

Chapter 5

TAXONOMY, BIOSTRATIGRAPHY, AND PHYLOGENY OF OLIGOCENE AND EARLY MIOCENE *PARAGLOBOROTALIA* AND *PARASUBBOTINA*

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ABSTRACT

The taxonomy, phylogeny, and biostratigraphy of Oligocene and early Miocene *Paragloborotalia* and *Parasubbotina* are reviewed. The two genera are closely related; *Paragloborotalia* was derived from *Parasubbotina* in the early Eocene. *Parasubbotina* was more diverse during the middle Eocene, while *Paragloborotalia* experienced considerable diversification during the mid-Oligocene and in the latest Oligocene-earliest Miocene. A significant finding has been the synonymization of *Globorotalia* (*Tuborotalia*) *mendacis* Blow, and *Tuborotalia primitiva* Brönnimann and Resig with *Globorotalia birnageae* Blow. The following species from the time interval of interest are regarded as valid: *Paragloborotalia acrostoma* (Wezel), *Paragloborotalia birnageae* (Blow), *Paragloborotalia continuosa* (Blow), *Paragloborotalia incognita* (Walters) *Paragloborotalia kugleri* (Bolli), *Paragloborotalia mayeri* (Cushman and Ellisor), *Paragloborotalia nana* (Bolli), *Paragloborotalia opima* (Bolli), *Paragloborotalia pseudocontinuosa* (Jenkins), *Paragloborotalia pseudokugleri* (Blow), *Paragloborotalia semivera* (Hornibrook), *Paragloborotalia*

siakensis (LeRoy), *Parasubbotina hagni* (Gohrbandt), and *Parasubbotina varianta* (Subbotina).

Paragloborotalia is a long-lived group of planktonic foraminifera that spanned the early Eocene to late Miocene and provided the root stock for the evolution of multiple smooth, nonspinose, and keeled globorotaliid lineages during the Neogene. The early Oligocene forms of *Paragloborotalia* (*nana*, *opima*, *siakensis*, *pseudocontinuosa*) have 4 or 5 globular chambers in the final whorl with radial spiral sutures and a broadly rounded periphery. A trend from radial to curved spiral sutures is observed in late Oligocene and earliest Miocene lineages. Most species of *Paragloborotalia* had wide distributions, but some were more common in tropical to warm subtropical waters (e.g., *siakensis*, *kugleri*) and were especially dominant in the equatorial Pacific divergence zone (e.g., *nana*, *opima*, and *pseudocontinuosa*) analogous to modern tropical upwelling *Neoglobobulimina*. Other species thrived in cool subtropical and temperate waters (e.g., *acrostoma*, *incognita*).

INTRODUCTION

There has been considerable debate about whether or not the genus *Paragloborotalia* was spinose or nonspinose. The spinosity controversy stems from two issues. Firstly, Cifelli (1982) erected the genus *Paragloborotalia* based on the coarsely cancellate wall and by analogy with Neogene *Globigerinoides*. His illustrated specimens, however, may not actually be *Paragloborotalia*; one of the illustrated specimens is not *P. opima* and there is a question about the other specimen. Evidence of spine bases or spine holes in the test is exceedingly rare, even in exceptionally well-preserved specimens (e.g., Pearson and Wade, 2009). Secondary calcification and wall thickening is a characteristic feature of *Paragloborotalia*, which obfuscates the problem of spinosity in this group and makes the detection of spine holes or spine bases problematic if not impossible. Despite these shortcomings, several species of *Paragloborotalia* that have been shown to possess unequivocal evidence for spines include: *P. pseudokugleri* (Rögl, 1996; this study), *P. kugleri* (Spezzaferri, 1991; Rögl, 1996), *P. semivera* (this study), and *P. siakensis* (Hilgen and others, 2000; Zachariasse and Sudijono, 2012; Sanchez and others, 2014). These taxa are not nearly as spinose as *Triloba-*

tus sacculifer, but they are representative of the genus *Paragloborotalia*, and therefore we conclude that the group was probably at least sparsely spinose during life.

The literature is filled with examples of different species concepts among the paragloborotaliids, and in several cases significant differences in reported stratigraphic ranges due to the interpretation of species concepts by different researchers. A case in point is the controversy about *mayeri* and *siakensis*; synonymous species or closely related but distinct taxa? We have tried to be thorough in our treatment of the species of *Paragloborotalia* presented here in hopes of stabilizing the taxonomy and concepts of each species, as well as establishing revised hypotheses about the phylogenetic relationships of *Paragloborotalia*.

Radial spiral sutures is an ancestral character in all Oligocene species of *Paragloborotalia*, while curved spiral sutures is a derived character more typical of later Oligocene and Miocene assemblages. Proposed phylogenetic relationships are based on the following ranked criteria: stratigraphic range, trends in spiral-side suture pattern (radial vs. gently to strongly curved), aperture position and height, compression of chambers (edge view; broadly rounded to subacute), and number of chambers in the final whorl. Evolution of multiple

lineages of *Paragloborotalia* gave rise to nonspinose descendants, including *Fohsella* from either *kugleri* or *mayeri* via *peripheroronda*, *Globoconella* from *incognita*, and perhaps *Neogloboquadrina* from *continua*. Some taxa display distinct and isochronous changes in size, specifically gigantism, which is the primary criterion to distinguish *opima* from *nana* (Bolli and Saunders, 1985; Wade and others, 2016). Other taxa are distinguished on subtle stratigraphic changes in morphology.

Globorotalia bella Jenkins was described from the lower Miocene of New Zealand, and has previously been placed in *Paragloborotalia* by several workers (e.g., Scott, 1992; Morgans and others, 2002; Li and others, 2003a; Kender and others, 2008; Aze and others, 2011). However, our new SEMs of the holotype (not shown) do not indicate a cancellate, *sacculifer*-type wall, but a smooth wall that is more like *Globoconella* than *Paragloborotalia*, therefore *bella* is not considered further in this work. Similarly, *Globorotalia acrostoma partimlabiata* Ruggieri and Sprovieri is a transitional, younger form that is restricted to the middle and late Miocene (e.g., Iaccarino and Salvatorini, 1979; Salvatorini and Cita, 1979; Zachariasse, 1992; Foresi and others, 1998, 2002) and is not considered here. *Parasubbotina hagni* and *P. varianta*, and the following species of *Paragloborotalia* are included in this chapter: *P. acrostoma*, *P. birnageae*, *P. continua*, *P. incognita*, *P. kugleri*, *P. mayeri*, *P. nana*, *P. opima*, *P. pseudocontinua*, *P. pseudokugleri*, *P. semivera*, and *P. siakensis*.

The early Oligocene forms of *Paragloborotalia* (*nana*, *opima*, *siakensis*, *pseudocontinua*) have 4-5 globular chambers in the final whorl with radial spiral sutures and a broadly rounded periphery. A trend from radial to curved spiral sutures is observed in late Oligocene and earliest Miocene lineages: 1) early *birnageae* to later forms of *birnageae*, 2) *siakensis* to *mayeri*, 3) *pseudocontinua* to *acrostoma*, 4) *pseudocontinua* to *incognita*; and 5) early *pseudokugleri* to later forms of *pseudokugleri*, and *pseudokugleri* to *kugleri*. *Paragloborotalia pseudocontinua* gave rise to *incognita* and the *Globoconella* lineage; and *kugleri*, or *mayeri* likely gave rise to *peripheroronda* and the *Fohsella* lineage in the early Miocene. Most species of *Paragloborotalia* had wide distributions, but some were more common in tropical to warm subtropical waters (e.g., *siakensis*, *kugleri*) and were especially dominant in the equatorial Pacific divergence zone (e.g., *nana*, *opima*, and *pseudocontinua*) analogous to modern tropical upwelling *Neogloboquadrina*. Other species thrived in

cool subtropical and temperate waters (e.g., *acrostoma*, *incognita*).

A significant finding of this study is the synonymization of *Globorotalia* (*Turborotalia*) *mendacis* Blow and *Turborotalia primitiva* Brönnimann and Resig with *Globorotalia birnageae* Blow.

Paragloborotalia is closely related to *Parasubbotina*; *Parasubbotina* was derived from *Hedbergella monmouthensis* in the basal Danian (Olsson and others, 1999), and *Paragloborotalia* was derived from *Parasubbotina varianta* in the early Eocene (Olsson and others, 2006). Both taxa are characterized by cancellate, spinose walls and low trochospiral coiling; *Paragloborotalia* has more embracing chambers, while *Parasubbotina* is more lobulate with more loosely coiled chambers (Olsson and others, 2006). *Parasubbotina* displays its greatest diversity in the middle Eocene, while *Paragloborotalia* had two pulses of accelerated diversification during the mid Oligocene and during the latest Oligocene and earliest Miocene. New observations on late Eocene-early Miocene assemblages since the publication of the *Atlas of Eocene Planktonic Foraminifera* (Pearson and others, 2006) have revealed an extended stratigraphic range for *Parasubbotina hagni* and *P. varianta* into the early Oligocene (Wade and Pearson, 2008; this study) and the reclassification of *Subbotina hagni* to *Parasubbotina* (Rögl and Egger, 2012). Updated stratigraphic ranges and a detailed taxonomic review of both genera are presented here.

SYSTEMATIC TAXONOMY

Order FORAMINIFERIDA d'Orbigny, 1826 **Superfamily GLOBIGERINOIDEA Carpenter, Parker, and Jones, 1862** **Family GLOBIGERINIDAE Carpenter, Parker, and Jones, 1862**

Genus *Paragloborotalia* Cifelli, 1982

Jenkinsella Kennett and Srinivasan, 1983:171.

TYPE SPECIES.— *Globorotalia opima* subsp. *opima* Bolli, 1957.

DESCRIPTION.

Type of wall: Normal perforate, coarsely cancellate, *sacculifer*-type wall texture (Olsson and others, 2006); spinose in life (Cifelli, 1982), although all

evidence to date suggests that the wall was sparsely or weakly spinose.

Test morphology: “Very low trochospiral, globular, compact, subquadrate to quadrate in outline, chambers globular, much embracing; in spiral view, 4 to 5 globular chambers, increasing rapidly, then moderately in size, strongly embracing chambers in ultimate whorl, ultimate chamber may be reduced in size, flattened or slightly concave, sutures slightly depressed, straight; in umbilical view 4 to 5 globular, embracing chambers that often close off umbilicus, sutures slightly depressed, straight; in edge view periphery rounded, aperture, umbilical-extraumbilical, a low arch, bordered by a narrow, thickened lip” (Olsson and others, 2006:88). *Paragloborotalia* species have a strong tendency to develop a calcite crust (Pearson and Wade, 2009; Chapter 3, this volume).

DISTINGUISHING FEATURES.— “The genus is distinguished by the very low trochospiral test, low-arched umbilical-extraumbilical aperture with a thick lip of constant thickness. Number of chambers 4-5 in ultimate whorl, and a coarsely cancellate, *sacculifer*-type wall” (Olsson and others, 2006:88), although the abundance and density of spines is significantly less than in the species of *Globigerinoides* and *Trilobatus*.

Characteristic features of the genus *Paragloborotalia* include the following (Cifelli, 1982; Spezzaferrri, 1994; Olsson and others, 2006):

- 1) Coarsely cancellate and (sparsely) spinose wall texture,
- 2) Polygonal to subhexagonal pores and pore pattern separated by ridges,
- 3) Low trochospiral test, with relatively compact and globular chambers,
- 4) Low or arched umbilical-extraumbilical or extra-umbilical aperture, usually bordered by a lip of relatively constant thickness,
- 5) Rounded peripheral margin, without a keel,
- 6) Generally, lobulate equatorial profile,
- 7) Radial to slightly curved spiral-side sutures.

DISCUSSION.— “The type species of *Paragloborotalia*, *P. opima* (Bolli), is an Oligocene taxon of great biostratigraphic utility that was originally described as belonging to the nonspinose genus *Globorotalia*. However, in an early application of wall texture based taxonomy, Cifelli (1982) showed that *opima* possesses

a cancellate wall and, on account of observed spine holes, must originally have been spinose” (Olsson and others, 2006:91).

Paragloborotalia experienced considerable evolutionary changes through the Oligocene – middle Miocene, particularly a period of accelerated evolutionary turnover (speciation and extinction) across the Oligocene/Miocene boundary and in the earliest Miocene (Figure 5.1). Major evolutionary trends include: 1) originally 4-5 chambers in the final whorl (ancestral condition), to 6 chambers in the mid- to late Oligocene, and finally up to 7 chambers in the early and middle Miocene; 2) radial spiral sutures through the mid Oligocene (Zone O5; ancestral condition), appearance of slightly curved spiral sutures in the late Oligocene (Zones O6-O7), to more strongly curved spiral sutures in some taxa in the early Miocene (Zone M1) – a trend also noted by Keller (1981); and 3) broadly rounded peripheral margin through the mid-Oligocene (Zone O5; ancestral condition) to some taxa with subacute margins in the late Oligocene and early Miocene. Species of *Paragloborotalia* range in size from small (<0.25 mm) to medium (0.25-0.35 mm) to large (>0.35 mm) (e.g., Spezzaferrri, 1994; Wade and others, 2007, 2016).

Kennett and Srinivasan (1983) erected *Jenkinsella* (type species *siakensis*) as a subgenus of *Globorotalia*, for low trochospiral forms with globular to subglobular chambers, a rounded peripheral margin, lacking a distinct carina, with an umbilical-extraumbilical aperture bordered by a rim. *Jenkinsella* included *opima*, *semivera*, *siakensis*, *bella*, *mayeri* and *acrostoma*. *Paragloborotalia* was erected by Cifelli in 1982 and therefore has seniority over *Jenkinsella*, which is here considered a junior synonym.

Paragloborotalia is distinguished from *Parasubbotina* by a slower rate of chamber growth and inflation, more embracing chambers, and generally more heavily encrusted test.

PHYLOGENETIC RELATIONSHIPS.— *Paragloborotalia* evolved from *Parasubbotina* in the early Eocene (Olsson and others, 2006). Multiple species and several lineages evolved from *Paragloborotalia nana* (Figure 5.1). The genus *Paragloborotalia* gave rise to the smooth, nonspinose genus *Globoconella* in the early Miocene, and the keeled genus *Fohsella* later in the early Miocene. *Paragloborotalia* may also be the direct ancestor of the nonspinose *Neogloboquadrina* in the late Miocene.

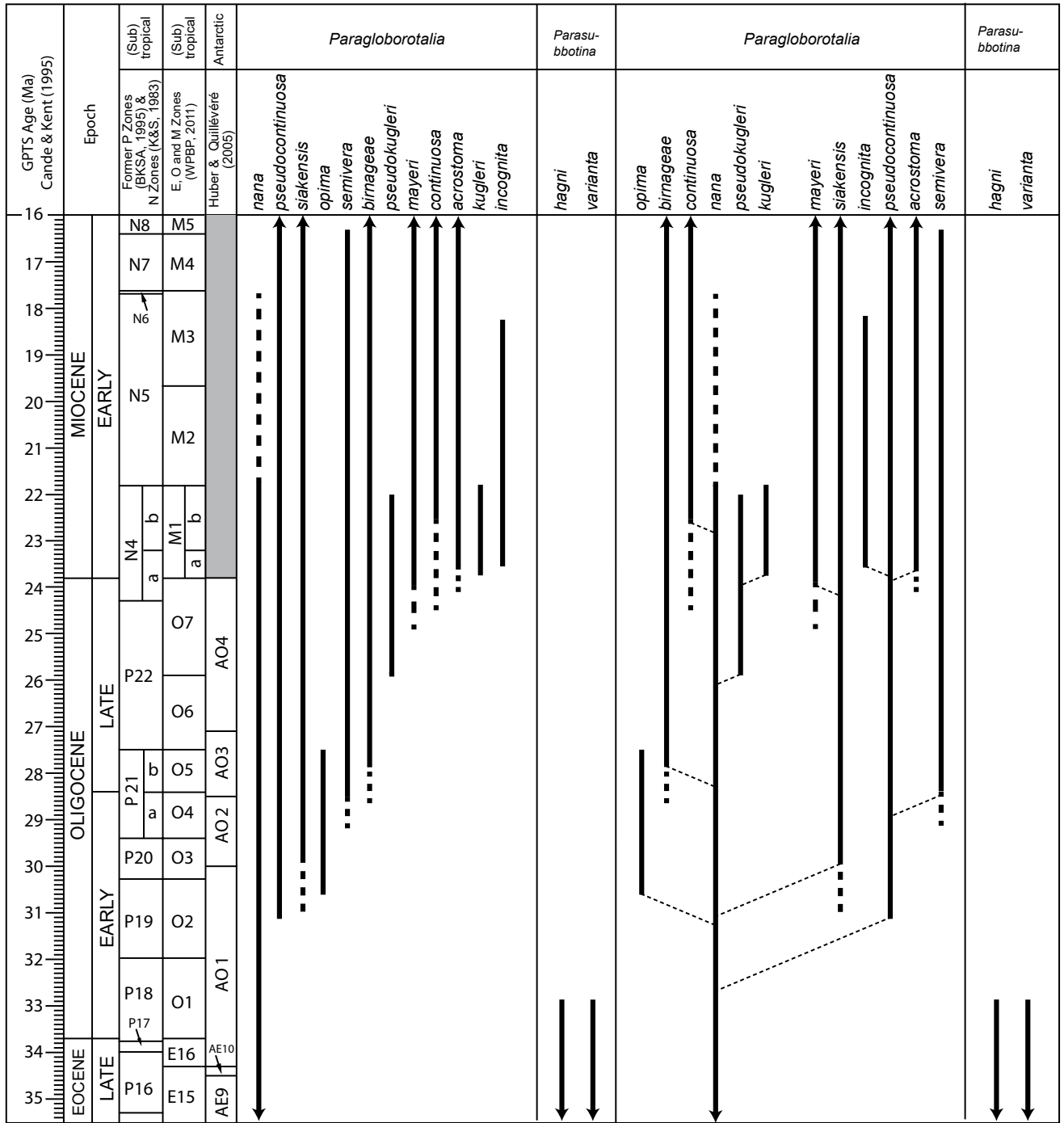


FIGURE 5.1 Stratigraphic ranges and inferred phylogenetic relationships of Eocene to early Miocene species of *Paragloborotalia* and *Parasubbotina* discussed in this chapter. BKSA, 1995 = Berggren and others, 1995; K&S, 1983 = Kennett and Srinivasan, 1983; WPBP, 2011 = Wade and others, 2011.

STRATIGRAPHIC RANGE.— Lower Eocene Zone E7 (Olsson and others, 2006) to Miocene Zone M13. The youngest recorded species attributed to *Paragloborotalia* is *P. continuosa*.

GEOGRAPHIC DISTRIBUTION.— Cosmopolitan, although most species are more typical of low to mid-latitudes (Jenkins, 1971; Kennett and Srinivasan, 1983; Leckie and others, 1993; Spezzaferri, 1994).

Paragloborotalia acrostoma (Wezel, 1966)

PLATE 5.1, FIGURES 1-16

“Globorotalia” acrostoma Wezel, 1966:1298-1301, pl. 101, figs. 1-8 [lower Miocene *Globigerinoides trilobus* Zone, Zona a scaglie tettoniche, Tempio River, Mirabella, Sicily, Italy].

Globorotalia (Turborotalia) acrostoma Wezel.—Poore, 1979:470, pl. 9, figs. 6-9 [lower Miocene Zone N7, DSDP Site 408; middle Miocene Zone N8-N11, DSDP Site 407, North Atlantic Ocean].—Iaccarino and Salvatorini, 1979:263, pl. 3, figs. 7, 8 [lower Miocene Zone N8, DSDP Site 398, eastern North Atlantic Ocean].—Salvatorini and Cita, 1979, pl. 9, figs. 19-21 [lower Miocene Zones N7 and N8, DSDP Site 397, eastern North Atlantic Ocean].—Keller, 1981, pl. 2, figure designations unspecified [lower Miocene Zone N4, DSDP Site 292, northwest Pacific Ocean].—Iaccarino, 1985:304, 306, figs. 6.13a-c [reillustration of holotype drawing of Wezel, 1966].

