowermost Core 120-749B-14X. The separation of *C. amekiensis* from *G. triseriata* must have been at a time earlier than the age of our oldest sample (120-749B-13X-CC, 0–3 cm), but future work will resolve this.

The evidence, therefore, suggests that Blow (1979) and Loeblich and Tappan (1988) are incorrect in their consideration of the nature of *C. amekiensis*. It is not an abortive variant of ?*Globigerinita,* as implied by Blow, because species of *Globigerinita,* although having a wall similar to *C. amekiensis,* have been suggested to have evolved from *Tenuitella* only from the Oligocene on (see Fleisher, 1974; Li, 1987). Neither is it a catapsydracid, as suggested by Loeblich and Tappan (1988), because all catapsydracids are characterized by a distinct cancellate wall rather than the microperforate wall found in *C. amekiensis*. The so-called "microcancellate wall" of Loeblich and Tappan (1988) is possibly a mistaken identification of a pattern produced by the heavy pustules in the type illustrations of *C. amekiensis*.

As pointed out by Stolk (1965), however, *C. amekiensis* is morphologically similar to species of *Cassigerinella,* as they have similar chamber arrangement patterns, which indeed has led some authors (e.g., Banner, 1982) to suppose affinity. A previous study by Li (1986), however, of the *Cassigerinella* species *C. chipolensis* and *C. boudecensis,* confirmed that

Table 1. Morphocharacters and ancestors of *Cassigerinelloita*, *Cassigerinella*, and *Riveroinella*.

Species	Wall texture	Coiling (pseudoplanispiral)	Range	Possible ancestor
Cassigerinelloita amekiensis	Microperforate, pustulate	Triserial	P10/AP8	*Guembelitria triseriata*
Cassigerinella boudecensis	Finely perforate, + pore mounds	Biserial	P18–?N14	*Chiloguembelina*
Cassigerinella chipolensis	Finely perforate, smooth	Biserial	[a]P18–?N14	*Chiloguembelina*
Riveroinella martinezpicoi	Finely perforate, smooth	Biserial	[b]early Miocene	?*Streptochilus*

[a]Blow (1979).
[b]Bermúdez and Seiglie (1967).

these are essentially biserial (but not triserial) planispires and that they evolved from a biserial *Chiloguembelina*. This contrasts with *Cassigerinelloita*, which is essentially triserial pseudoplanispiral and probably evolved from triserial *Guembelitria*. In addition, *C. amekiensis* can be distinguished from *Cassigerinella*, as well as from *Riveroinella martinezpicoi* (SEM illustrations in Saito and Biscaye, 1977), by its microperforate, pustulate wall rather than by a finely perforate, smooth wall or a wall with distinct pore mounds (Table 1).

OCCURRENCE

Stolk (1965) recorded *C. amekiensis*, together with *Guembelitria* "*columbiana*" (= *G. triseriata*), as ranging from the ?uppermost lower Eocene to the lower middle Eocene (the *C. amekiensis* Zone), confirmed by Petters (1983). Other species occurring in this interval include *Globigerina linaperta* Finlay, *G. yeguaensis* Weinzierl and Applin, *G. boweri* Bolli, *Globorotalia pseudomayeri* Bolli, *G. renzi* Bolli, *Pseudohastigerina micra* (Howe), and, in the lower part, "*G. pseudomenardii*" sensu Loeblich and Tappan (1957). Although lacking some diagnostic species (e.g., *Acarinina primitiva* Finlay and *Globigerinatheka index* Finlay), this faunal assemblage represents the early to middle Eocene in modern biostratigraphy (Blow, 1979; Toumarkine and Luterbacher, 1985; Berggren and Miller, 1988), which conforms with the original age determination by Stolk (1965).

Surprisingly, the fossil fauna from the interval with *C. amekiensis* in Hole 749B is similar, if not identical in age, to the one recorded by Stolk in Nigeria. *Acarinina primitiva* and *Guembelitria triseriata* occurred throughout the range of *C. amekiensis*, and *G. index* made its first appearance some 10 m above the extinction of *C. amekiensis* (Fig. 2). This approximates Zones P10 to lower P11 because, according to McGowran (1977) and McGowran and Beecroft (1985), the last appearance datum (LAD) of *Planorotalites australiformis* (Jenkins) and the first appearance datum (FAD) of *G. index* can be correlated to within Zone P11. Just below this, in the lower part of Zones P11 and P10, *Guembelitria* occurred in southern Australia and in Sites 214 and 264 in the eastern Indian Ocean. Because *C. amekiensis* disappeared much earlier than the extinction level of *Guembelitria* at Hole 749B, we now propose a range for *C. amekiensis* to be within Zone P10, or Zone AP8 (of Stott and Kennett, 1990) in the early middle Eocene (Fig. 2; see also Li et al., this volume).

Stott and Kennett (1990) recorded some similar forms in Hole 689B (Leg 113, Maud Rise, Antarctica) in their Zone AP8, equivalent to tropical Zone P10 (upper part), in Chron 21, about 50 Ma in the chronostratigraphy of Berggren et al. (1985). Their specimens, figured as *Globigerina*? sp. B on Plate 5, Figures 11–14, appear to belong to *C. amekiensis*.

PALEOCEANOGRAPHIC SIGNIFICANCE

Modern representatives of triserial *Guembelitria*, the microperforate *Gallitellia vivans* (Cushman), inhabit the water column between *Globigerinoides trilobus* (surface dweller) and *Globorotalia menardii* (deep dweller) in open-marine environments. They are especially common, however, in unstable conditions such as upwelling waters (Kroon and Nederbragt, 1988). Except in its smooth wall and lipless, asymmetric aperture, *Gallitellia vivans* closely resembles the fossil *Guembelitria triseriata*. The latter has been reported as occurring from the middle Eocene to the lower Oligocene (Beckmann, 1957, as *G. columbiana*), but it became common to abundant only in sediments of the early middle Eocene (Zones P10–P11), a period of cooling according to McGowran and Beecroft (1985), for example. The onset of the middle Eocene saw a drop in global temperature after a long warm period in the early Eocene, as recorded by isotopic studies (e.g., Shackleton and Kennett, 1975, Tasman Sea; Shackleton, 1986, summary of Paleogene; Boersma et al., 1987, Atlantic Ocean). In response to this cooling, however, planktonic foraminifers showed a gradual transformation rather than a rapid faunal turnover from morozovellid to subbotinid assemblages (see Haq et al., 1977, and Premoli Silva and Boersma, 1988, for the Atlantic Ocean).

McGowran and Beecroft (1985) first proposed that *G. triseriata* might be a cool-water indicator based on the disappearance of large benthic foraminifers in the early middle Eocene. Whether *G. triseriata*, as well as its probable offshoot *Cassigerinelloita amekiensis*, was an upwelling inhabitant, as is its present-day counterpart *Gallitellia vivans*, or a cool-water indicator, or both, is not yet fully understood. However, the invasion of *G. triseriata* alone is insufficient to indicate such a cooling event in the early middle Eocene. It is unlikely that Nigeria (equatorial) and southern Australia and the Kerguelen Plateau (subantarctic) were all under similar cool-water conditions, as indicated by a similar fauna, including *G. triseriata*, found in these areas during the early middle Eocene.

The evidence listed below supports our view that *G. triseriata* is an indicator of unstable (upwelling) waters:

1. Upwelling waters are presently usually dominated by small forms (Duplessy et al., 1981), such as *Gallitellia vivans* (Kroon and Nederbragt, 1988).
2. *Guembelitria triseriata* first occurred at the beginning of the middle Eocene, a period of invigorated upwelling accompanied by a strong, widely developed oxygen minimum, as indicated by high abundances of biserial *Chiloguembelina* in Atlantic regions (Boersma and Premoli Silva, 1988).
3. A synchronous hiatus has been widely recorded near the early Eocene–middle Eocene boundary in the Southern Oceans (McGowran, 1977; Stott and Kennett, 1990), indicating unstable marine environments (McGowran, 1978).
4. A change of sedimentation rates from >70 m/m.y. (early Eocene) to about 8 m/m.y. (middle to late Eocene) was recorded at Hole 749B (Schlich, Wise, et al., 1989), and at that level both *Guembelitria triseriata* and *Cassigerinelloita amekiensis* occurred (this study). This indicates that environmental changes such as increasing productivity might have caused the evolution of these taxa.