Globorotalia (Turborotalia) acrostoma Wezel.—Molina, 1979:244-246, pl. 29, figs. 1A-D [lower Miocene *P. glomerata curva* Zone, Lavigado ES-5, Spain].

Globorotalia (Jenkinsella) acrostoma Wezel.—Kennett and Srinivasan, 1983:176, pl. 43, figs. 7-9 [lower Miocene Zone N8, DSDP Site 408, North Atlantic Ocean].

Paragloborotalia acrostoma (Wezel).—Spezzaferri, 1994:56, pl. 21, figs. 5a-d [lower Miocene, Zone N7/N8, DSDP Hole 548A, Goban Spur, eastern North Atlantic Ocean], pl. 22, figs. 3a-c [lower Miocene Zone N7/N8, DSDP Hole 548A, Goban Spur, eastern North Atlantic Ocean].

DESCRIPTION.

Type of wall: Normal perforate, coarsely cancellate, probably sparsely spinose in life, heavy game-togenetic calcification is often present.

Test morphology: Test small to large in size; very low trochospiral, moderately lobulate in equatorial outline, chambers globular, inflated, embracing; typically 5, sometimes with 4 or 4½ chambers in ultimate whorl, increasing rapidly in size; in spiral view chambers initially reniform becoming subspherical, arranged in 2½-3 whorls, sutures slightly depressed, slightly curved becoming radial between ultimate and penultimate chamber; in umbilical view chambers subspherical, sutures depressed, radial, umbilicus very narrow to nearly closed, moderately deep; aperture umbilical-extraumbilical, high arch bordered by a continuous imperforate rim or thin lip; in edge view chambers globular to subglobular, spiral side nearly flat to slightly convex, umbilical side more convex, periphery broadly but asymmetrically rounded.

Size: Maximum diameter of holotype and paratypes 0.23-0.36 mm, minimum diameter 0.19-0.32 mm, maximum thickness 0.16-0.26 mm (original measurements); holotype maximum diameter 0.33 mm, maximum thickness 0.23 mm (remeasured this study).

DISTINGUISHING FEATURES.— Typical 5 chambered forms are pentagonal in outline, but not very lobulate. *Paragloborotalia acrostoma* is similar to *semivera* in having 5 chambers in the final whorl and a compact test with a narrow umbilicus, but it differs from *semivera* by its distinctly higher arched, semi-circular aperture bordered by an imperforate rim or thin lip. It is distinguished from *siakensis* by its higher arched aperture and tendency for curved spiral-side sutures. Specimens of *acrostoma* with 4½ chambers in the final whorl (e.g., Spezzaferri, 1994) closely resemble *pseudocontinua*, but are differentiated from the latter by having a higher arched aperture. *Paragloborotalia acrostoma* differs from *continua* in the same ways that it does with *pseudocontinua*, but *acrostoma* is also distinguished by its more umbilical-extraumbilical aperture, compared with a more extraumbilical aperture in *continua*.

Paragloborotalia acrostoma is distinguished from *mayeri* by its slightly greater spiral-side convexity, narrower umbilicus, fewer chambers (typically 5

Plate 5.1 *Paragloborotalia acrostoma* (Wezel, 1966)

1-3 (holotype, IGC 26); 5-7 (paratype, IGC 29); 9-11 (paratype, IGC 64), lower Miocene *Globigerinoides trilobus* Zone, Tempio River, Mirabella Area, Sicily; 4, 8, 12 (same specimen, Spezzaferri, 1994, pl. 22, figs. 3a-c), and 13-15 (same specimen, Spezzaferri, 1994; pl. 21, figs. 5a-c), Zone N7-N8, ODP Hole 548A, Goban Spur, eastern North Atlantic Ocean; 16 (Poore, 1979, pl. 9, fig. 7), Zone N8-N11, DSDP Site 407, North Atlantic Ocean. Scale bar: 1-16 = 100 µm.

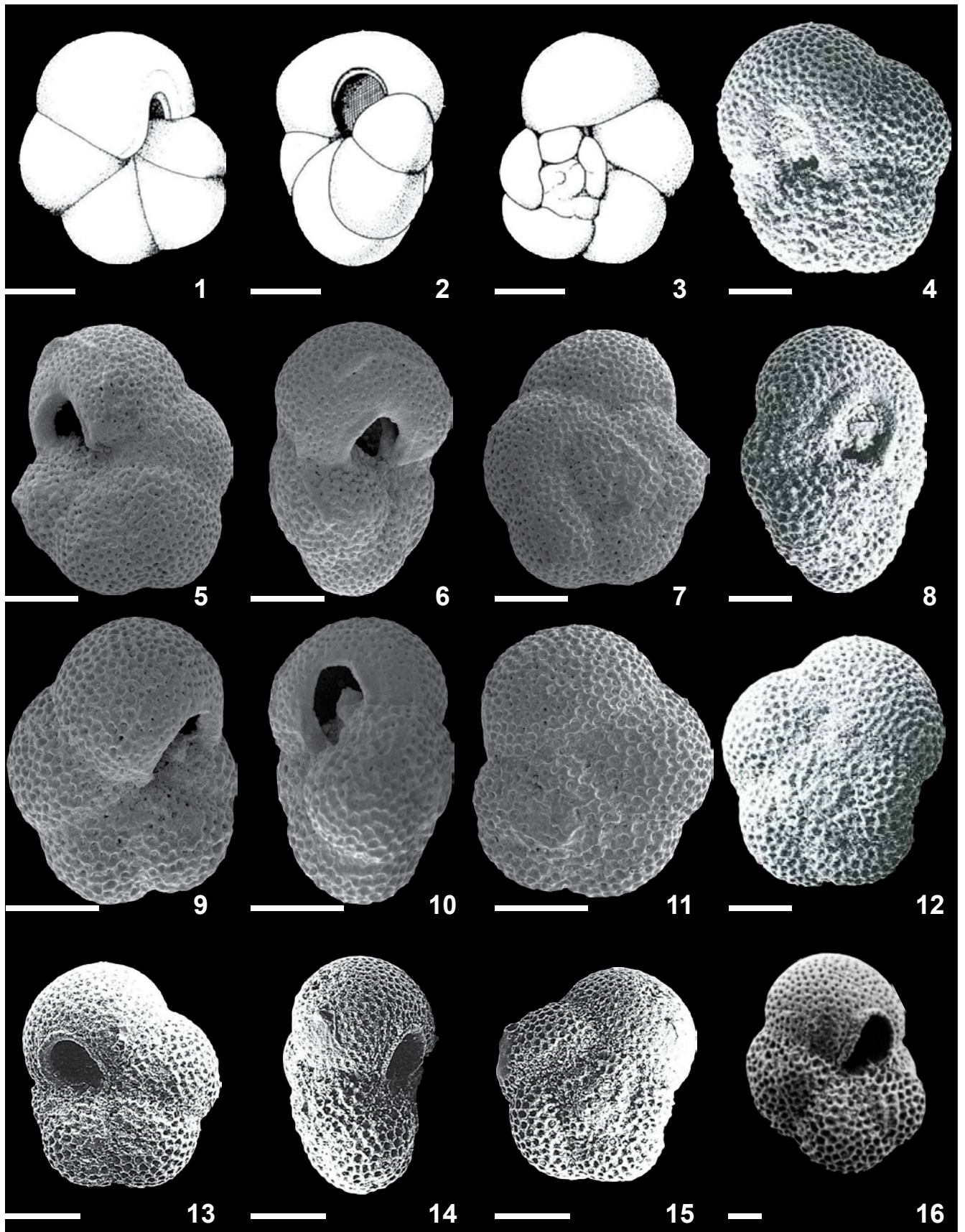


PLATE 5.1 *Paragloborotalia acrostoma* (Wezel, 1966)

compared with 6), and more umbilical-extraumbilical aperture. *Paragloborotalia acrostoma* is transitional in morphologic character between *semivera* and *mayeri*, however, the similar first occurrences of *acrostoma* and *mayeri* during the latest Oligocene suggest that *acrostoma* either falls within the range of variability for early forms of *mayeri*, or that the two taxa are more distantly related homeomorphs. Because of the more compact nature of *acrostoma*, including its narrow umbilicus, and its distinctive semi-circular apertural characteristics and one fewer chamber than typical *mayeri*, we have retained *acrostoma* as a valid taxon.

DISCUSSION.— Wezel (1966) tentatively attributed *acrostoma* to the genus “*Globorotalia*” in quotation marks because of its cancellate rather than smooth wall of typical *Globorotalia* or *Turborotalia*; he further suggested that a new subgenus should be erected to accommodate “*G.*” *acrostoma* as well as other species like “*G.*” *mayeri* and “*G.*” *continiosa*.

Jenkins (1977) suggested that *acrostoma* is a junior synonym of *semivera*, while Poore (1979) suggested that *acrostoma* could be considered as a subspecies of *mayeri*. Despite the close morphologically similar characteristics with both *semivera* and *mayeri*, we recognize *acrostoma* as a unique taxon in large part because of its distinctive aperture and relatively limited biogeographic range in and around the Mediterranean and tropical Atlantic Ocean (e.g., Iaccarino, 1985).

PHYLOGENETIC RELATIONSHIPS.— Spezzaferri (1994) has proposed that *P. acrostoma* evolved from *P. semivera* during the early Miocene, however other authors have suggested the species evolved from *P. mayeri/siakensis* (Keller, 1981; Kennett and Srinivasan, 1983; Aze and others, 2011). Based on the similarity of 4 chambered *pseudocontiniosa* and the 4½ chambered forms of *acrostoma*, we propose that *pseudocontiniosa* is the likely ancestor of *acrostoma*.

TYPE LEVEL.— Lower Miocene, upper part of the *Globigerinoides trilobus* Zone, Tempio River, Mirabella Region, Sicily, Italy.

STRATIGRAPHIC RANGE.— Lower Miocene Subzone M1a to Zone M5. Wezel (1966) recorded a range from the *Catapsydrax dissimilis* Zone to *Globigerinatella insueta* Zone with questionable occurrences in or near the *Globigerina ciperoensis ciperoensis-Globorotalia kugleri* zonal boundary (Oligocene/Miocene boundary). Spezzaferri (1994) recorded a lowest occurrence of *acrostoma* near the Oligocene/Miocene boundary Subzone N4a. Multiple authors record *acrostoma* in Zone N8 (M5).

GEOGRAPHIC DISTRIBUTION.— Warm to cool subtropical (Kennett and Srinivasan, 1983). *Paragloborotalia acrostoma* is a common component of Mediterranean and North Atlantic samples (Iaccarino and Salvatorini, 1979; Salvatorini and Cita, 1979; Iaccarino, 1985; Gennari and others, 2013; Foresi and others, 2014), but has also been reported in the equatorial and northwest Pacific Ocean (Keller, 1981), and in northern high latitude Atlantic Ocean sites (Poore, 1979; Spezzaferri, 1998). No occurrences have been recorded in the Southern Hemisphere.

STABLE ISOTOPE PALEOBIOLOGY.— No data available.

REPOSITORY.— Holotype (no. IGC 26) and 99 paratypes (nos. 27-125; figs. 1-8, nos. IGC 73, 70, 29, 108, 64, 88, 95, and 112, respectively) deposited in the collections of the Institute of Geology, University of Catania, Sicily.

Paragloborotalia birnageae (Blow, 1959)

PLATE 5.2, FIGURES 1-9; PLATE 5.3, FIGURES 1-16
(Pl. 5.2, Figs. 1-3: new SEMs of holotype of
Globorotalia birnageae Blow)
(Pl. 5.2, Figs. 4-6: new SEMs of holotype of
Globorotalia (Turborotalia) mendacis Blow)
(Pl. 5.2, Figs. 7-9: new SEMs of holotype of
Turborotalita primitiva Brönnimann and Resig)

Globorotalia birnageae Blow, 1959:210-211, pl. 17, figs. 108a-c [lower Miocene *Globigerinatella insueta*

Plate 5.2 *Paragloborotalia birnageae* (Blow, 1959)

1-3, (holotype, USNM 625709), lower Miocene *Globigerinatella insueta* Zone, Pozón Fm., Venezuela; 4-6 (holotype of *Globorotalia (Turborotalia) mendacis* BMNH 49718 Blow, 1969), upper Oligocene Zone N3, JOIDES drillhole 3, western North Atlantic Ocean; 7-9 (holotype of *Turborotalia primitiva* USNM 486363 Brönnimann and Resig, 1971) upper Oligocene Zone N3, DSDP Hole 64.1, Ontong Java Plateau, western equatorial Pacific Ocean. Scale bar 1-9 = 100 µm.

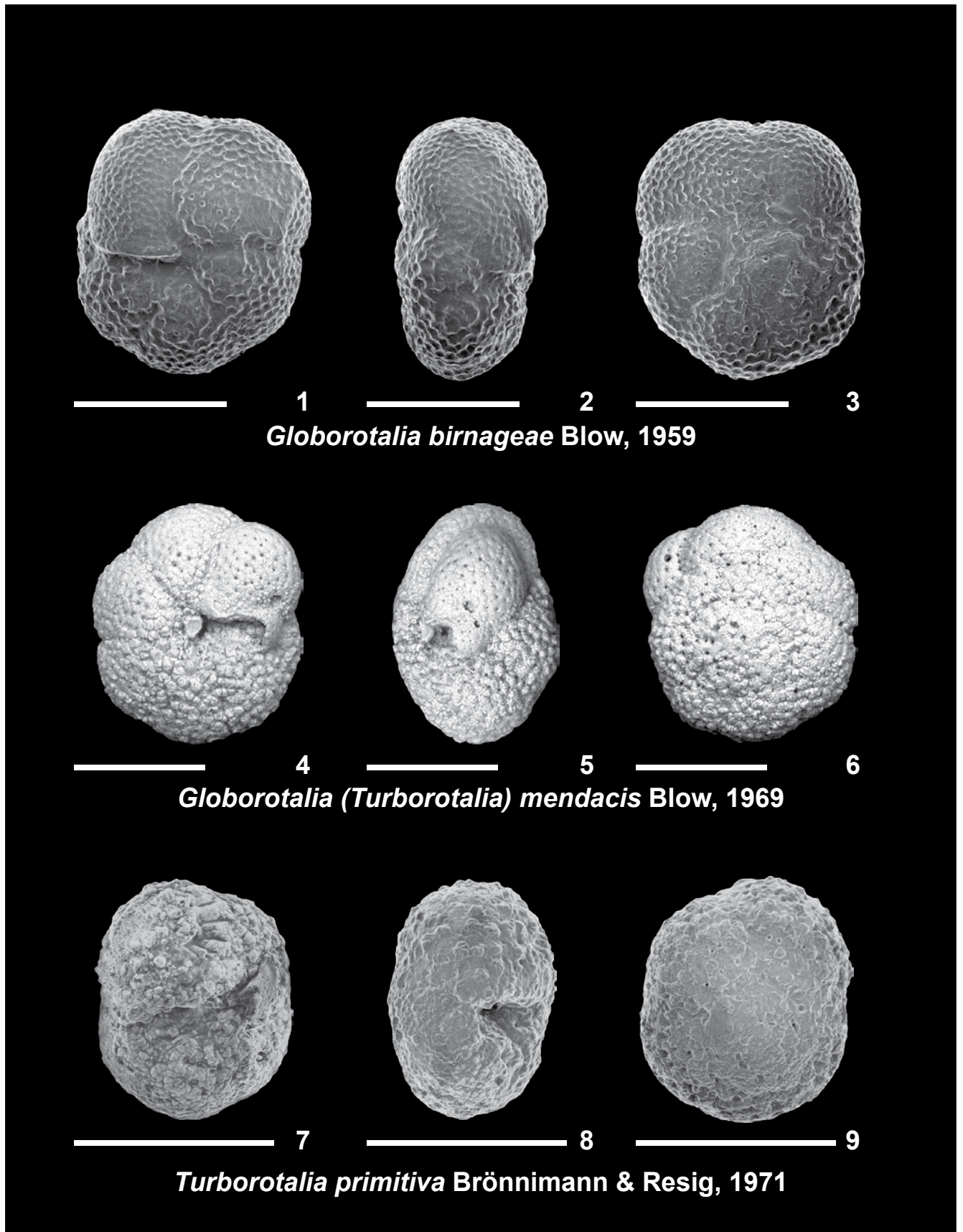


PLATE 5.2 *Paragloborotalia birnageae* (Blow, 1959)

Zone, Pozón Fm., eastern Falcón, Venezuela].—Poore, 1979:470, pl. 10, figs. 4, 5, 7, 8 [lower Miocene Zone N7, DSDP Site 407, North Atlantic Ocean].—Salvatorini and Cita, 1979, pl. 9, figs. 10, 15, 16 [lower Miocene Zones N7 and N8, DSDP Site 397, eastern North Atlantic Ocean].—Chaisson and Leckie, 1993:160, pl. 4, figs. 19-22 [lower Miocene Subzone N4b, Hole 806B, Ontong Java Plateau, western equatorial Pacific Ocean].—Spezzaferri, 1994:58, pl. 26, figs. 1a-c [lower-middle Miocene Zone N8/9, DSDP Hole 17A, eastern South Atlantic Ocean], fig. 3 [lower Miocene Subzone N4b, ODP Hole 667A, eastern equatorial Atlantic Ocean].

Globorotalia (Fohsella) sp. cf. G. (F.) birnageae Blow.—Chaproniere, 1981:125-126, figs. 12Fa-c [upper Oligocene to lower Miocene, Ashmore Reef No. 1 Well, northwest Australia].

Globorotalia (Fohsella) birnageae Blow.—Kennett and Srinivasan, 1983:94, pl. 21, figs. 6-8 [lower Miocene Zone N8, DSDP Site 289, Ontong Java Plateau, western equatorial Pacific Ocean].

Fohsella birnageae (Blow).—Norris, 1998:466, pl. 1, fig. 5 [middle Miocene Zone N8, ODP Hole 959A, eastern equatorial Atlantic Ocean].

Globorotalia (Turborotalia) mendacis Blow, 1969:390-391, pl. 38, figs. 5, 6 [upper Oligocene Zone N3, JOIDES Drillhole 3, Blake Plateau, western North Atlantic Ocean].

Globorotalia (Fohsella) kugleri mendacis Blow.—Chaproniere, 1981:126, figs. 12Ca-c [upper Oligocene to lower Miocene, Ashmore Reef No. 1 Well, northwest Australia].

Turborotalita primitiva Brönnimann and Resig, 1971:1287-1288, pl. 26, figs. 5-9 [upper Oligocene Zone N2, DSDP Hole 64.1, Ontong Java Plateau, western equatorial Pacific Ocean].

Paragloborotalia? laccadivensis (Fleisher).—Spezzaferri, 1994:57, pl. 9, figs. 2a-c [lower Miocene Zone N5, DSDP Hole 526A, Walvis Ridge, eastern South Atlantic Ocean], pl. 9, figs. 3a-d [upper Oligocene Zone P22, DSDP Hole 526A, Walvis Ridge, eastern South Atlantic Ocean]. [Not Fleisher, 1974.]

Not *Turborotalia (Turborotalia) birnageae* (Blow).—Fleisher, 1974:1035, pl. 18, fig. 9 [lower Miocene Zone N7-N8, DSDP Site 219, Arabian Sea] = ?*Paragloborotalia siakensis* (LeRoy).

Not *Globorotalia (Turborotalia) mendacis* Blow.—Brönni-

mann and Resig, 1971:1314, pl. 39, figs. 6-8 [lower Miocene Zone N4, DSDP Hole 64.1, Ontong Java Plateau, western equatorial Pacific Ocean].—Quilty, 1976:646, pl. 12, figs. 21, 22 [lower Miocene Zone N4, DSDP Site 320, southeastern Pacific Ocean] = *Paragloborotalia kugleri* (Bolli).

DESCRIPTION.

Type of wall: Normal perforate, coarsely cancellate, probably sparsely spinose in life, heavy gameogenetic calcification is often present.

Test morphology: Test small to medium in size; low trochospiral, weakly lobulate in equatorial outline, chambers subglobular, inflated, embracing; 5½-7, typically 6 chambers in the ultimate whorl, increasing slowly in size, ultimate chamber may be smaller than penultimate chamber (kummerform); in spiral view chambers subspherical, arranged in 2½-3 whorls, sutures slightly depressed, nearly radial to curved; in umbilical view chambers subspherical, sutures slightly depressed, radial, umbilicus narrow, moderately deep; may have an ampullate final chamber; aperture a low slit extending midway onto the peripheral edge, typically bordered by a lip or flap-like flange (apertural plate) as in *Turborotalita quinqueloba* and *Neogloboquadrina acostaensis*; in edge view chambers spherical, spiral side flat to slightly convex, umbilical side slightly convex, periphery broadly rounded to slightly subacute.

Size: Maximum diameter of holotype 0.22 mm (original measurement); 0.18 mm (remeasured this study); thickness 0.10 mm (this study).

DISTINGUISHING FEATURES.—*Paragloborotalia birnageae* is distinguished from *P. pseudokugleri* in having less depressed sutures, a less lobulate test, and a lower aperture. It differs from *P. siakensis*, *P. mayeri*, *P. semivera*, and *P. kugleri* in being less ovate and more circular in equatorial profile, and in having a nearly closed to closed umbilicus with a distinctive low aperture with lip or apertural flap/flange. The last chamber and aperture may resemble *Turborotalita quinqueloba*, but *P. birnageae* has a cancellate wall and a less lobulate equatorial profile (e.g., see Pearson and Wade, 2009).

Plate 5.3 *Paragloborotalia birnageae* (Blow, 1959)

1-3 (same specimen), Zone O7, ODP Hole 628A/16H/5, 100-102 cm, Little Bahama Bank, western North Atlantic Ocean; **4**, Zone M1, ODP Hole 806B/76X/2, 30-32 cm, Ontong Java Plateau, western equatorial Pacific Ocean; **5-7**, (Kennett and Srinivasan, 1983, pl. 21, figs. 6-8), Zone N8, DSDP Site 289, Ontong Java Plateau, western equatorial Pacific Ocean; **8, 12** (Chaisson and Leckie 1993, pl. 4, figs. 19, 20), Subzone N4b, ODP Hole 806B Ontong Java Plateau, western equatorial Pacific Ocean; **9-11**, Subzone N4a, ODP Hole 709B/21X/6, 78-80 cm; **13-15** (same specimen), Zone O7, ODP Hole 709B/22X/4, 125-127 cm, Madingley Rise, Indian Ocean; **16**, Zone O7, DSDP Hole 64A/7R/2, 33-35 cm, Ontong Java Plateau, western equatorial Pacific Ocean. Scale bar: **1-16** = 100 µm (scale bars estimated for **5-8, 12**).

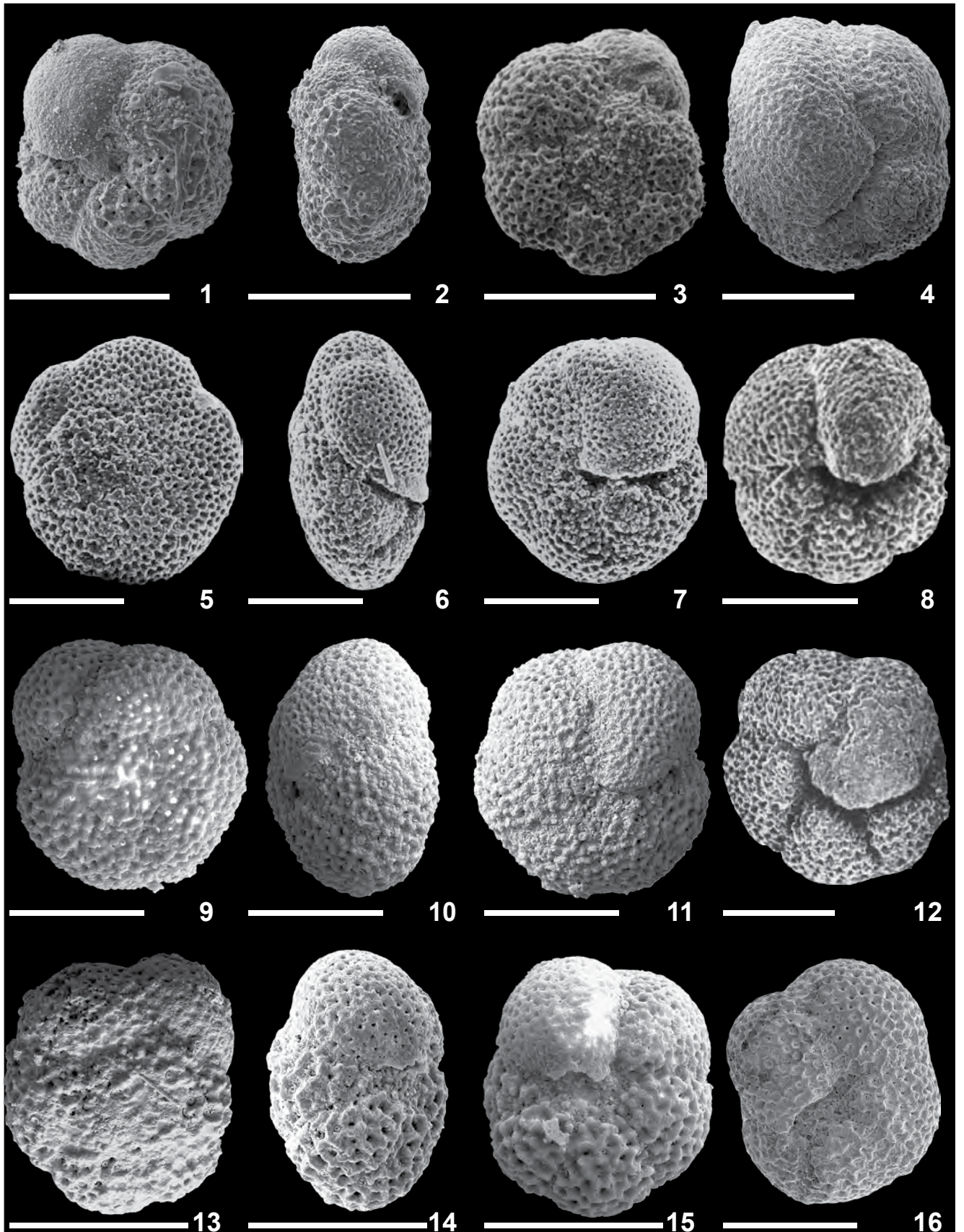


PLATE 5.3 *Paragloborotalia birnageae* (Blow, 1959)

DISCUSSION.— *Paragloborotalia birnageae* and its junior synonyms have previously been attributed to a number of genera, including *Globorotalia*, *Fohsella*, and *Turborotalita*, but is placed here within *Paragloborotalia* based on its coarsely cancellate wall, and close resemblance with the *P. nana*-*P. pseudokugleri*-*P. kugleri* lineage. As part of our investigations, we have examined the topotypes of *P. birnageae* housed at the Natural History Museum in London, Blow collection (P49680, P49688); they are very consistent with the holotype, including the extended final chamber.

Globorotalia mendacis (Blow, 1969) is considered to be a junior synonym of *P. birnageae*. Both taxa have ~6 embracing chambers in the final whorl, a compact test with mostly closed umbilicus and a low aperture with a thin lip, and slightly curved dorsal sutures. Blow (1969) chose a distinctly biconvex specimen with a subacute peripheral margin (Pl. 5.2, Figs. 4-6) for the holotype. However, there is a complete gradation between forms with a broadly rounded margin (*P. birnageae* s.s.) and specimens that have a subacute margin. *Globorotalia mendacis* has long been considered a junior synonym of *P. kugleri* (Stainforth and others, 1975; Bolli and Saunders, 1985). However, our investigations of the holotype reveal that it is synonymous with *P. birnageae* based on the circular, weakly lobulate equatorial outline, kummerform final chamber with low aperture and flap-like lip. Blow (1979:148) notes that “superficially it [*birnageae*] bears some general morphological resemblances to *G. (T.) kugleri*, *G. (T.) pseudokugleri* and, especially, *G. (T.) mendacis*”.

Specimens of *Paragloborotalia? laccadivensis* reported by Spezzaferri (1994) are also likely synonymous with *birnageae*. The tiny, 5-6 chambered *laccadivensis* consistently first appears in mid-Oligocene Subzone P21a (= Zone O3/O4; Spezzaferri, 1994). Therefore, these mid-Oligocene to early Miocene forms are probably not the same taxon described by Fleisher (1974) as *Globanomalina laccadivensis* from the upper Eocene of the Arabian Sea. In her description of the forms she attributed to *P.? laccadivensis*, Spezzaferri (1994:57) notes: “Sutures are slightly depressed and radial on both sides”. As observed in other lineages of *Paragloborotalia*, radial spiral sutures are the ancestral condition in all early and mid Oligocene taxa (through Subzone P21a = O3-O4); spiral sutures of *birnageae* become more curved in the late to latest Oligocene (Zone P22 = O6 and O7).

Turborotalita primitiva was described by Brönnimann and Resig from the upper Oligocene of the southwestern Pacific Ocean and is considered here to be within the morphologic variability of *P. birnageae*. Although the type specimen is of rather poor quality and equivocal in its identification, it fits best as within the *birnageae* plexus. Moreover, we have re-examined the type level of *T. primitiva* in DSDP Hole 64A and found specimens attributable to *P. birnageae* (Pl. 5.3, Fig. 16).

PHYLOGENETIC RELATIONSHIPS.— *Paragloborotalia birnageae* evolved from *P. nana* in the mid-Oligocene by developing a kummerform final chamber, a less lobulate equatorial periphery, and more than 4 chambers in the final whorl. A reference to intergradation between *P. birnageae* and *Trilobatus trilobus* by Gradstein and others (2012:1093) is unfounded.

TYPE LEVEL.— Lower Miocene *Globigerinatella insueta* Zone, Pozón Fm., Venezuela.

STRATIGRAPHIC RANGE.— As defined here, *P. birnageae* has a much longer stratigraphic range than *P. pseudokugleri* and *P. kugleri*, which are more restricted. *Paragloborotalia birnageae* was previously used as a marker to designate the base of Subzone M4b (late early Miocene; Berggren and others, 1995), however, multiple authors have reported this taxon in the lower Miocene and upper Oligocene (e.g., Blow, 1979; Chaisson and Leckie, 1993; Spezzaferri, 1994). For example, Blow (1979) reported *G. mendacis* (= *P. birnageae*) as low as Zone N2 (= Zone P21). In addition, Spezzaferri (1994) recorded the lowest/oldest confirmed occurrence of *P.? laccadivensis* (= *P. birnageae*) in mid-Zone O5 (= Subzone P21b), with more questionable occurrences as low as mid-Zone O4 (=Subzone P21a). These reported occurrences clearly pre-date the lowest occurrence of *P. pseudokugleri*.

GEOGRAPHIC DISTRIBUTION.— Low to mid-latitudes.

STABLE ISOTOPE PALEOBIOLOGY.— No data available.

REPOSITORY.— Holotype (USNM 625709) deposited at the Smithsonian Museum of Natural History, Washington, D.C.

***Paragloborotalia continua* (Blow, 1959)**

PLATE 5.4, FIGURES 1-4, 8

(Pl. 5.4, Figs. 1-3: new SEMs of holotype of *Globorotalia opima* subsp. *continua* Blow)

Globorotalia opima subsp. *continua* Blow, 1959:218-219, pl. 19, figs. 125 a-c [middle Miocene *Globorotalia mayeri* Zone, Pozón Fm., eastern Falcón, Venezuela].

Globorotalia (Turborotalia) mayeri continua Blow.—Jenkins, 1971:120, pl. 11, figs. 294-296 [middle Miocene *G. (T.) mayeri mayeri* Zone, Waiau Stage, North Island, New Zealand].

Globorotalia continua Blow.—Kennett, 1973, pl. 14, figs. 3-6 [middle Miocene *G. mayeri* Zone and upper Miocene *G. continua* Zone, DSDP Site 206, New Caledonia Basin, western South Pacific Ocean].—Poore, 1979:471, pl. 9, figs. 10-12 [upper Miocene Zone “N16?”, DSDP Site 408, North Atlantic Ocean].—Bolli and Saunders, 1982a:49-50, pl. 4, figs. 10-27 [lower to middle Miocene *Globigerinatella insueta* Zone to *Globorotalia mayeri* Zone, Ciperó Fm., Trinidad].—Hoskins, 1984, figs. 2:7-12 [middle Miocene *Praeorbulina glomerosa curva* Zone, Clifdenian Stage New Zealand], figs. 8:1-4 [middle Miocene *Orbulina suturalis* Zone, Lillburnian Stage, New Zealand].

Neogloboquadrina continua (Blow).—Kennett and Srinivasan, 1983:192, pl. 47, figs. 3-5 [lower Miocene Zone N6, DSDP Site 289, Ontong Java Plateau, western equatorial Pacific Ocean].—Chaisson and Leckie, 1993:164, pl. 8, figs. 12, 13 [lower Miocene Zone N5, ODP Hole 806B, Ontong Java Plateau, western equatorial Pacific Ocean], pl. 8, figs. 14, 15 [middle Miocene Zone N8/N9, ODP Hole 806B, Ontong Java Plateau, western equatorial Pacific Ocean].

Paragloborotalia continua (Blow).—Spezzaferri, 1994:54, pl. 20, figs. 7a-c [lower Miocene Zone N5, DSDP Site 151, Gulf of Mexico].—Fox and Wade, 2013:401, fig. 14.1a-c [lower Miocene Zone M5a, IODP Hole U1338B, eastern equatorial Pacific Ocean].

Globorotalia (Turborotalia) aff. mayeri Cushman and Ellis.—Quilty, 1976:646, pl. 12, figs. 19, 20 [middle Miocene Zone N12, DSDP Site 319, southeastern Pacific Ocean].

Paragloborotalia nana (Bolli).—Chaisson and Leckie, 1993:165, pl. 8, figs. 10, 11 [lower Miocene Zone N5, ODP Hole 806B, Ontong Java Plateau, western equatorial Pacific Ocean]. [Not Bolli, 1957.]

Not *Globorotalia opima nana* Bolli.—*Globorotalia continua* Blow transition.—Bolli and Saunders, 1982a, pl. 4, figs. 28-39 [uppermost Oligocene to lower Miocene, *Globigerina ciperóensis ciperóensis* Zone to *Catapsydrax dissimilis* Zone, Ciperó Fm., Trinidad] (= *Paragloborotalia nana*).

DESCRIPTION.

Type of wall: Normal perforate, coarsely cancellate, possibly sparsely spinose in life, heavy game-to-genetic calcification is often present.

Test morphology: Test small to medium in size; very low trochospiral, quadrate and lobulate in equatorial outline, chambers globular, inflated, embracing; 4 chambers in ultimate whorl, increasing rapidly in size; in spiral view chambers moderately inflated, ovate to subspherical, arranged in 2½ whorls, sutures slightly depressed, radial; in umbilical view chambers strongly inflated, sutures slightly depressed, radial, umbilicus narrow, moderately deep; aperture a moderately high comma-shaped arch extending midway onto the peripheral edge, more extraumbilical than umbilical-extraumbilical, bordered by a narrow, thickened, continuous lip; in edge view chambers ovate to subspherical, spiral side flat, periphery broadly rounded.

Size: Maximum diameter of holotype 0.26 mm (original measurement); 0.19 mm (remeasured this study); thickness 0.11 mm (this study).

DISTINGUISHING FEATURES.—*Paragloborotalia continua* was originally recognized as having four chambers in the final whorl and a high-arched aperture with a distinctive comma shape (Blow, 1959). It is differentiated from *P. nana* by having a higher arched aperture with a more distinctive lip, and a less compact, more lobulate equatorial outline. *Paragloborotalia continua* is small, like *P. nana*, which is the primary way both taxa are distinguished from *P. opima*. Additionally, *P. continua* is distinguished from *P. opima* by its higher-arched, extraumbilical aperture. It is differentiated from *P. siakensis* and *P. mayeri* by being more subquad-rangular in profile with fewer (only 4) chambers in the final whorl (Fox and Wade, 2013). Bolli and Saunders (1982a, 1985) stated that the morphology of *P. continua* and *P. mayeri* is identical with the main difference being fewer chambers in the final whorl of *continua*, and the overall smaller test size.

Paragloborotalia continua differs from *pseudocontinua* by its more extraumbilical aperture, less spherical chambers (ovate to subspherical), and flatter spiral side. Rate of chamber inflation in *continua* is less than observed in *pseudocontinua* and *incognita*; this is particularly evident in edge view by the smaller, less inflated final chamber. It differs from *acrostoma* in having only 4 chambers in the final whorl, a lower apertural arch, and radial spiral sutures.

DISCUSSION.— Jenkins (1971) considered *Globorotalia continuosa* to be a subspecies of *G. mayeri*. Bolli and Saunders (1982a) considered *continuosa* to be a 4 chambered variant of *mayeri*, and therefore placed *continuosa* in synonymy with *mayeri*. We disagree with this assessment and consider the 4 chambered *P. continuosa* as distinct. Bolli and Saunders (1982a) further state that *G. continuosa* has the same range as *G. mayeri*, both of which have a first occurrence in the upper Oligocene *Globigerina ciperoensis ciperoensis* Zone (= Zone O6, *G. ciperoensis* Partial Range Zone; Wade and others, 2011). This conclusion has possible implications about the relationship, if any, between *Paragloborotalia continuosa* and *P. pseudocontinuosa*. Jenkins (1971), on the other hand, reported similar, middle Miocene first occurrences for both *mayeri* and closely related *continuosa*. These varying ranges and phylogenetic relationships are not supported by this study.

Paragloborotalia continuosa may have been derived directly from *nana* rather than *pseudocontinuosa* based on the small size and extraumbilical position of the aperture, flat spiral side, radial spiral-side sutures, and quadrilobate test like *nana*, albeit not as compact and distinctly more lobulate than *nana*. Both *nana* and *continuosa* have a smaller, less inflated final chamber than *pseudocontinuosa* and *incognita*. *P. continuosa* is a continuation of the *nana*-like quadrilobate form well into the Miocene.

Paragloborotalia continuosa has a widely varying stratigraphic range owing to its very close similarity, if not direct phyletic relationship with *P. pseudocontinuosa* (see additional discussion under that species). Jenkins (1960, 1967, 1971, 1975, 1978) reports distinct ranges for the two taxa: upper Oligocene to lower Miocene for *P. pseudocontinuosa* and middle to upper Miocene for *P. continuosa*. Jenkins maintained that *P. pseudocontinuosa* was derived from *P. nana* and the ancestor of *Globorotalia (Globoconella) zealandica* Hornibrook in the lower Miocene *G. trilobus trilobus*

Zone, and that *P. continuosa* was derived from *P. mayeri* in the lower middle Miocene *G. mayeri mayeri* Zone. However, a number of researchers report a lower Miocene first occurrence for *continuosa* (e.g., Kennett and Srinivasan, 1983; Chaisson and Leckie, 1993).

PHYLOGENETIC RELATIONSHIPS.— Jenkins (1971) described very little morphologic difference between homeomorphs *continuosa* and *pseudocontinuosa*; Jenkins recognized the two taxa based on phylogenetic and stratigraphic evidence with *pseudocontinuosa* being derived from *nana* in the Oligocene and *continuosa* derived from *mayeri* in the middle Miocene. We agree that the two taxa are sufficiently distinct based primarily on their stratigraphic ranges, as well as subtle differences in their morphology, but we suggest that *continuosa* was also derived from *nana*.