5. The scattered geographic record of *C. amekiensis* suggests that this species is an indicator of unusual conditions.

6. The middle Eocene in the Gulf of Guinea, including the type locality of *C. amekiensis,* is characterized by coastal upwelling and phosphate sedimentation (Petters, 1981, 1983).

Originating from *G. triseriata, C. amekiensis* might have inhabited similar unstable environments such as upwelling waters but with a rather limited spatial dispersal.

CONCLUSIONS

Cassigerinelloita amekiensis possesses a microperforate, pustulate wall and a peculiar, triserial, pseudoplanispiral coiling mode. It resembles a co-occurring triserial species, *Guembelitria triseriata,* in many morphological aspects. *C. amekiensis* may have evolved from *G. triseriata* by a change of coiling mode from triserial and rectilinear coiling to triserial and pseudoplanispiral coiling, in unstable or upwelling waters at about 50 Ma, equivalent to Zone P10, or Zone AP8, in the early middle Eocene.

Accordingly, the genus *Cassigerinelloita* should be classified in the family Guembelitriidae (given below), rather than in the families Catapsydracidae or Cassigerinellidae, as proposed elsewhere.

The phylogenetic importance of wall texture, as discovered earlier by Lipps (1966) and Steineck and Fleisher (1978), is confirmed again by a reconstruction of the *G. triseriata–C. amekiensis* lineage in this study.

SYSTEMATIC DESCRIPTION

Family GUEMBELITRIIDAE Montanaro Gallitelli, 1957
Genus *CASSIGERINELLOITA* Stolk, 1965, emended
(type species: *C. amekiensis* Stolk, 1965)

Emended Description. Test small, about 70–120 μm in diameter, globular; chambers spherical, six to eight visible in the complete test, arranged triserially and pseudoplanispirally, without a true umbilicus; wall microperforate and pustulate; aperture interiomarginal, low arched, with or without a thin lip, situated on the suture and sited between the last two chambers and the early chambers of the outer whorl; rarely, up to three nontriserial additional chambers are formed terminally with their own sutural apertures.

Range. Zone P10/AP8 (lower middle Eocene).

Distribution. Nigeria, southern Indian Ocean, Weddell Sea.

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POSTSCRIPT

Since this report was written, we have been informed that *Cassigerinelloita amekiensis* also occurs in a level equivalent to Zones P9 (upper part) and P10 at Holes 698A, 699A, 700B, 702B, 703A, and 704B in the subantarctic South Atlantic Ocean (Nocchi et al., 1991).