TYPE LEVEL.— Miocene, Vindobonian, Pozón Formation, Husito marly clay member, *Globorotalia mayeri* Zone s.l., *Globorotalia mayeri/Globigerina nepenthes* Subzone, near Pozón, east Falcón, Venezuela.

STRATIGRAPHIC RANGE.— *Paragloborotalia continuosa* first appeared in the uppermost Oligocene or lowermost Miocene (Chaisson and Leckie, 1993; Spezzaferri, 1994). It ranges into the upper Miocene Zone M13 (Spiegler and Jansen, 1989; Berggren, 1992; Chaisson and Leckie, 1993; Chaisson and Pearson, 1997; Chaisson and D'Hondt, 2000).

GEOGRAPHIC DISTRIBUTION.— Cosmopolitan.

STABLE ISOTOPE PALEOBIOLOGY.— Majewski (2003) reported a shallow depth habitat for late middle Miocene *continuosa* based on stable isotope analyses from ODP Site 744 in the southern Indian Ocean.

REPOSITORY.— Holotype (USNM 625711) deposited

Plate 5.4, 1-4, 8, *Paragloborotalia continuosa* (Blow, 1959); 5-7, *Paragloborotalia incognita* (Walters, 1965); 9-16, *Paragloborotalia pseudocontinuosa* (Jenkins, 1967)

Paragloborotalia continuosa **1-3** (holotype of *Globorotalia opima* subsp. *continuosa*, USNM 625711), middle Miocene *Globorotalia mayeri* Zone, Pozón Fm., Venezuela; **4** (Chaisson and Leckie, 1993; pl. 8, fig. 15), Zone N8/N9, ODP Hole 806B, Ontong Java Plateau, western equatorial Pacific Ocean; **8** (Chaisson and Leckie, 1993; pl. 8, fig. 13); Zone N5, ODP Hole 806B, Ontong Java Plateau, western equatorial Pacific Ocean.

Paragloborotalia incognita **5-7** (holotype, TF 1487-1), lower Miocene *Globigerinoides triloba* Zone, Awamoan Stage, Waiomoko River section, South Island, New Zealand.

Paragloborotalia pseudocontinuosa **9-11** (holotype, TF 1530), lower Miocene *Globigerinoides triloba triloba* Zone, Victoria, Australia; **12, 16** (Spezzaferri, 1994; pl. 20, figs. 1b-c) Subzone P21a, ODP Hole 538A, Gulf of Mexico; **13-15** (paratype), lower Miocene *Globigerinoides triloba triloba* Zone, Victoria, Australia. Scale bar: **1-16** = 100 μ m (scale bars estimated for **4, 8**).

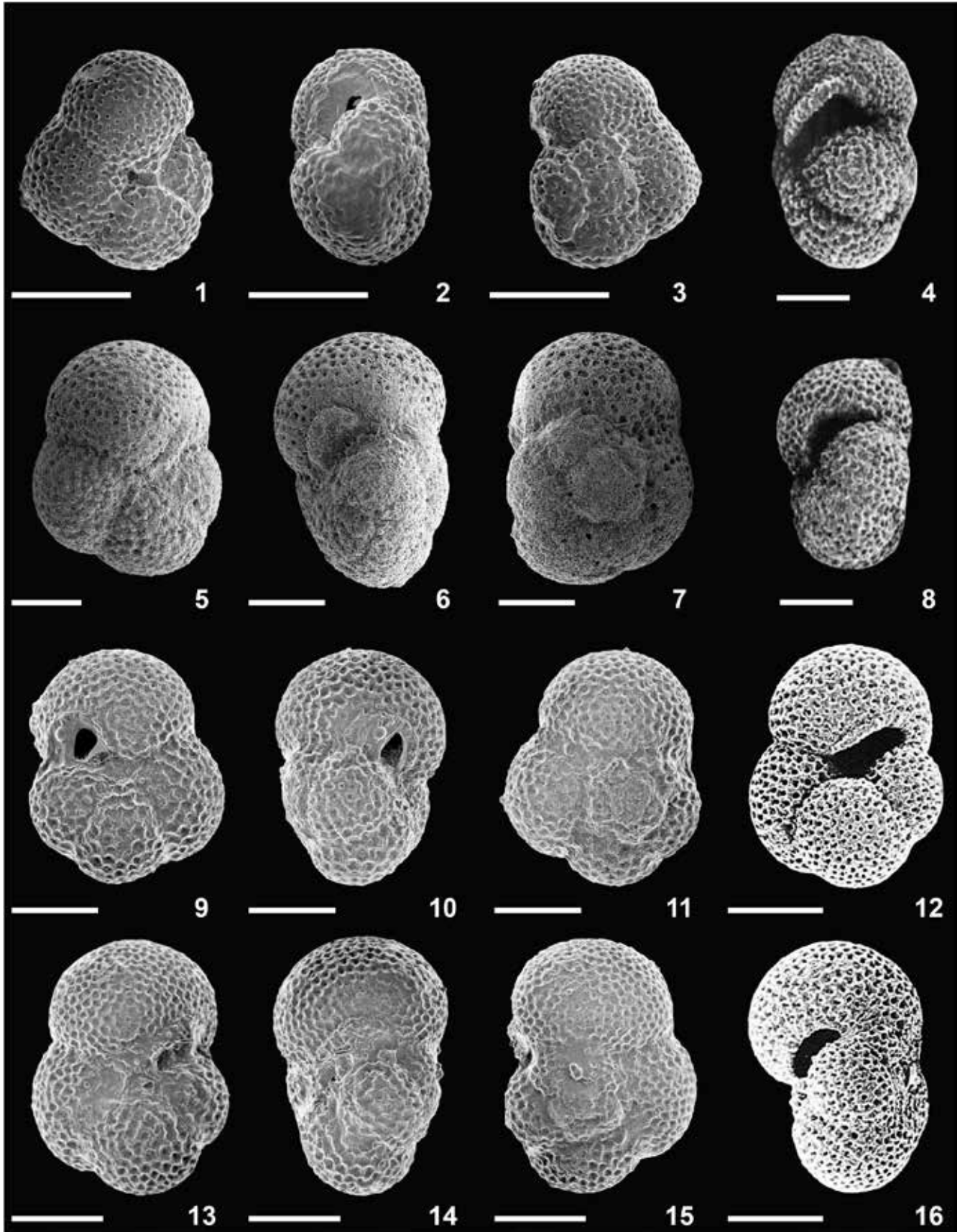


PLATE 5.4, 1-4, 8, *Paragloborotalia continua* (Blow, 1959); 5-7, *Paragloborotalia incognita* (Walters, 1965); 9-16, *Paragloborotalia pseudocontinua* (Jenkins, 1967) 139

at the Smithsonian Museum of Natural History, Washington, D.C.

***Paragloborotalia incognita* (Walters, 1965)**

PLATE 5.4, FIGURES 5-7

(Pl. 5.4, Figs. 5-7: new SEMs of holotype of *Globorotalia zealandica incognita* Walters)

Globorotalia zealandica incognita Walters, 1965:120, figs. 6a-j [lower Miocene *Globigerinoides triloba* Zone, Awamoan Stage, Waiomoko River section, South Island, New Zealand].—Tjalsma, 1977:501, pl. 6, figs. 1-3 [lower Miocene Zone N6/N7, DSDP Site 329, Falkland Plateau, western South Atlantic Ocean].

Globorotalia incognita Walters.—Cifelli and Scott, 1983:163, 165, figs. 1A, B; pl. 1, figs. 1-3 (reillustration of holotype), figs. 4-12 (reillustration of paratypes) [lower Miocene *Globigerinoides triloba* Zone, Awamoan Stage, Waiomoko River section, South Island, New Zealand].—Berggren and others, 1983:701-703, pl. 3, figs. 6-7; pl. 5, fig. 1 [lower Miocene Zone N5 and Zone N6, DSDP Site 516, Rio Grande Rise, western South Atlantic Ocean].—Cifelli and Scott, 1986, figs. 9a, 9b, and 9e [lower Miocene, Amamoia Drillhole, New Zealand].

Globorotalia (Globoconella) incognita Walters.—Kennett and Srinivasan, 1983:106, pl. 24, figs. 6-8 [lower Miocene *G. incognita* Zone, DSDP Site 206, New Caledonia Basin, western South Pacific Ocean].

Paragloborotalia incognita (Walters).—Berggren, 1992:641, pl. 2, figs. 6-8 [lower Miocene *G. praescitula* Zone, ODP Hole 748B, Kerguelen Plateau, southern Indian Ocean].—Spezzaferri, 1994:54-55, pl. 20, figs. 2a-c [lower Miocene Subzone N4b, DSDP Hole 516F, Rio Grande Rise, western South Atlantic Ocean], 3a-c [lower Miocene Subzone N4b, DSDP Site 593, Challenger Plateau, western South Pacific Ocean].—Morgans and others, 2002:164, figs. 12M-T [lower Miocene *Globorotalia incognita* Zone, Altonian Stage, North Island, New Zealand].—Li and others 2003a, pl. 1, fig. 30 [lower Miocene Zone SAN2, ODP Hole 1134B, Great Australian Bight, Indian Ocean].

Not *Globorotalia (Turborotalia) zealandica incognita* Walters.—Jenkins, 1971:132, pl. 13, figs. 374-376 [lower Miocene *G. trilobus trilobus* Zone, Awamoan Stage, North Island, New Zealand] (= *Globorotalia zealandica*).

DESCRIPTION.

Type of wall: Normal perforate, coarsely cancellate, unclear if spinose in life, heavy gametogenetic calcification is often present.

Test morphology: Test medium to large in size;

low trochospiral, quadrate and lobulate in equatorial outline, chambers spherical to subspherical, inflated, embracing; typically 4, occasionally 4½ chambers in ultimate whorl, increasing rapidly in size; may possess small kummerform final chamber or chamberlet; in spiral view chambers weakly inflated, longer than broad in the direction of coiling, arranged in 2½-3 whorls, sutures slightly depressed, slightly curved; in umbilical view chambers moderately inflated, sutures slightly depressed, radial to slightly curved, umbilicus narrow, shallow; aperture umbilical-extraumbilical, moderately high arch, bordered by a narrow, thickened, continuous lip; in edge view chambers subspherical, spiral side nearly flat, umbilical side more strongly convex, periphery broadly rounded.

Size: Maximum diameter of holotype 0.36 mm; maximum thickness 0.23 mm (original measurements); diameter 0.35 mm; thickness 0.23 mm (remeasured this study).

DISTINGUISHING FEATURES.— This species is distinguished from *P. nana* by its larger size, and in having a more rapid rate of chamber expansion, a less compact test, a higher arched aperture, elongation of the chambers in the direction of coiling, and slightly curved spiral sutures. It is distinguished from *P. opima* in having a distinctly more higher arched aperture, and asymmetrical final chamber. The species had been synonymized with *P. pseudocontiniosa* (e.g., Li and others, 1992), but can be differentiated by the more extraumbilical aperture, flatter spiral side with slightly curved spiral-side sutures, and subspherical final chamber in axial profile (edge view). *Paragloborotalia incognita* is distinguished from *P. continiosa* by having a larger, more inflated, but subspherical final chamber, slight chamber elongation, and slightly curved spiral sutures. It is distinguished from *G. zealandica pseudomiozea* Walters in having a distinctly more cancellate wall, more rounded periphery, and a less flattened spiral side.

DISCUSSION.— Kennett and Srinivasan (1983) consider *incognita* to be the senior synonym of *pseudocontiniosa*. Following Cifelli and Scott (1983), we consider *P. incognita* to be a valid transitional taxon between *P. pseudocontiniosa* and *Globoconella zealandica*.

PHYLOGENETIC RELATIONSHIPS.— *Paragloborotalia incognita* is transitional in morphology between ancestral *P. pseudocontiniosa* and the *G. zealandica*

lineage (Cifelli and Scott, 1983), including *G. pseudo-miozea*, following Berggren and others (1983). *Paragloborotalia incognita* evolved from *P. pseudocontinua* in the earliest Miocene (Subzone M1a).

TYPE LEVEL.— Lower Miocene Awamoan Stage (the base is defined by the lowest occurrence of *Globigerinoides triloba* and the lowest occurrence of *Sphaeroidinella disjuncta*), Waiomoko River, North Island, New Zealand.

STRATIGRAPHIC RANGE.— Lower Miocene Subzone M1a (Spezzaferri, 1994) or M1b (Keller, 1981; Berggren and others, 1983; Cifelli and Scott, 1983; Berggren, 1992; Harwood and others, 1992) to Zone M3 (Barron and others, 1991; Huber, 1991; Berggren, 1992; Harwood and others, 1992; Spezzaferri, 1994; Ali and Vandamme, 1998); the range may extend into the middle Miocene at high latitudes. Morgans and others (2002) report a LAD of *P. incognita* in Chron C5En.

GEOGRAPHIC DISTRIBUTION.— Cool temperate waters in mid to high latitudes, nearly all recorded occurrences are between 30°-60°S in the South Atlantic and South Pacific Ocean (e.g., Berggren and others, 1983; Jenkins, 1971, 1978; Morgans and others, 2002). In addition, Keller (1981) reported *incognita* from the equatorial and northwest Pacific Ocean.

STABLE ISOTOPE PALEOBIOLOGY.— No data available.

REPOSITORY.— Institute of Geological and Nuclear Sciences, National Paleontological Collection, New Zealand: TF 1487-1 (holotype) and TF 1487-2 to 1487-6 (5 paratypes).

Paragloborotalia kugleri (Bolli, 1957)

PLATE 5.5, FIGURES 1-16
(Pl. 5.5, Figs. 1-3: new SEMs of holotype of
Globorotalia kugleri Bolli)

Globorotalia kugleri Bolli, 1957:118, pl. 28, figs. 5a-6 [lower Miocene *Globorotalia kugleri* Zone, Cipero Fm., Trinidad].—Jenkins and Orr, 1972:1100, pl. 25, figs. 9-11 [lower Miocene *G. kugleri* Zone, DSDP Site 79, eastern equatorial Pacific Ocean].—Berggren and Am-durer, 1973, pl. 28, figs. 3-5 [lower Miocene Zone N4, DSDP Site 18, South Atlantic Ocean].—Stainforth and

others, 1975:289, fig. 126.5a-c (holotype), fig. 126.1, 3, 6-7 (topotypes), fig. 126.4 (paratype) [lower Miocene *Globorotalia kugleri* Zone, Cipero Fm., Trinidad].—Krasheninnikov and Pflaumann, 1978:593, pl. 6, figs. 1-3 ["Oligocene", DSDP Hole 366A, eastern equatorial Atlantic Ocean].—Poore, 1979:471, pl. 10, figs. 1-3 [lower Miocene Zone N4, DSDP Site 407, North Atlantic Ocean].—Stainforth and Lamb, 1981:26 (partim), pl. 7, figs. 5a-6b [lower Miocene *Globorotalia kugleri* Zone, Atlantic Slope Project corehole 5, western North Atlantic Ocean] (not pl. 7, fig. 4a-c = *P. pseudokugleri*).—Berggren and others, 1983, pl. 3, figs. 1-3 [lower Miocene Zone N4, DSDP Site 516, Rio Grande Rise, western South Atlantic Ocean].—Bolli and Saunders, 1985:203 (partim), fig. 26.1a-c, fig. 26.2 [reproduction of paratype drawing from Bolli, 1957], fig. 26.4-6 [lower Miocene *G. primordius* Zone, Cipero Fm., Trinidad] (not fig. 26.3 = *P. pseudokugleri*).—Vincent and Toumarkine, 1990:802, pl. 3, figs. 8-11 [lower Miocene Zone N4, ODP Hole 707A, western equatorial Indian Ocean].

Globorotalia (Turborotalia) kugleri Bolli.—Blow, 1969:350-351, pl. 10, figs. 1-3 [holotype images reproduced from Bolli, 1957, pl. 28, fig. 5], pl. 38, figs. 1-4 [lower Miocene *Globorotalia (Turborotalia) kugleri* Zone, Cipero Fm., Trinidad].—Brönnimann and Resig, 1971:1313-1314, pl. 39, figs. 1, 3-5 [lower Miocene Zone N4, DSDP Hole 64.1, Ontong Java Plateau, western equatorial Pacific Ocean].—Quilty, 1976:646, pl. 12, figs. 15, 16 [lower Miocene Zone N4, DSDP Site 320, eastern equatorial Pacific Ocean].—Blow, 1979:152, pl. 10, figs. 1-3 [holotype and paratype images reproduced from Bolli, 1957, pl. 28, figs. 5-6], pl. 38, figs. 1-4 [reproduced from Blow, 1969, pl. 38, figs. 1-4].

Globorotalia (Fohsella) kugleri kugleri Bolli.—Chaproniere, 1981:126, pl. 12, figs. A, B [lower Miocene Cartier beds, Ashmore Reef No. 1 well, northwest Australia].

Globorotalia (Fohsella) kugleri Bolli.—Kennett and Srinivasan, 1983:94, pl. 21, figs. 1, 3-5 [lower Miocene Subzone N4a, DSDP Site 289, Ontong Java Plateau, western equatorial Pacific Ocean].

"*Globorotalia*" *kugleri* Bolli.—Premoli Silva and Spezzaferri, 1990:303, pl. 3, figs. 5a-c [lower Miocene Zone N4, ODP Hole 709B, Madingley Rise, western equatorial Indian Ocean].

Paragloborotalia kugleri (Bolli).—Spezzaferri, 1991:317, pl. 1, fig. 5a-c [reproduced from Premoli Silva and Spezzaferri, 1990, pl. 3, figs. 5a-c], pl. 2, figs. 1a-d [lower Miocene Subzone N4a, ODP Hole 709C, Madingley Rise, western equatorial Indian Ocean].—Chaisson and Leckie, 1993:164, pl. 3, figs. 16-18 [lower Miocene Subzone N4a, ODP Hole 806B, Ontong Java Plateau, western equatorial Pacific Ocean].—Leckie and others, 1993:124, pl. 8, figs. 1-5 [lower Miocene Zone N4, ODP Hole 803D, Ontong Java Plateau, western equatorial

Pacific Ocean].—Spezzaferri, 1994:57, pl. 23, fig. 5 [reproduced from Premoli Silva and Spezzaferri, 1990, pl. 3, figs. 5a-c], pl. 24, fig. 1a-2d [reproduced from Spezzaferri, 1991, pl. 2, figs. 1a-2d].—Pearson, 1995:51, pl. 1, fig. 6 [lower Miocene Zone N6/7 (reworked), ODP Hole 871A, Limalok Guyot, western equatorial Pacific Ocean].—Rögl, 1996:151, pl. 1, figs. 1-3, pl. 2, figs. 1, 2, 4, 5 [lower Miocene, Cipero Fm., Trinidad], pl. 1, figs. 4-6 [lower Miocene, Scaglia Cinerea Fm., Marche region, Italy], figs. 7-9 [lower Miocene, Rigoroso Fm., Piedmont Basin, Italy].—Pearson and Chaisson, 1997:63, pl. 2, fig. 17 [lower Miocene Zone N4, ODP Hole 926A, Ceara Rise, western equatorial Atlantic Ocean].—Li and others, 2005:19, pl. 3, fig. 30 [lower Miocene “Zone P22” slumped zone (level equivalent to Zone M1), ODP Site 1148, South China Sea], 31-39, pl. 4, figs. 1-3 [lower Miocene Subzone N4b, ODP Hole 1148A, South China Sea].—Rincón and others, 2007:305, pl. 2, fig. 3a-d [lower Miocene *Globigerinoides primordius* Zone – *G. diminuta* Subzone, Buena Vista-1 well, Planto Basin, Colombia], pl. 10, fig. 3a-c [lower Miocene *Globigerinoides primordius* Zone – *Paragloborotalia kugleri* Subzone, Carmen Fm., Bolívar, Colombia].

Fohsella kugleri (Bolli).—van Eijden and Smit, 1991:112, pl. 4, figs. 13, 14 [lower Miocene Zone N4/P22, ODP Hole 757B, Ninetyeast Ridge, eastern Indian Ocean].

Paragloborotalia cf. kugleri (Bolli).—Spezzaferri, 1994, pl. 24, fig. 2 [lower Miocene Subzone N4b, ODP Hole 709B, Madingley Rise, equatorial Indian Ocean].

“*Globorotalia*” *pseudokugleri* Blow/“*G.*” *kugleri* Bolli transition.—Premoli Silva and Spezzaferri, 1990:303, pl. 3, figs. 3a-c [lower Miocene Zone N4, ODP Hole 709B, Madingley Rise, western equatorial Indian Ocean].

Paragloborotalia pseudokugleri Blow/*P. kugleri* Bolli transition.—Spezzaferri, 1991:315, pl. 1, fig. 4a-c [reillustrated from Premoli Silva and Spezzaferri, 1990, pl. 3, figs. 3a-c].—Spezzaferri, 1994:142, pl. 23, fig. 4a-c [reproduced from Premoli Silva and Spezzaferri, 1990, pl. 3, figs. 3a-c].—Li and others, 2005, pl. 3, figs. 21-29 [lower Miocene Subzone N4a, ODP Hole 1148A, South China Sea].

Not *Globorotalia kugleri* Bolli, 1957.—Postuma, 1971:324, pl. on p. 325 [lower Miocene *Globorotalia kugleri* Zone, San Fernando, Trinidad] (= *Paragloborotalia pseudokugleri* Blow).

DESCRIPTION.

Type of wall: Normal perforate, coarsely cancellate, sparsely spinose in life, heavy gametogenetic calcification is often present.

Test morphology: Test small to medium in size; low trochospiral; 6 to typically 7, rarely 8 chambers in the final whorl, increasing slowly in size; equatorial outline slightly lobulate, circular to slightly ovate depending on the size of the final chamber which is often smaller than the penultimate chamber; in spiral view chambers arranged in 2½-3 whorls, sutures slightly depressed, strongly curved; in umbilical view chambers wedge-shaped, weakly inflated, sutures slightly depressed, radial or slightly curved, umbilicus narrow and moderately deep; aperture umbilical-extraumbilical, a low arch, frequently hooked, typically bordered by a lip; in edge view spiral side nearly flat to moderately convex, umbilical side more convex, periphery of final chamber subacute.

Size: Maximum diameter of holotype 0.30 mm (original measurement); 0.27 mm (remeasured this study); thickness 0.15 mm (this study).

DISTINGUISHING FEATURES.—*Paragloborotalia kugleri* would appear to have evolved from *P. pseudokugleri* by gradual evolutionary transition (Blow, 1969, 1979; Chaproniere, 1981; Keller, 1981; Premoli Silva and Spezzaferri, 1990; Spezzaferri, 1991; Leckie and others, 1993; Pearson, 1995; Pearson and Chaisson, 1997). No detailed morphometric study has yet been attempted, but the overall features of the evolutionary trend are generally agreed by workers. Because it is a gradual transition, the distinction of the two taxa is an arbitrary divide, and the lowermost specimens of *kugleri* in a given section are usually rare and found among an intergrading population that is predominantly assigned to *pseudokugleri*. The frequency of *kugleri* versus *pseudokugleri* typically increases up-section, with the *pseudokugleri* morphospecies often persisting through much of the range of *kugleri*.

Because *kugleri* is an important zone fossil whose lowermost occurrence defines Zone M1 and approximates the Oligocene/Miocene boundary

Plate 5.5 *Paragloborotalia kugleri* (Bolli, 1957)

1-3 (holotype, USNM P5663), lower Miocene *Globorotalia kugleri* Zone, Cipero Fm., Trinidad; 4, 8, 12, 16 (Leckie and others, 1993, pl. 8, figs. 1, 2, 5, 4), Subzone N4a, ODP Hole 803D, Ontong Java Plateau, western equatorial Pacific Ocean; 5-7 (Spezzaferri, 1994, pl. 23, figs. 5a-c), Subzone N4b, ODP Hole 709B, Madingley Rise, Indian Ocean; 9-11, *Globorotalia kugleri* Zone, Mosquito Creek, Trinidad; 13, 14, Zone M1, ODP Site 904/13/2, 43”, New Jersey slope, North Atlantic Ocean; 15, RDL sample, *kugleri* type locality, Trinidad. Scale bar: 1-16 = 100 µm. (scale bars estimated for 4, 8, 12, 16).

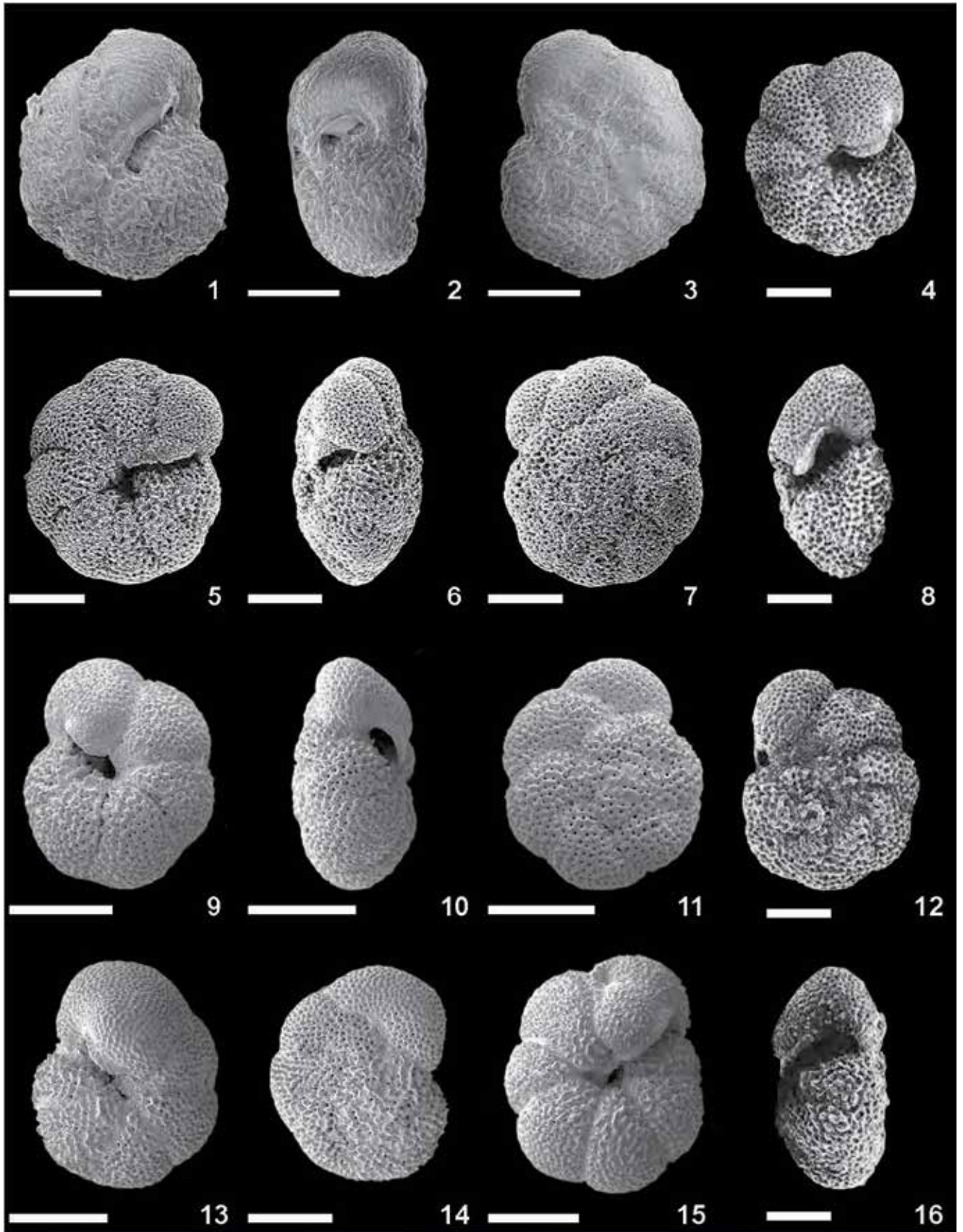


PLATE 5.5 *Paragloborotalia kugleri* (Bolli, 1957)

(Steininger and others, 1997), it is important to establish clear criteria for distinguishing the morphospecies. The method for doing this should involve careful consideration of the morphology of two holotype specimens (which are shown here in SEM for the first time on their respective plates) and trying to draw the line half way between them, rather than by trying to develop an idealized view of what a quintessential *kugleri* and *pseudokugleri* should look like. This point is stressed because the *pseudokugleri* holotype is quite an ‘advanced’ form for the morphospecies, and shows various features that tend to be more clearly associated with *kugleri*, especially the number of chambers in the final whorl and curved spiral sutures, as discussed further below. A mosaic of characters is involved when trying to draw a subjective line in the evolutionary transition between the morphospecies. It is a multidimensional problem that ultimately may benefit from a quantitative, morphometric approach using multivariate statistics. At present, however, we rely on our subjective appreciation of shape to accomplish this task.

Before proceeding, it is worth mentioning that some authors (Premoli Silva and Spezzaferri, 1990; Spezzaferri and Premoli Silva, 1991; Spezzaferri, 1994; Rögl, 1996) have recognized on their range charts a third morphotype in open nomenclature as “*pseudokugleri* - *kugleri* transition”. To operate that distinction, it would be necessary (using the same principles described above) to define arbitrary divisions between 1) *pseudokugleri* s.s. and “*pseudokugleri* - *kugleri* transition”; and 2) between “*pseudokugleri* - *kugleri* transition” and *kugleri* s.s. Moreover, the lowermost *kugleri* s.s. is likely to be drawn at somewhat higher level if transitional forms are entered in to a separate category. We have elected not to do this and assign all ‘transitional’ forms to one or the other morphospecies.

The principal morphological changes that occur from ‘primitive’ *pseudokugleri* to ‘advanced’ *kugleri* are as follows;

- 1) An increase in the number of chambers in the final whorl from 5-6 to 7 and more rarely 8,
- 2) A concomitant reduction in the rate of chamber enlargement, making successive chambers more equal in size,
- 3) Reduced inflation and increasing compression and appression of the chambers,
- 4) A concomitant reduction in the lobateness of the periphery, which ranges from ovate to more circular,
- 5) A transition from straight to strongly curved sutures on the spiral side,
- 6) An increase in the tendency for weakly curved sutures on the umbilical side,
- 7) Less marked depression of the spiral side sutures,
- 8) Flattening of the spiral side generally, although some ‘advanced’ forms are convex on both sides and biconvex - lensoidal in overall morphology,
- 9) Increased pinching of the periphery of the final one or more chambers, which go from sub-rounded to sub-acute,
- 10) A slight increase in average size, after an initially more rapid increase near the very beginning of the stratigraphic range (Spezzaferri, 1994).

As mentioned above, the holotype of *pseudokugleri* is a considerable way along this transition. It has 7 chambers in the final whorl, which expand fairly slowly in size; fairly inflated chambers and a distinctly lobulate periphery with, nevertheless moderate chamber appression; slightly curved sutures on the spiral side throughout ontogeny (see the SEMs of the holotype, Pl. 5.9, Figs. 1-3; these are seemingly exaggerated on Bolli’s original drawing; Blow (1969) on the other hand, originally described the sutures as straight); straight sutures on the umbilical side; moderately depressed spiral side sutures with a moderately flattened spiral side; and a fully rounded periphery. A rounded periphery is the key feature of *pseudokugleri* s.s. (e.g., Leckie and others, 1993). Pearson and Wade (2009) collected more specimens from the ‘cotype locality’ at Mosquito Creek, Trinidad, which show a similar set of characters. The holotype of *kugleri* shows 8 chambers of gradually increasing size in the final whorl, although the final chamber is unusually large; low chamber inflation and high appression making the periphery almost entire and non-lobulate; strongly curved spiral side sutures and fairly straight umbilical side sutures; a very flat spiral side and a somewhat pinched/subacute periphery to the final chamber. An asymmetrically subacute periphery is a key feature of *kugleri* s.s.

It is clear from this that the number of chambers in the final whorl and the presence of curved spiral sutures are of less importance in distinguishing the morphospecies than some of the other features. Accordingly, we suggest the following guidelines for distinguishing *kugleri*: most importantly, the final chamber should show a distinct pinching and not be broadly rounded (contra Rögl, 1996); the chambers are less inflated and more appressed and the outline is more ovate and less lobulate;

and spiral side sutures are more strongly curved and less depressed than is typical in *pseudokugleri*; and the spiral side is generally flatter. A combination of these features allows for the most reliable means to differentiate the two taxa and recognize the base of Zone M1 near the Oligocene/Miocene boundary.

Finally, although the spiral side in *kugleri* is usually flat, it can also be convex, rendering the test markedly biconvex (e.g., Premoli Silva and Spezzaferri, 1990, pl. 3, fig. 5a-c; Spezzaferri, 1991, fig. 1a-d). These variants have sometimes been identified as *Globorotalia* (*Turborotalia*) *mendacis* Blow but the holotype of that species is regarded here as a synonym of *P. birnageae*. *Paragloborotalia kugleri* is distinguished from *P. birnageae* by its more asymmetrically subacute peripheral margin, more ovate equatorial outline, flatter spiral side, and higher aperture with smaller lip (*P. kugleri* lacks an appressed final chamber with flap-like flange or apertural plate). It is distinguished from *Fohsella? peripheroronda* by its generally greater number of chambers in the final whorl (typically 7 compared with 6) and slower rate of chamber expansion giving *kugleri* a more circular equatorial outline compared with a more ovate outline of *peripheroronda*.

DISCUSSION.— When *Paragloborotalia kugleri* was described by Bolli (1957), he included within the concept forms which were later separated as *pseudokugleri* by Blow (1969) (see also Postuma, 1971). Most authors since the 1990s have followed Blow, as we do here, although influential works by Stainforth and others (1975), Kennett and Srinivasan (1983), and Bolli and Saunders (1985) continued to recognize only *kugleri*. Spezzaferri (1991) and Rögl (1996) recognized spine holes, and Spezzaferri (1991; pl. 1, fig. 6) illustrated calcite build-ups ('rises') at the intersections of cancellate ridges that may represent gametogenic calcification over spine holes as observed in *Trilobatus sacculifer* (e.g., Hemleben and Olsson, 2006). However, Pearson and Wade (2009) considered that evidence questionable and failed to find evidence of spine holes or spines embedded in the wall in well-preserved populations from Trinidad. Hence they, and Aze and others (2011), regarded the species as probably nonspinose and referred it, and the closely related *pseudokugleri*, only questionably to the genus *Paragloborotalia*. Our ongoing investigations have produced unequivocal evidence of true spines in *pseudokugleri* (Plate 5.9, Figs. 4, 8), supporting the original evidence of Spezzaferri (1991) and Rögl (1996) and

confirming the generic assignment. Like most species of *Paragloborotalia*, *P. kugleri* was subject to heavy gametogenic calcification (Hemleben and others, 1989) making spines often difficult to detect.

PHYLOGENETIC RELATIONSHIPS.— Evolved by gradual transition from *P. pseudokugleri* (Blow, 1969, and subsequent authors; see discussion above). Many have proposed that *kugleri* is the direct ancestor of *F.? peripheroronda* and the *Fohsella* lineage (e.g., Fleisher, 1974, Stainforth and others, 1975; Keller, 1981; Kennett and Srinivasan, 1983; Cifelli and Scott, 1986; Chaisson and Leckie, 1993). An alternate hypothesis is that *kugleri* became extinct with no descendants. Olsson (1972) proposed that *mayeri* was the ancestor of *peripheroronda*, while Jenkins (1960, 1971) and Blow (1969) suggested that *mayeri* was the descendant of *peripheroronda*.

TYPE LEVEL.— Lower Miocene *Globorotalia kugleri* Zone type locality sensu Bolli, 1957, Ciperó Fm., Trinidad (same sample as holotype of *P. pseudokugleri*).

STRATIGRAPHIC RANGE.— Base of Zone M1, by definition, to top of Zone M1, also by definition (Berggren and others, 1995; Wade and others, 2011; see discussion in Chapter 2, this volume). The base of Zone M1 occurs two meters above the 'golden spike' for the Neogene Period, Miocene Epoch, and Aquitanian Stage, at Lemme-Carrosio, Italy (Steininger and others, 1997) hence it is used to approximate these levels in planktonic foraminiferal biostratigraphy.

GEOGRAPHIC DISTRIBUTION.— According to Kennett and Srinivasan (1983) and Rögl (1996), this species is limited to the tropics and subtropics, but in fact it has been found nearly as far north as the Reykjanes Ridge and east Greenland margin in the North Atlantic Ocean (Poore, 1979; Spezzaferri, 1998).

STABLE ISOTOPE PALEOBIOLOGY.— *Paragloborotalia kugleri* has low $\delta^{18}\text{O}$ and high $\delta^{13}\text{C}$ relative to other species suggesting it was a mixed-layer dweller (Douglas and Savin, 1973; Biolzi, 1983; van Eijden and Ganssen, 1995; Pearson and others, 1997; Spezzaferri and Pearson, 2009).

REPOSITORY.— Holotype (USNM P5663) and paratype (USNM P5664) deposited at the Smithsonian Museum of Natural History, Washington, D.C.

***Paragloborotalia mayeri* (Cushman and Ellisor, 1939)**

PLATE 5.6, FIGURES 1-16

Globorotalia mayeri Cushman and Ellisor, 1939:11, pl. 2, figs. 4a-c [Miocene, Humble Oil and Refining Company No. 1 Ellender, Louisiana].—Postuma, 1971:332, pl. on p. 333 [Hermitage, Trinidad].—Berggren and Amdurer, 1973, pl. 28, fig. 14 [middle Miocene Zone N9, DSDP Site 30, Aves Ridge, Caribbean Sea].—Kennett, 1973, pl. 13, figs. 12-16 [middle Miocene *G. mayeri* Zone, DSDP Site 206 and Hole 207A, New Caledonia Basin and Lord Howe Rise, western South Pacific Ocean].—Poore, 1979:471, pl. 9, figs. 1, 2 [middle Miocene Zone N14, DSDP Site 408, North Atlantic Ocean], figs. 3-5 [middle Miocene Zone N8-N11, DSDP Site 407, North Atlantic Ocean].—Salvatorini and Cita, 1979, pl. 9, figs. 5, 9, 12-14 [middle Miocene Zone N13 and in a slump within upper Miocene Zone N16, DSDP Site 397, eastern North Atlantic Ocean].—Bolli and Saunders, 1982a, pl. 1 (partim), figs. 22-24, 27-29, 31-35, 37, 39; pl. 2, figs. 7, 11-13, 18-20, 32, 37, 39-42, 46, 47; pl. 3, figs. 7, 10, 12, 19-21, 30, 31 [lower to middle Miocene *Globigerinita insueta* Zone to *Globorotalia mayeri* Zone, Bodjonegoro-1 well, Java].—Hoskins, 1984, figs. 2:1-6 [middle Miocene *P. glomerosa curva* Zone, Clifdenian Stage, South Island, New Zealand].—Zachariasse and Sudijono, 2012:161-166, fig. 10 (holotype of *Globorotalia mayeri*) [Miocene, Humble Oil and Refining Company No. 1 Ellender, Louisiana].

Globorotalia (Turborotalia) mayeri mayeri Cushman and Ellisor.—Jenkins, 1971:120, pl. 11, figs. 297-302 [middle Miocene *Globorotalia (Turborotalia) mayeri mayeri* Zone, Waiauuan stage, Tukituki River section and Muddy Creek section, New Zealand].

Globorotalia (Jenkinsella) mayeri Cushman and Ellisor.—Kennett and Srinivasan, 1983:174, pl. 43, figs. 4-6 [lower Miocene *Globorotalia miozea* Zone, DSDP Site 206, New Caledonia Basin, western South Pacific Ocean].

Paragloborotalia mayeri s.l. (Cushman and Ellisor).—Chaisson and Leckie, 1993:164-165, pl. 8 (partim), figs. 18-20 [lower Miocene Zone N5 and middle Miocene Zone N10, ODP Hole 806B, Ontong Java Plateau, western equatorial Pacific Ocean].