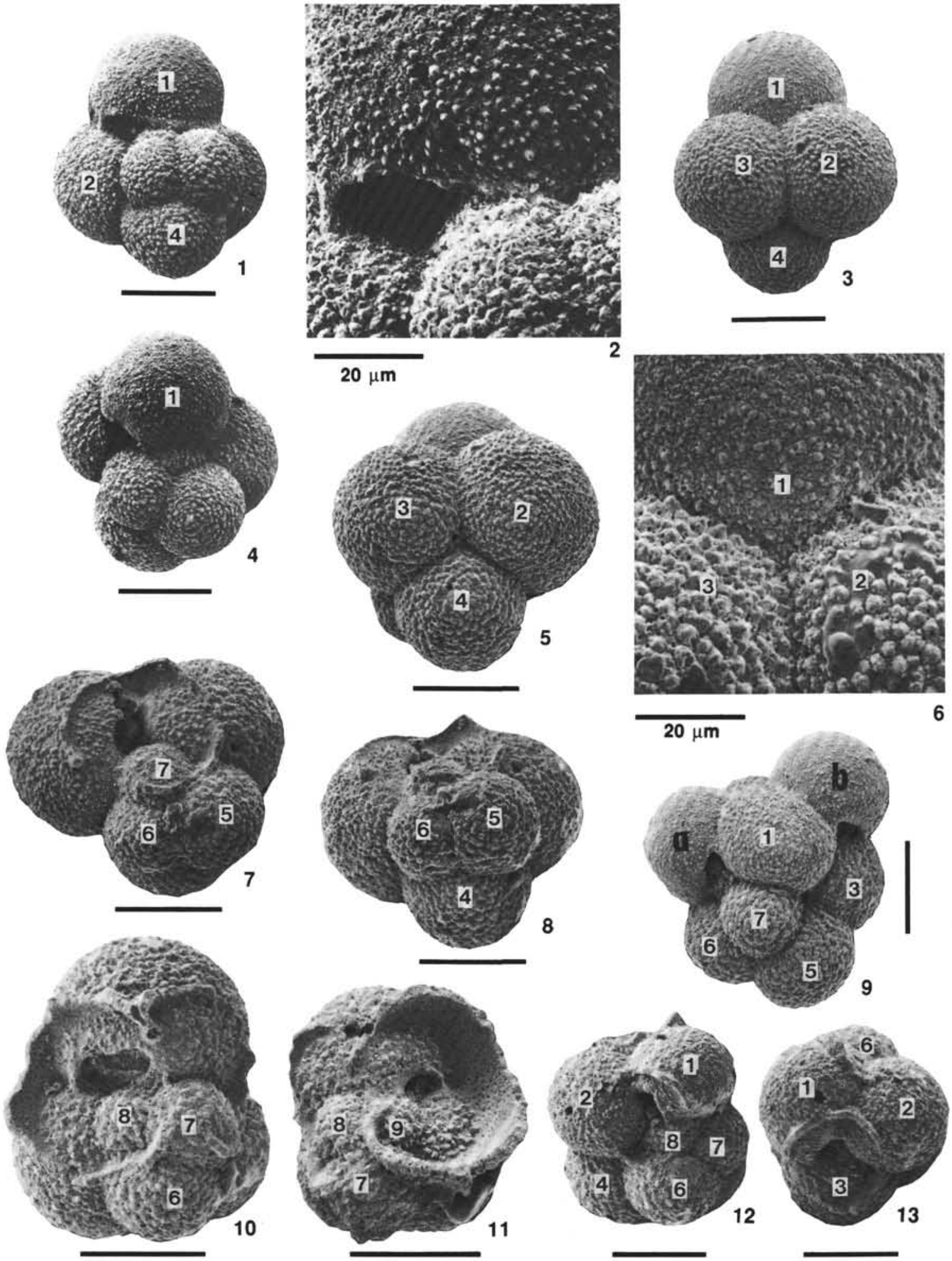

Plate 1. Scale bar for all specimens = 50 μm, unless otherwise indicated. **1–8, 10, 11.** A single specimen of *Cassigerinelloita amekiensis* from Sample 120-749B-11X-CC, 0–3 cm; (1) apertural view; (2) apertural closeup showing a weakly developed lip and microperforate, pustulate wall; (3) side view of the last four chambers that shows the trigonal pattern of last three successive chambers; (4) tilted view of Plate 1, Figure 1; (5) tilted view of Plate 1, Figure 3, showing chambers 2, 3, and 4, which constitute another trigonal pattern; (6) enlargement of Plate 1, Figure 3; (7) final chamber removed to show the early aperture and trigonal pattern formed by chambers 5, 6, and 7; (8) tilted view of Plate 1, Figure 7; (10) final two chambers removed; (11) final three chambers removed to show the thickened wall and heavy pustules in early chambers. **9, 12, 13.** A single specimen of *C. amekiensis* with supplementary apertures and additional chambers from Sample 120-749B-11X-2, 50–53 cm; (9), whole specimen with two additional chambers (**a** and **b**), which are not coiled triserially or planispirally; (12) additional chambers removed, to show the primary aperture on which additional chamber **a** formed; (13) tilted view of Plate 1, Figure 12, showing the additional aperture on which additional chamber **b** formed.