Paragloborotalia mayeri (Cushman and Ellisor).—Spezzaferrri, 1994:55, pl. 21, figs. 3a-c [lower Miocene Zone N5,

ODP Hole 709C, Madingley Rise, western equatorial Indian Ocean].—Pearson, 1995:51, pl. 1, fig. 7 [middle Miocene Zone N12, ODP Hole 871A, Limalok Guyot, western equatorial Pacific Ocean].

Paragloborotalia semivera Hornibrook/*Paragloborotalia mayeri* group (Cushman and Ellisor).—Leckie and others, 1993:125, pl. 7, figs. 5, 10-11 [upper Oligocene Zone P22, ODP Hole 628A, Little Bahama Bank, western North Atlantic Ocean], figs. 6-8, 12-14 [upper Oligocene Zone P22, ODP Hole 803D, Ontong Java Plateau, western equatorial Pacific Ocean].

Globorotalia siakensis LeRoy.—Postuma, 1971:358, pl. on p. 359 [Trinidad]. [Not Leroy, 1939.]

Not *Globorotalia* cf. *mayeri* Cushman and Ellisor.—Keller, 1981:125-127, pl. 2, 7 figures [upper Oligocene Zone P22, DSDP Site 292, Benham Rise, northwest Pacific Ocean] (= *Paragloborotalia siakensis*).

Not *Globorotalia mayeri* Cushman and Ellisor.—Bolli and Saunders, 1982a, pl. 1, figs. 25, 26, 30, 36, 38; pl. 2, figs. 1-6, 8, 9, 14-17, 21-31, 36, 38, 43-45; pl. 3, 1-6, 13-18, 22-29, 32-43 [lower to middle Miocene *Globigerinita insueta* Zone to *Globorotalia mayeri* Zone, Bodjonegoro-1 well, Java] (= *Paragloborotalia siakensis*).

Not *Paragloborotalia mayeri* s.l. (Cushman and Ellisor).—Chaisson and Leckie, 1993:164-165, pl. 8, figs. 16, 17 [lower Miocene Subzone N4b, ODP Hole 806B, Ontong Java Plateau, western equatorial Pacific Ocean] (= *P. semivera*).

DESCRIPTION.

Type of wall: Normal perforate, coarsely cancellate, probably sparsely spinose in life, heavy game-togenetic calcification is often present.

Test morphology: Test medium to large in size; low trochospiral, moderately lobulate in equatorial outline, chambers subglobular, inflated, slightly embracing; 5 to typically 6 chambers in the ultimate whorl of late Oligocene forms, up to 7 chambers in early and middle Miocene forms, increasing rapidly in size in initial whorl and slowly in the final whorl; in spiral view chambers subspherical, arranged in 2½-3 whorls, sutures depressed, slightly curved; in umbilical view chambers spherical to subspherical, sutures depressed, radial, umbilicus narrow, moderately deep; aperture umbilical-extraumbilical, moderately high arch, bordered

Plate 5.6 *Paragloborotalia mayeri* (Cushman and Ellisor, 1939)

1-3 (holotype; USNM 25236), Miocene, Humble Oil and Refining Company No. 1 Ellender, Louisiana; **4, 8**, Zone M3/M4, ODP Hole 871A/12H/2 59-61 cm, Limalok Guyot, western equatorial Pacific Ocean; **5-7** (Spezzaferrri, 1994; pl. 21, figs. 3a-c), Zone N5, ODP Hole 709C, Madingley Rise, western Indian Ocean; **9-11** (same specimen), and **13-15** (same specimen), Zone M9, ODP Hole 871A/6H/5 60-62 cm, Limalok Guyot, western equatorial Pacific Ocean; **12**, Zone M3/M4, ODP Hole 871A/10H/2 78-80 cm, Limalok Guyot, western equatorial Pacific Ocean; **16**, Zone M5, ODP Hole 871A/8H/1 59-61 cm, Limalok Guyot, western equatorial Pacific Ocean. Scale bar: **1-16** = 100 µm.

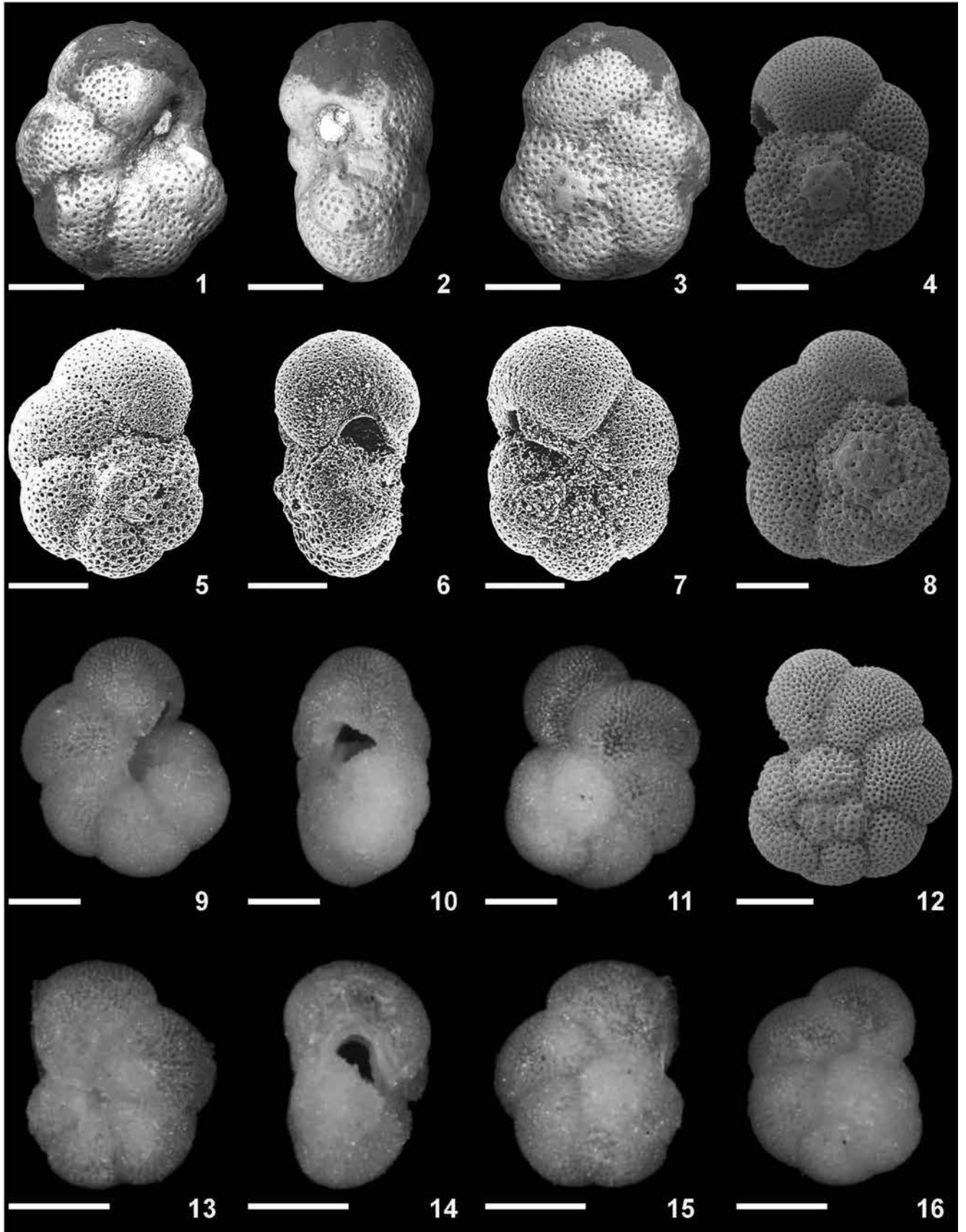


PLATE 5.6 *Paragloborotalia mayeri* (Cushman and Ellisor, 1939)

by an imperforate rim or thin lip; in edge view chambers spherical, spiral side flat to slightly convex, umbilical side slightly convex, periphery broadly rounded.

Size: Maximum diameter of holotype and other specimens from the type level 0.35–0.40 mm; minimum diameter 0.27–0.30 mm; maximum thickness 0.22 mm (original measurements); maximum diameter of holotype 0.34 mm, maximum thickness 0.21 mm (this study).

DISTINGUISHING FEATURES.— The holotype of *P. mayeri* lacks a prominent lip but appears to have an imperforate rim bordering the aperture. In their original description of *Globorotalia mayeri*, Cushman and Ellisor (1939) noted the presence of a slight lip. *Paragloborotalia mayeri* and *P. siakensis* bear close similarities and both species were originally described as having about six chambers in the final whorl, depressed sutures, a moderately high arched umbilical to extraumbilical aperture with a distinctive lip, and a distinctly rounded peripheral margin (Cushman and Ellisor, 1939; LeRoy, 1939). These close similarities, led to the suggestion that *P. siakensis* is a junior synonym of *P. mayeri* (Bolli and Saunders, 1982a, b). While some authors have followed this synonymy (e.g., Bolli and Saunders, 1985; Chaisson and Leckie, 1993; Pearson, 1995; Hilgen and others, 2000), others have differentiated between the two taxa (e.g., Kennett and Srinivasan, 1983; Premoli Silva and Spezzaferri, 1990; Spezzaferri, 1994; Hilgen and others, 2003; Stewart and others, 2004; Pearson and Wade, 2009). *Paragloborotalia mayeri* is distinguished from *P. siakensis* by its slightly curved spiral sutures and generally higher arched aperture, and less strongly developed lip.

Paragloborotalia mayeri is distinguished from *P. semivera* in having a flatter spiral side, more rapid rate of chamber expansion and ovate equatorial outline, wider, more open umbilicus, and generally greater number of chambers in the final whorl (typically 6 in *mayeri* compared with 5 in *semivera*). It is distinguished from *acrostoma* by its flatter spiral side, wider umbilicus, generally greater number of chambers in the final whorl (typically 6 compared with 5), and more extraumbilical aperture. *Paragloborotalia mayeri* is distinguished from *P. pseudokugleri* by its greater rate of chamber expansion and more ovate equatorial outline, and higher arched aperture, and from *P. kugleri* by its more inflated chambers and lobulate equatorial profile with fewer chambers in the final whorl (typically 6 compared with 7–8 in *kugleri*), and higher arched aperture. *Paragloborotalia*

mayeri is distinguished from *Globorotalia acrostoma partimlabiata* by its more spherical chambers and less asymmetrical flattening of the spiral side.

DISCUSSION.— Bolli and Saunders (1982a, 1985) wrote extensively about the distinction between *mayeri* and *siakensis*, and concluded that the two taxa, both named in 1939, are synonymous, with *mayeri* having priority (Bolli and Saunders, 1982b). We reject this synonymy here. Zachariasse and Sudijono (2012) argued the two taxa could not be synonymised as *P. mayeri* has curved spiral-side sutures, while *P. siakensis* possesses straight sutures. Interestingly, these curved sutures are not included in the original type description as a distinguishing feature (Cushman and Ellisor, 1939). A lack of spinosity in *P. mayeri* (Hilgen and others, 2000; Zachariasse and Sudijono, 2012), and a wider, deeper umbilicus in *P. siakensis* (Kennett and Srinivasan, 1983) have also been suggested as means of differentiation. *Paragloborotalia siakensis* is the ancestral form derived directly from *P. nana*.

Low latitude early and middle Miocene assemblages contain specimens of the *mayeri-siakensis* plexus with all manner of variability and transitional specimens in terms of spiral suture orientation, relative lobateness of the test outline, and height of the arched aperture, suggesting that the two forms are very closely related (e.g., Bolli and Saunders, 1982a; Zachariasse and Sudijono, 2012). In this study, specimens illustrated by Bolli and Saunders (1982a) with radial sutures are assigned to *siakensis*, while those with curved spiral sutures are here assigned to *mayeri*. *Paragloborotalia mayeri* is a more evolved form of *P. siakensis*; several *Paragloborotalia* lineages have straight spiral sutures in the Oligocene that become curved in the latest Oligocene and early Miocene (*siakensis* to *mayeri*; *pseudocontinua* to *acrostoma*; *pseudokugleri* to *kugleri*), and then become increasingly curved to crescentic as they gave rise to *Fohsella* and *Globoconella*. Both *P. mayeri* and *P. siakensis* have the same last occurrence in the early late Miocene (10.53 Ma; Wade and others, 2011; also see Kennett and Srinivasan, 1983; Berggren and others, 1995) further supporting the close relationship of the two forms.

The paratype assigned to *P. mayeri* by Blow and Banner has been reassigned to *Fohsella? peripheroronda* (Bolli and Saunders, 1982a; Zachariasse and Sudijono, 2012). We reject Hoskins' (1984) proposed synonymy of *G. pseudocontinua*, *G. semivera*, *G. continua*,

and *G. mayeri nympha* with *G. mayeri* for the reasons outlined above.

Zachariasse and Sudijono (2012) suggested that *Globorotalia partimlabiata* Ruggieri and Sprovieri is synonymous with *P. mayeri*, although we note the more flattened dorsal side of *partimlabiata* and resultant asymmetrical shape of the final chamber in axial (edge) view.

PHYLOGENETIC RELATIONSHIPS.— The ancestry of *P. mayeri* has been widely debated. Kennett and Srinivasan (1983) suggested that *P. mayeri* was derived from *siakensis* in the latest Oligocene. This evolutionary relationship was further supported by Spezzaferri and Premoli Silva (1991) who proposed that *P. mayeri* s.s. originated from *P. siakensis* in the latest Oligocene as the *mayeri-siakensis* plexus increased in size (>250 μm ; also see Spezzaferri, 1994). Both taxa share the same (or close) last occurrence in the early late Miocene (Kennett and Srinivasan, 1983; Spezzaferri, 1994); the extinction of *P. mayeri* is used to define the base of Zone M12 (Wade and others, 2011).

Jenkins (1971) suggested that “pre-*Orbulina*” (i.e., early Miocene) specimens of *G. (T.) mayeri mayeri* may be better assigned to *siakensis*. Jenkins (1978) reported the lowest occurrence of *G. mayeri mayeri* in the middle Miocene *G. mayeri mayeri* Zone at DSDP Site 360 and 362 in the southeast Atlantic Ocean. Jenkins (1960, 1966, 1971, 1975) and Jenkins and Srinivasan (1986) proposed that *mayeri* evolved from *peripheroronda* in the late middle Miocene. Jenkins and Srinivasan (1986) speculated that *G. challengerii* Srinivasan and Kennett was an intermediate species between *peripheroronda* and *mayeri*. We reject these proposed phylogenetic relationships because of the latest Oligocene/earliest Miocene first appearance of *mayeri* precedes *peripheroronda* (Kennett and Srinivasan, 1983; Chaisson and Leckie, 1993; Spezzaferri, 1994). We conclude that *mayeri* was derived from *siakensis* in the latest Oligocene.

Some authors have proposed that *P. mayeri* gave rise to *Fohsella? peripheroronda* in the earliest Miocene (Bolli and Saunders, 1982a; Spezzaferri, 1994; see transitional specimens illustrated on pl. 25, figs. 4a-c and 5a-c), while others have proposed that *P. kugleri* was the direct ancestor of *F.? peripheroronda* (e.g., Fleisher, 1974; Stainforth and others, 1975; Kennett and Srinivasan, 1983; Chaisson and Leckie, 1993). The generic assignment of *peripheroronda* remains unsettled and therefore a discussion of this taxon and the origin of the

genus of *Fohsella* is not considered further in this work.

TYPE LEVEL.— Miocene, core sample at 9,612 feet from Humble Oil and Refining Company’s No.1 Ellender, Terrebonne Parish, Louisiana. The original type sample from Humble Oil Well No. 1 Ellender, Terrebonne Parish, Louisiana containing *P. mayeri*, which is also the type level of *Globorotalia fohsi* Cushman and Ellis, is no longer available (Bolli and Saunders, 1982a, b; Zachariasse and Sudijono, 2012).

STRATIGRAPHIC RANGE.— Uppermost Oligocene – lower upper Miocene (Zone O7 through Zone M11; Bolli and Saunders, 1982a; Kennett and Srinivasan, 1983; Spezzaferri and Premoli Silva, 1991; Spezzaferri, 1994; Wade and others, 2011). Berggren and others (1983), like many others (e.g., Jenkins, 1960, 1966, 1971, 1975), reported a lowest occurrence in the middle Miocene.

GEOGRAPHIC DISTRIBUTION.— According to Kennett and Srinivasan (1983), *siakensis* is more common in equatorial and warm subtropical locations, while *mayeri* is more common in temperate locations. As documented in the synonymy list above, *mayeri* also occurred in equatorial and tropical waters.

STABLE ISOTOPE PALEOBIOLOGY.— Biolzi (1983) reported negative $\delta^{18}\text{O}$ values in comparison to the rest of the assemblage indicating a mixed-layer dwelling habitat, however, the taxonomic concepts are not discussed and no specimens are illustrated. Gasperi and Kennett (1993) reported consistently low $\delta^{18}\text{O}$ values and low $\delta^{13}\text{C}$ values through the lower and middle Miocene of DSDP Site 289 in the western equatorial Pacific suggesting a mixed-layer habitat.

REPOSITORY.— Holotype (USNM 25236) deposited at the Smithsonian Museum of Natural History, Washington, D.C.

***Paragloborotalia nana* (Bolli, 1957)**

PLATE 5.7, FIGURES 1-16

Globorotalia opima nana Bolli, 1957:118, pl. 28, fig. 3a-c [Oligocene *Globorotalia opima opima* Zone, Cipero Fm., Trinidad; max. diameter = 0.30 mm (original measurement), 0.319 mm (re-measured herein)].—Raju, 1971:33, pl. 10, figs. 3a-b [lower Oligocene *G. sastrii* Zone, Well No. KKL-4, Cauvery Basin, southern India;

- max. diameter = 0.20 mm].—Berggren and Amdurer, 1973, pl. 27, figs. 8-10 [upper Oligocene Zone P21, DSDP Hole 17B, South Atlantic Ocean].—Stainforth and others, 1975:297, fig. 131.1-3, 5-7 [lower Oligocene *Globigerina ampliapertura* Zone, Ciperó Fm., Trinidad; max. diameters = 0.30 mm, 0.29 mm, 0.28 mm, 0.27 mm, 0.23 mm, and 0.22 mm], 4 (holotype drawing reproduced)].—Toumarkine, 1978:714, pl. 8, figs. 3-4 [Oligocene *Globorotalia opima opima* Zone, DSDP Site 360, southeast Atlantic Ocean; max. diameters = 0.24 mm].—Bolli and Saunders, 1982a, pl. 4, figs. 40-42 [Oligocene *Globorotalia opima opima* Zone, Ciperó Fm., Trinidad].—Bolli and Saunders, 1985:202-203, fig. 26.16a-c (holotype re-illustrated from Bolli, 1957, pl. 28, figs. 3a-c), figs. 26.15, 17-20 (“paratypes”, actually topotypes) [Oligocene *Globorotalia opima opima* Zone, Ciperó Fm., Trinidad; max. diameters = 0.15 mm, 0.14 mm, 0.18 mm, 0.19 mm, and 0.18 mm].
- Globorotalia (Turborotalia) opima nana* Bolli.—Jenkins, 1971:123-124, pl. 11, figs. 303-305 [upper Eocene, Kaiatan Stage, South Island, New Zealand; max. diameters = 0.20 mm and 0.17 mm], pl. 11, figs. 306-308 [lower Miocene *G. (G.) woodi woodi* Zone, North Island, New Zealand].—Quilty, 1976:646, pl. 13, figs. 10, 11 [Oligocene Zone N2/N3, DSDP Site 320, southeastern Pacific Ocean; max. diameters = 0.17 mm and 0.19 mm].
- Turborotalia (Turborotalia) opima nana* (Bolli).—Fleisher, 1974:1036, pl. 19, fig. 11 [lower Oligocene Zone P18/P19, DSDP Site 219, Arabian Sea; max. diameter = 0.30 mm].
- Globorotalia nana* Bolli.—Krashennikov and Pflaumann, 1978:592, pl. 6, figs. 10-11c [Oligocene, DSDP Hole 369A, eastern North Atlantic Ocean; max. diameter = 0.25 mm and 0.21 mm].
- Turborotalia siakensis nana* (Bolli).—Chaproniere, 1981:124, figs. 11.Ba-c, Ea-c [upper Oligocene Zone N3/N4, Ashmore Reef No. 1 well, eastern Indian Ocean; max. diameters = 0.23 mm and 0.25 mm].
- “*Globorotalia*” *nana* Bolli.—Kennett and Srinivasan, 1983:106, pl. 24, figs. 3-5 [lowermost Miocene Subzone N4a, DSDP Hole 206C, New Caledonia Basin, western South Pacific Ocean; max. diameters = 0.29 mm, 0.27 mm, and 0.27 mm].
- Paragloborotalia opima nana* (Bolli).—Spezzaferri and Premoli Silva, 1991:248, pl. XI, figs. 4a-c [lower Oligocene Subzone P21a, DSDP Hole 538A, Gulf of Mexico; max. diameter = 0.26 mm].
- Paragloborotalia nana* (Bolli).—Leckie and others, 1993:124, pl. 7, fig. 1 [upper Oligocene Zone P22, ODP Hole 628A, Little Bahama Bank, western North Atlantic Ocean; max. diameter = 0.28 mm], pl. 7, fig. 2 [lower Oligocene Zone P19, ODP Hole 628A, Little Bahama Bank, western North Atlantic Ocean; max. diameter = 0.27 mm].—Spezzaferri, 1994:54, pl. 20, figs. 4a-c (image reproduced from Spezzaferri and Premoli Silva, 1991).—Pearson, 1995:51, pl. 1, fig. 5 [Oligocene Zone P21/P22, ODP Hole 872C, Lo-En Guyot, western equatorial Pacific Ocean; max. diameter = 0.28 mm].—Morgans and others, 2002, figs. 13M-P [lower Miocene *P. incognita* Zone, Altonian Stage, North Island, New Zealand].—Li and others, 2005:19, pl. 2, figs. 20-22 [upper Oligocene Zone P22, ODP Site 1148, South China Sea; max. diameters = 0.32 mm, 0.29 mm], pl. 2, figs. 23, 24 [lower Oligocene Zone P21a, ODP Site 1148, South China Sea; max. diameters = 0.28 mm, 0.26 mm].—Olsson and others, 2006:95-96, pl. 5.8, figs. 1-3 (holotype re-illustrated by SEM).—Wade and others, 2007, pl. I, figs. a-g [upper Oligocene Zone O6, ODP Site 1218, equatorial Pacific Ocean; max. diameters = 0.20 mm, 0.20 mm, 0.22 mm, 0.19 mm, 0.24 mm, and 0.30 mm].—Rincón and others, 2007:305, pl. 10, figs. 5a-c [lower Oligocene *Turborotalia ampliapertura* Zone, San Jacinto Fm., Colombia; max. diameter = 0.26 mm].—Pearson and Wade, 2009:208, pl. 6, figs. 1a-2d [upper Oligocene Zone O6 (=O7 of this work), Ciperó Fm., Trinidad; max. diameters = 0.16 mm and 0.18 mm].—Wade and others, 2016:440, pl. 1, figs. 1a-c (holotype SEM re-illustrated), pl. 2, figs. 1a-b [upper Oligocene Zone O6, IODP Hole U1334A, equatorial Pacific Ocean; max. diameter = 0.20 mm], pl. 2, figs. 2a-2e, 4a-4d [lower Oligocene Zone O3/O4, IODP Hole U1334A, equatorial Pacific Ocean; max. diameters = 0.23 mm, 0.28 mm], pl. 2, figs. 3a-3d [upper Oligocene Zone O5, IODP Hole U1334A, equatorial Pacific Ocean; max. diameter = 0.27 mm].
- Jenkinsella opima nana* (Bolli).—Poag and Commeau, 1995:149, pl. 6, figs. 21, 22, pl. 7, figs. 20, 21 [Oligocene, Hammond Well, Maryland; max. diameters = 0.24 mm, 0.24 mm, 0.20 mm and 0.20 mm].
- Globorotalia opima nana* Bolli/*Globorotalia continuosa* Blow transition.—Bolli and Saunders, 1982a, pl. 4, figs. 28-39

Plate 5.7 *Paragloborotalia nana* (Bolli, 1957)

1-3 (holotype, USNM P5661), *Globorotalia opima opima* Zone, Ciperó Fm., Trinidad (max. size 0.319 mm); **4, 8, 12** (same specimen), Zone O7, ODP Site 628/16/5 100-102 cm, Little Bahama Bank, western North Atlantic Ocean (max. size 0.27 mm); **5-7** (same specimen), Zone O6, ODP Site 628/18/1 100-102 cm, Little Bahama Bank, western North Atlantic Ocean (max. size 0.20 mm); **9-11** (same specimen), Zone O5?, ODP Site 628/24/1 100-102 cm, Little Bahama Bank, western North Atlantic Ocean (max. size 0.22 mm); **13** (Wade and others, 2016; pl. 2, fig. 1a), Zone O6, IODP Hole U1334A, equatorial Pacific Ocean (max. size 0.20 mm); **14-16** (same specimen), specimen transitional to *Paragloborotalia pseudokugleri*, Zone O7, ODP Site 628/16/5 100-102 cm, Little Bahama Bank, western North Atlantic Ocean (max. size 0.20 mm). Scale bar: **1-16** = 100 μ m.

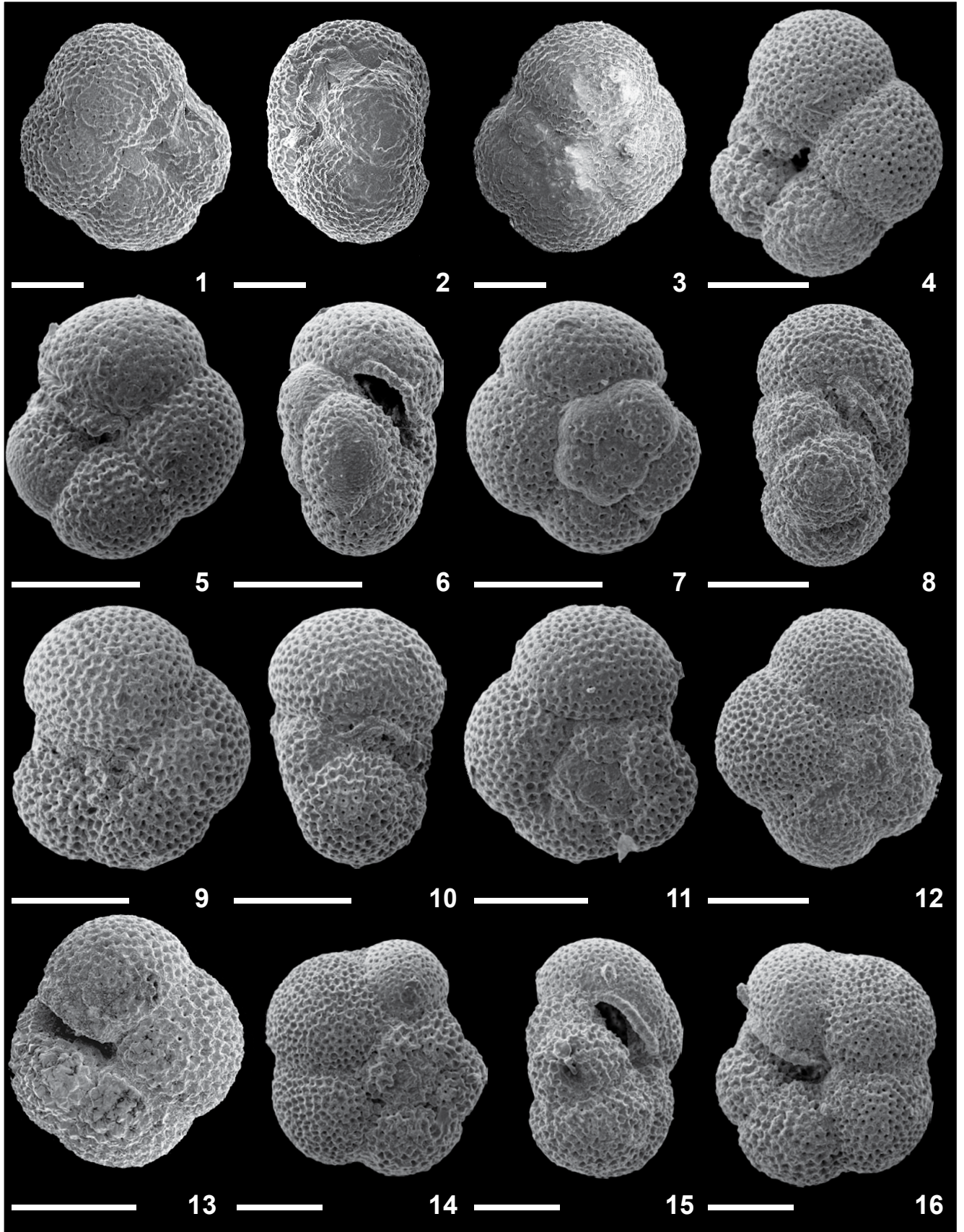


PLATE 5.7 *Paragloborotalia nana* (Bolli, 1957)

[uppermost Oligocene to lower Miocene, *Globigerina ciperoensis ciperoensis* Zone to *Catapsydrax stainforthi* Zone, Ciperó Fm., Trinidad].

Turborotalia siakensis opima (Bolli).—Chaproniere, 1981:124, figs. 11.Ca-c [Oligocene Zone N3/N4, Ashmore Reef No. 1 well, eastern Indian Ocean; max. diameter = 0.31 mm]. [Not Bolli, 1957.]

Paragloborotalia opima opima (Bolli).—Cifelli, 1982 (partim), pl. 2, fig. 2 [upper Oligocene *Globorotalia opima* Zone, Ciperó Fm., Trinidad (given in plate caption as *Globorotalia opima*); max. diameter 0.22 mm]. [Not Bolli, 1957.]

Paragloborotalia opima (Bolli).—Li and others, 2005:19, pl. 2, figs. 25, 26 [upper Oligocene Zone P22, ODP Site 1148, South China Sea; max. diameters = 0.27 mm, and 0.30 mm], figs. 27, 29 [lower Oligocene Zone P21a, ODP Site 1148, South China Sea; max. diameters = 0.22 mm, 0.24 mm, and 0.27 mm], fig. 30 [Oligocene Zone P22 (?reworked), ODP Site 1148, South China Sea; max. diameter of specimen = 0.27 mm]. [Not Bolli, 1957.]

Paragloborotalia opima transitional form to *P. nana*.—Rincón and others, 2007:305, pl. 10, figs. 6 a-c [lower Oligocene *Turborotalia ampliapertura* Zone, San Jacinto Fm., Colombia; max. diameter = 0.29 mm]. [Not Bolli, 1957.]

Not *Globorotalia (Turborotalia) opima nana* Bolli.—Blow, 1969:352-3, pl. 39, fig. 1 [lower Oligocene Zone P20, Ciperó Fm., Trinidad; max. diameter = 0.33 mm] (species uncertain).

Not *Globorotalia nana* Bolli.—Postuma, 1971:340, pl. on p. 341 [Oligocene, Trinidad; max. diameter = 0.33 mm] (= *P. opima*).

Not *Globorotalia opima nana* Bolli.—Stainforth and Lamb, 1981:25, pl. 4, fig. 1a-c [upper Eocene, Atlantic Slope Project corehole 5B, western North Atlantic Ocean] (= *Parasubbotina varianta*).

Not *Paragloborotalia nana* (Bolli).—Huber, 1991:440, pl. 7, fig. 15 [upper Eocene Zone AP12, ODP Site 738, Kerguelen Plateau, Southern Ocean] (?= *Tenuitella munda*).—Chaisson and Leckie, 1993:165, pl. 8, figs. 10, 11 [lower Miocene Zone N5, ODP Hole 806B, Ontong Java Plateau, western equatorial Pacific Ocean; max. diameter = 0.35 mm] (= *P. continuosa*).

DESCRIPTION.

Type of wall: Normal perforate, coarsely cancellate, probably sparsely spinose in life, heavy game-togenic calcification is often present.

Test morphology: Test small to medium in size; very low trochospiral, quadrate to slightly lobulate in equatorial outline, chambers spherical to subspherical, inflated, embracing; typically 4-4½, occasionally 5 chambers in ultimate whorl, increasing slowly in size; in spiral view chambers moderately inflated,

spherical to subspherical, arranged in 2 whorls, sutures slightly depressed, radial; in umbilical view chambers moderately inflated, sutures slightly depressed, radial, forming a cross, umbilicus very narrow, moderately deep, sometimes closed off by surrounding chambers, ultimate chamber may be slightly reduced in size; aperture umbilical-extraumbilical, low arch, bordered by a narrow, often thickened, continuous lip; in edge view chambers globular, spiral side flat, periphery broadly rounded (modified after Olsson and others, 2006, and Wade and others, 2016).

Size: Maximum diameter of holotype 0.30 mm (original measurement), 0.319 mm (re-measured this study); maximum thickness 0.217 mm (this study). All specimens restricted to <0.32 mm in size as per Bolli and Saunders (1985) and Wade and others (2016).

DISTINGUISHING FEATURES.—*Paragloborotalia nana* is distinguished from *P. opima* on size alone, with all specimens smaller than 0.32 mm attributed to *P. nana*. Previous authors have suggested that *P. nana* is more quadrate than *P. opima*, with a lower rate of chamber expansion. However, Wade and others (2016) conducted morphometric analyses on specimens of *P. opima* and *P. nana* from the equatorial Pacific Ocean and were unable to distinguish the forms on outline (quadrateness), or number of chambers, and concluded that size was the only effective means to separate the two forms.

Paragloborotalia nana differs from *P. siakensis* in typically having only 4 chambers in the final whorl, compared with 5 or 6 in *P. siakensis*, and in being distinctly less lobulate and less ovate in equatorial profile. As stated by Blow (1959), *P. continuosa* can be distinguished from *P. nana* by a more ovate outline and higher arched aperture. In addition, *P. continuosa* can attain sizes greater than *P. nana*. *Paragloborotalia pseudocontinua* is more lobulate and has a large, nearly circular, umbilical-extraumbilical aperture rimmed by the lip. It can be distinguished from *Parasubbotina varianta* by its lower rate of chamber expansion, and lower arched aperture, particularly in edge view. *Paragloborotalia nana* differs from bulla-less forms of *Globorotaloides suteri* (see Chapter 4, Fig. 4.10, this volume) by the less cancellate wall, more extraumbilical position of the aperture, and distinctive lip.

DISCUSSION.— Bolli and Saunders (1985) originally proposed the use of size as the principle criterion to distinguish *nana* and *opima* with specimens <0.32

mm assigned to *nana*. Spezzaferri (1994) rejected this size criterion because of the possible implication that *nana* was the juvenile and *opima* the adult of the same species. However, large-sized, 4-5 chambered *Paragloborotalia* have a short, distinct range in the mid- to early late Oligocene, while the smaller *nana* s.s. has a much longer range. In a quantitative study of *Paragloborotalia* size changes in the equatorial Pacific, Wade and others (2007, 2016) concluded that Bolli's size criteria for distinguishing the *opima-nana* plexus are robust. They documented a sharp decline in the sizes of 4 and 5 chambered *Paragloborotalia* within Chron C9n marking the highest occurrence of *P. opima* and the O5/O6 zonal boundary. We continue to favor the use of size as a primary criterion to distinguish *P. nana* from *P. opima* because the smaller *nana* co-occurs with its larger descendant *opima* in the mid Oligocene, but then continues to range beyond the highest occurrence of *opima* into the early Miocene (e.g., Leckie and others, 1993; Morgans and others, 2002; Wade and others, 2007, 2016).

PHYLOGENETIC RELATIONSHIPS.— According to Olsson and others (2006), *P. nana* evolved from *P. griffinoidea* in the middle Eocene by developing more inflated, embracing chambers, with a slower rate of chamber size increase in the ultimate whorl. We conclude here that *P. nana* was ancestral to *P. opima*, *P. pseudocontinua*, *P. siakensis*, *P. pseudokugleri*, *P. continua*, and *P. birnageae*.

TYPE LEVEL.— Sample JS 20 (TTOC 193265), *Globorotalia opima opima* zone, Ciperó Fm, Trinidad (same sample as holotype of *Globorotalia opima opima*).

STRATIGRAPHIC RANGE.— Zone E13 to Zone M2. According to Blow (1979) and Toumarkine and Luterbacher (1985), *P. nana* first appeared in upper Eocene Zone E13. Forms transitional with its proposed ancestor, *P. griffinoidea*, have been reported as low as Zone E7 in Tanzania (Olsson and others, 2006). *Paragloborotalia nana* persisted into the lower Miocene Zone N4 (Kennett and Srinivasan, 1983). Jenkins (1978) reports a last occurrence of *P. nana* in the lower Miocene *G. woodi* Zone in the southeast Atlantic Ocean (DSDP Site 362). A number of oceanic sites show highest occurrences within the early Miocene (Chaisson and Leckie, 1993; Pearson and Chaisson, 1997; Spezzaferri, 1998).

GEOGRAPHIC DISTRIBUTION.— Global in low and mid-latitudes.

STABLE ISOTOPE PALEOBIOLOGY.— Several studies (e.g., Wade and others, 2007; Pearson and Wade, 2009; Matsui and others, 2016) indicate that *P. nana* calcified in the upper thermocline. However, some records have indicated a more positive oxygen isotope signature suggesting a deeper thermocline habitat (e.g., Douglas and Savin, 1978; Poore and Matthews, 1984) while Boersma and Shackleton (1978) suggested a mixed-layer habitat.

REPOSITORY.— Holotype (USNM P5661) deposited at the Smithsonian Museum of Natural History, Washington, D.C.

Paragloborotalia opima (Bolli, 1957)

PLATE 5.8, FIGURES 1-16

Globorotalia opima opima Bolli, 1957:117-118, pl. 28, figs. 1a-c (holotype), fig. 2 (paratype) [Oligocene *Globorotalia opima opima* Zone, Ciperó Fm., Trinidad; max. diameter = 0.45 mm (re-measured herein)].—Berggren and Am-durer, 1973, pl. 27, fig. 7 [upper Oligocene Zone P21, DSDP Hole 17B, South Atlantic Ocean].—Stainforth and others, 1975:300, fig. 132.1-7 [Oligocene *Globorotalia opima opima* Zone, Ciperó Fm., Trinidad; max. diameters = 0.40 mm, 0.39 mm, 0.39 mm, 0.35 mm, 0.41 mm, 0.33 mm, and 0.35 mm], 8 (holotype drawing reproduced).—Toumarkine, 1978:714, pl. 8, figs. 7, 8 [mid Oligocene *Globorotalia opima opima* Zone, DSDP Site 360, southeast Atlantic Ocean; max. diameters = 0.34 mm and 0.34 mm].—Stainforth and Lamb, 1981:25, pl. 4, fig. 2a-c [Oligocene *Globorotalia opima opima* Zone, Atlantic Slope Project corehole 5B, western North Atlantic Ocean; max. diameter = 0.55 mm].—Bolli and Saunders, 1985:202, fig. 26.30a-c (holotype re-illustrated), figs. 26.24-29 (given as "paratypes", actually topotypes) [Oligocene *Globorotalia opima opima* Zone, Ciperó Fm., Trinidad; max. diameters = 0.43 mm, 0.47 mm, 0.48 mm, 0.53 mm, 0.50 mm, and 0.53 mm].—Martinotti, 1986, pl. 1, fig. 1 [Oligocene *Globorotalia opima opima* Zone, Ashqelon 4 Borehole, Israel; max. diameter = 0.41 mm], pl. 1, fig. 2 [Oligocene *Globorotalia opima opima* Zone, Shiqma 1 Borehole, Israel; max. diameter = 0.36 mm], pl. 1, fig. 3 [Oligocene *Globorotalia opima opima* Zone, Ashdod 1 Borehole, Israel; max. diameter = 0.36 mm], pl. 1, fig. 4 [Oligocene *Globorotalia opima opima* Zone, Beeri structure Hole 4, Israel; max. diameter = 0.45 mm].