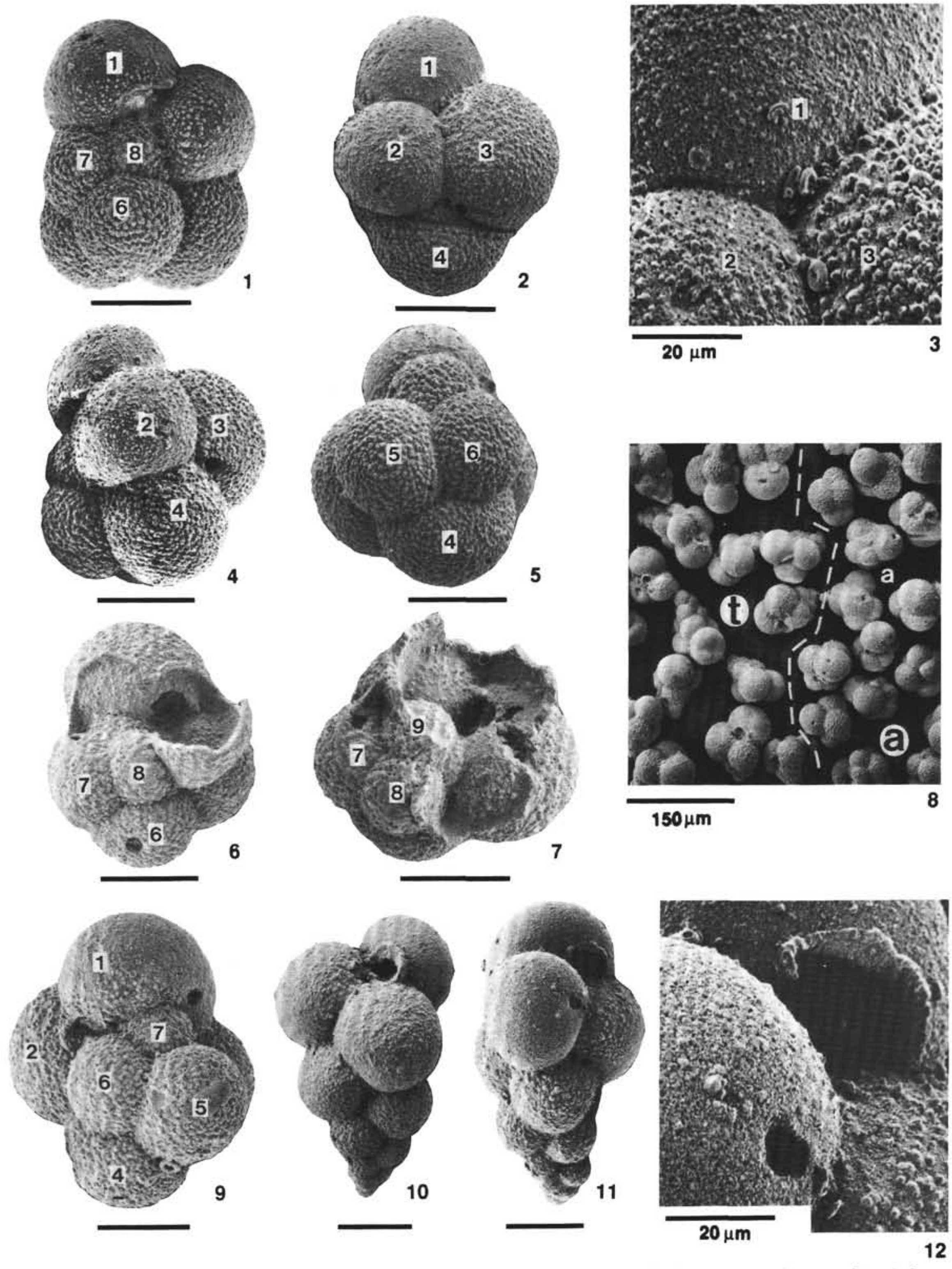

Plate 2. Scale bar for all specimens = 50 μm, unless otherwise indicated. **1–7.** A single specimen of *C. amekiensis* from Sample 120-749B-11X-2, 50–53 cm; (1) aperture view; (2) outer marginal view showing trigonal patterns of chambers 1, 2, and 3 and 2, 3, and 4, respectively; (3) enlarged from Plate 2, Figure 2; (4 and 5) tilted views of Plate 2, Figure 1; (6) last two chambers removed to show early aperture and chambers; and (7) last three chambers removed. **8.** Population of *G. triseriata* (**t**) and *C. amekiensis* (**a**) from Sample 120-749B-13X-CC, 0–3 cm. Note that their tests are almost equally small. **9.** A single specimen of *C. amekiensis* with a small aperture from Sample 120-749B-11X-2, 50–53 cm. **10–12.** Two specimens of *G. triseriata* from Sample 120-749B-10X-4, 50–53 cm; (10) specimen with spherical chambers; (11) specimen with oval to spherical chambers; (12) enlargement of Plate 2, Figure 11, showing the microperforate, pustulate wall and well-developed apertural lip.