- Globorotalia (Turborotalia) opima opima* Bolli.—Blow, 1969:353, pl. 39, fig. 3 [lower Oligocene Zone N1 (=P20), Cipero Fm., Trinidad; max. diameter = 0.60 mm].—Jenkins, 1971:128, pl. 13, figs. 354-357 [Oligocene, Duntroonian-Whaingaroan Stage, South Island, New Zealand; max. diameter = 0.49 mm and 0.40 mm].—Quilty, 1976:646, pl. 13, figs. 12, 13 [Oligocene Zone N2/N3, DSDP Hole 320B, southeastern Pacific Ocean; max. diameters = 0.34 mm and 0.37 mm].
- Globorotalia opima* Bolli.—Postuma, 1971:344, pl. on p. 345 [Oligocene, Cipero Fm., Trinidad; max. diameter = 0.50 mm].
- Turborotalia (Turborotalia) opima opima* (Bolli).—Fleisher, 1974:1036, pl. 19, fig. 12 [lower Oligocene Zone P20/P21, DSDP Site 223, Arabian Sea; max. diameter = 0.45 mm].
- Paragloborotalia opima* (Bolli).—Cifelli and Scott, 1986, figs. 1c and 1g [?Trinidad].—Leckie and others, 1993:125, pl. 7, figs. 3 [upper Oligocene Subzone P21b, ODP Hole 803D, Ontong Java Plateau, western equatorial Pacific Ocean; max. diameter = 0.54 mm], 4 [upper Oligocene Zone P22, ODP Hole 628A, Little Bahama Bank, western North Atlantic Ocean; max. diameter = 0.42 mm (?specimen reworked)], 9 [lower Oligocene Zone P20, ODP Hole 803D, Ontong Java Plateau, western equatorial Pacific Ocean; max. diameter = 0.44 mm].—Olsson and others, 2006, pl. 5.8, figs. 13-15 (holotype re-illustrated by SEM).—Rincón and others, 2007:305, pl. 2, fig. 5a-c [upper Oligocene *Paragloborotalia opima* Zone, Carmen Fm., Colombia; max. diameter = 0.41 mm].—Wade and others, 2007:pl. I, figs. n-o [upper Oligocene Zone O5, ODP Hole 1218B, equatorial Pacific Ocean; max. diameters = 0.40 mm, 0.46 mm].—Wade and others, 2016:440-441, pl. 1, fig. 2 (holotype SEM re-illustrated), pl. 1, fig. 3 (new SEM of paratype of *Globorotalia opima opima* Bolli), pl. 3, figs. 1a-1d, 4a-4d, pl. 4, fig. 5 [lower Oligocene Zone O3/O4, IODP Hole U1334A, equatorial Pacific Ocean; max. diameters = 0.35 mm, 0.37 mm, 0.48 mm], pl. 3, figs. 2a-2d, pl. 4, figs. 1a-4, pl. 5, figs. 1a-5d [upper Oligocene Zone O5, IODP Hole U1334A, equatorial Pacific Ocean; max. diameters = 0.35 mm, 0.38 mm, 0.40 mm, 0.46 mm, 0.49 mm, 0.50 mm, 0.51 mm, 0.54 mm], pl. 3, figs. 3a-3b [lower Oligocene Zone O1/O2, IODP Hole U1334A, equatorial Pacific Ocean; max. diameter = 0.36 mm].
- Paragloborotalia opima opima* (Bolli).—Spezzaferri and Premoli Silva, 1991:248, pl. XI, figs. 5a-6b [lower Oligocene Subzone P21a, DSDP Hole 538A, Gulf of Mexico; max. diameter = 0.40 mm and 0.38 mm].—Spezzaferri, 1994:53-54, pl. 20, figs. 5a-c (reproduced from Spezzaferri and Premoli Silva, 1991).
- Specimen ex interc. *Globorotalia (Turborotalia) opima nana/G. (T.) opima opima* (Bolli).—Blow, 1969, pl. 39, fig. 2 [lower Oligocene Zone N1 (=P20), Cipero Fm., Trinidad; max. diameter = 0.37 mm].
- Globorotalia nana* Bolli.—Postuma, 1971:340, pl. on p. 341 [Oligocene, Trinidad; max. diameter = 0.33 mm]. [Not Bolli, 1957.]
- Globorotalia opima nana-opima opima* Bolli transition.—Bolli and Saunders, 1985, fig. 26.21-23 [Oligocene *Globorotalia opima opima* Zone, Cipero Fm., Trinidad; max. diameters = 0.42 mm, 0.38 mm, and 0.40 mm].
- Paragloborotalia opima-nana* (Bolli) transition.—Wade and others, 2007:pl. I, figs. h-m [upper Oligocene Zone O5, ODP Hole 1218B, equatorial Pacific Ocean; max. diameters = 0.35, 0.35 mm, 0.36 mm, and 0.37 mm].
- Paragloborotalia pseudocontinua* (Jenkins).—Wade and others, 2007, pl. II, figs. l, m [upper Oligocene Zone O5, ODP Hole 1218B, equatorial Pacific Ocean; max. diameters = 0.47 mm and 0.40 mm (scales corrected)]. [Not Jenkins, 1967.]
- Not *Globorotalia opima* subsp. *opima* Bolli.—Jenkins, 1960:366, pl. 5, fig. 3a-c [upper Oligocene pre-*Globorotalia dehiscens dehiscens* Zone, Lakes Entrance Oil Shaft, Victoria, Australia] (= *Ciperoella ciperoensis*).
- Not *Turborotalia siakensis opima* (Bolli).—Chaproniere, 1981:124, figs. 11.Ca-c [Oligocene Zone N3/N4, Ashmore Reef No. 1 well, eastern Indian Ocean; max. diameter = 0.31 mm] (= *P. nana*).
- Not *Paragloborotalia opima opima* (Bolli).—Cifelli, 1982 (partim), pl. 2, fig. 1 [upper Oligocene *Globorotalia opima* Zone, Cipero Fm., Trinidad (given in plate caption as *Globorotalia opima*); max. diameter 0.25 mm] (?= *Globorotaloides*), fig. 2 [upper Oligocene *Globorotalia opima* Zone, Cipero Fm., Trinidad (given in plate caption as *Globorotalia opima*); max. diameter 0.22 mm] (= *P. nana*).
- Not *Paragloborotalia opima* (Bolli).—Li and others, 2005:19, pl. 2, figs. 25, 26 [upper Oligocene Zone P22, ODP Site 1148, South China Sea; max. diameter of specimens = <0.30 mm], figs. 27-29 [lower Oligocene Zone P21a, ODP Site 1148, South China Sea; max. diameter of

Plate 5.8 *Paragloborotalia opima* (Bolli, 1957)

1-3 (holotype, USNM P5659), *Globorotalia opima opima* Zone, Cipero Fm., Trinidad (max. size 0.45 mm); 4, 8, (same specimen, Wade and others, 2007; pl. I, figs. i, j), Zone O5, ODP Hole 1218B, equatorial Pacific Ocean (max. size 0.35 mm); 5-7 (same specimen, Wade and others, 2016; pl. 3, figs. 2a-c), Zone O5, IODP Hole U1334A, equatorial Pacific Ocean (max. size 0.35 mm); 9-11 (paratype, USNM P5660), *Globorotalia opima opima* Zone, Cipero Fm., Trinidad (max. size 0.48 mm); 12, Zone O2-O4, Sample PR139/11, Juana Diaz Fm., Puerto Rico (max. size 0.39 mm); 13-16 (13, 14, same specimen), RDL sample 410, *Globorotalia opima opima* Zone, Cipero Fm., Trinidad (max. size 0.35 mm, 0.35 mm, 0.36). Scale bar: 1-16 = 100 μ m.

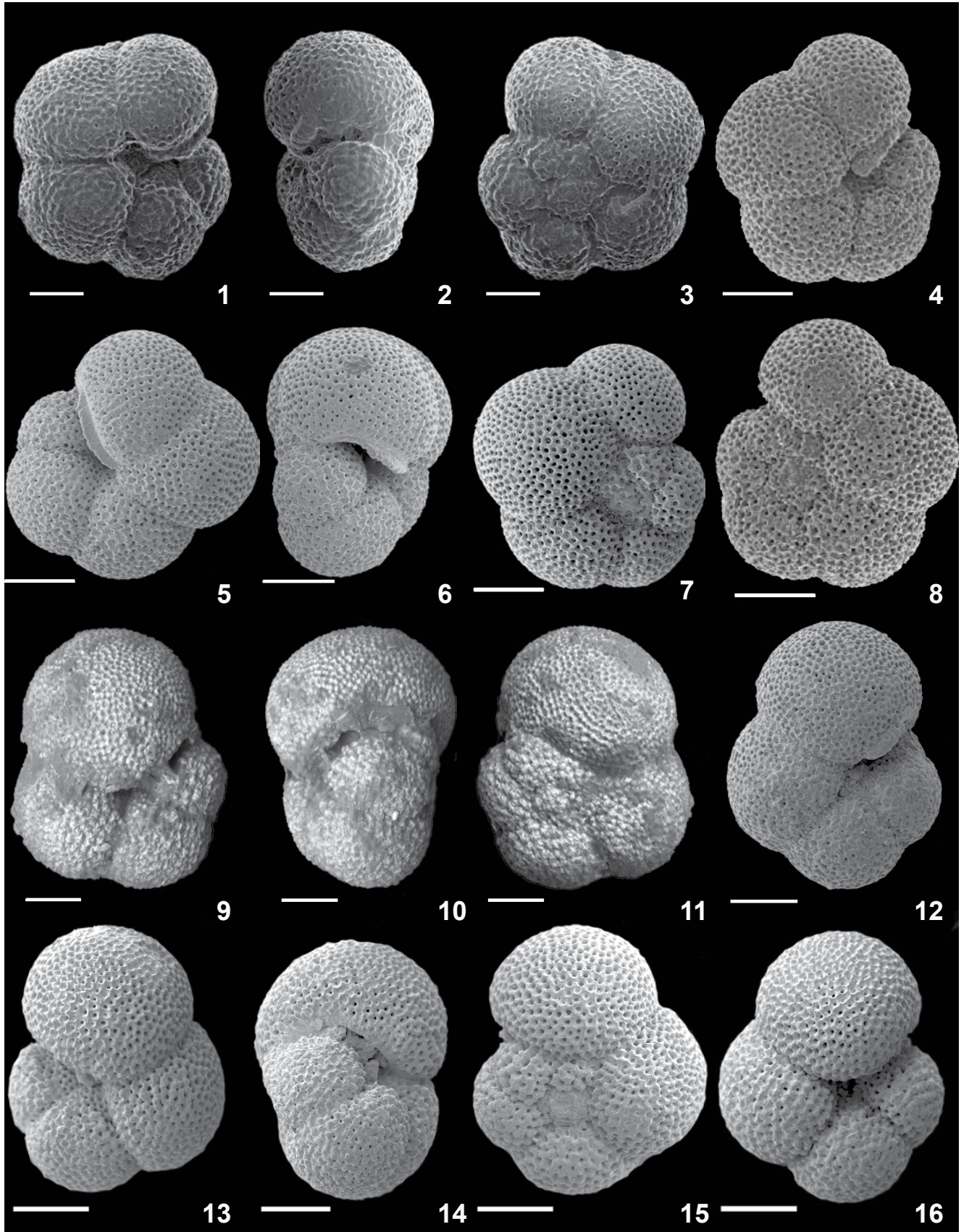


PLATE 5.8 *Paragloborotalia opima* (Bolli, 1957)

specimens = <0.30 mm], fig. 30 [Oligocene Zone P22 (?reworked), ODP Site 1148, South China Sea; max. diameter of specimen = 0.27 mm] (= *P. nana*).

Not *Paragloborotalia opima* (Bolli) transitional form to *P. nana* (Bolli).—Rincón and others, 2007:305, pl. 10, fig. 6 a-c [lower Oligocene *Turborotalia ampliapertura* Zone, San Jacinto Fm., Colombia; max. diameter = 0.29 mm] (= *P. nana*).

DESCRIPTION.

Type of wall: Normal perforate, coarsely cancellate, probably sparsely spinose in life, heavy game-genetic calcification is often present.

Test morphology: Test large in size; very low trochospiral, generally quadrate to slightly lobulate in equatorial outline, chambers globular, inflated, embracing; commonly 4, sometimes 4½-5 chambers in ultimate whorl, increasing moderately in size; in spiral view chambers moderately to strongly inflated, spherical to subspherical, arranged in 2-2½ whorls, sutures depressed, radial, ultimate chamber may be slightly reduced in size; in umbilical view chambers strongly inflated, spherical, sutures depressed, radial, umbilicus very narrow to nearly closed, moderately deep, sometimes closed off by surrounding chambers, ultimate chamber may be slightly reduced in size; aperture umbilical-extraumbilical, low arch, bordered by a narrow, often thickened, continuous rim or lip; in edge view chambers globular, spiral side nearly flat to slightly depressed, periphery broadly rounded.

Size: Maximum diameter of holotype 0.45 mm, maximum thickness 0.31 mm (this study).

DISTINGUISHING FEATURES.— The criterion for separating *P. opima* from *P. nana* is strictly size, with <0.32 mm being the size criterion for recognition of *P. nana* (Bolli and Saunders, 1985; Wade and others, 2016). The holotype of *P. opima* has 5 chambers in the final whorl, and a diminutive final chamber (Pl. 5.8, Figs. 1-3). As stated by Bolli and Saunders (1985), the 5 chambered forms are typically rare and we consider the 4 chambered paratype with its large, embracing final chamber (Pl. 5.8, Figs. 9-11) to be more characteristic of the form based on our experiences. In general, the lip in *P. opima* is less pronounced and thinner than in *P. nana*. The position of the final chamber against the first chamber (of the final whorl) also prevents the cross-shaped suture pattern that is a common feature of *P. nana* s.s. Greater chamber inflation is common in the largest specimens of *P. opima*, resulting in a bulbous final

chamber (Wade and others, 2016). In addition, some larger specimens of *opima* may display a more rapid expansion in thickness resulting in the slight depression of the inner spire.

Paragloborotalia opima is distinguished from *P. pseudocontinua* by its more compact test and lower arched aperture. Bolli and Saunders (1985) suggested that the forms they considered as *opima-nana* transitions (between 0.32 and 0.39 mm), which more commonly have 5 chambers, may be ancestral to *P. mayeri*. We reject this hypothesis and consider *P. siakensis* as the direct ancestor of *P. mayeri*. *Paragloborotalia opima* can be distinguished from *P. mayeri*, by its lower arched aperture, radial spiral sutures, and fewer number of chambers in the final whorl. It can be distinguished from *P. siakensis* by its rounder, more embracing chambers, less well developed lip, and less lobulate periphery. *Paragloborotalia opima* is distinguished from *Parasubbotina varianta* by a slower rate of chamber growth and inflation, more embracing chambers, a lower aperture, and generally more heavily encrusted test.

DISCUSSION.— As *P. opima* and *P. nana* are distinguished by their size (e.g., Bolli and Saunders, 1985; Wade and others, 2016) it is very important to determine the size of their holotypes. Bolli (1957) stated that the holotype of *P. opima* was 0.55 mm, however, our investigations indicate this is incorrect. Adding to the confusion, the holotype of *P. opima* was first illustrated by SEM in Olsson and others (2006) (pl. 5.8, figs. 13-15), however, the scale bar in the figure is not accurate. Through this work we re-examined the holotype at the USMN have determined that the 5 chambered holotype specimen (USNM P5659) is 0.45 mm, and the 4 chambered paratype (USNM 5660) is 0.48 mm.

Bolli and Saunders (1985) referred to specimens of the *opima-nana* plexus that were between 0.32 and 0.39 mm as ‘transitional’ intermediate forms. However, given the stratigraphic utility of *P. opima* it is critical to classify the transitional forms for recognition of the base of Zone O6. Morphometric analysis was conducted on specimens of the *opima-nana* plexus from IODP Site U1334 in the equatorial Pacific Ocean by Wade and others (2016). They determined that shape outline (quadrateness) and number of chambers were not useful criteria to separate the two forms and concluded that size was the only delimiting character. The ‘transitional’ forms of Bolli and Saunders (1985) (i.e., >0.32 mm) are thus consistent with *P. opima*.

Both *P. nana* and *P. opima* typically possess the same number of chambers in the final whorl, indicating that the increased size in *P. opima* is not a form of heterochrony but gigantism of the ancestral *P. nana* form (Wade and others, 2016).

PHYLOGENETIC RELATIONSHIPS.— Evolved from *P. nana* in lower Oligocene Zone O2, and did not leave any descendants.

TYPE LEVEL.— Sample JS 20 (TTOC 193265), *Globorotalia opima opima* Zone, Ciperó Fm, Trinidad (same sample as holotype of *Globorotalia opima nana*).

STRATIGRAPHIC RANGE.— *Paragloborotalia opima* has a restricted stratigraphic range relative to *P. nana* and *P. siakensis*, a feature that has been utilized in biostratigraphic schemes (e.g., Bolli, 1957; Bolli and Saunders, 1985; Berggren and others, 1995; Berggren and Pearson, 2005; Wade and others, 2011). Its base occurrence has been calibrated to 30.6 Ma (Berggren and others, 1995). The highest occurrence of *P. opima* defines the O5/O6 zonal boundary at 27.5 Ma within Chron C9n (Wade and others, 2007, 2011, 2016).

GEOGRAPHIC DISTRIBUTION.— Cosmopolitan, including the tropics and high northern latitudes, e.g., Site 407 (63°N) (Poore, 1979). Larger and more abundant in eutrophic environments (Wade and others, 2007, 2016).

STABLE ISOTOPE PALEOBIOLOGY.— Multispecies stable isotope analyses by Biolzi (1983) and Poore and Matthews (1984) suggest a thermocline habitat, consistent with Wade and others (2007) and Matsui and others (2016).

REPOSITORY.— Holotype (USNM P5659) and paratype (USNM P5660) deposited at the Smithsonian Museum of Natural History, Washington, D.C.

***Paragloborotalia pseudocontiniosa* (Jenkins, 1967)**

PLATE 5.4, FIGURES 9-16

(Pl. 5.4, Figs. 9-11: new SEMs of holotype of *Globorotalia nana pseudocontiniosa* Jenkins)

(Pl. 5.4, Figs. 13-15: new SEMs of paratype of *Globorotalia nana pseudocontiniosa* Jenkins)

Globorotalia opima Bolli subsp. *continiosa* Blow.—Jenkins, 1960:366, pl. 5 (partim), figs. 4a-c [lower Miocene *Globigerinoides triloba triloba* Zone, Lakes Entrance Oil Shaft, Victoria, Australia]. [Not Blow, 1959.]

Globorotalia continiosa Blow.—Jenkins, 1966:9-10, pl. 2, figs. 9a-c [lower Miocene, lower Aquitanian stage, southwest France]. [Not Blow, 1959.]

Globorotalia nana pseudocontiniosa Jenkins, 1967:1074-1077, fig. 4.20-22 (holotype), fig. 4.23-25 (paratype) [lower Miocene, *G. (G.) woodi connecta* Zone, Otaian Stage, North Island, New Zealand].

Globorotalia (Turborotalia) nana pseudocontiniosa Jenkins.—Jenkins, 1971:124-125, pl. 12, figs. 336-341 [re-illustrated from Jenkins, 1967, pl. 1074, figs. 4.20-25].

Globorotalia pseudocontiniosa Jenkins.—Berggren and Am-durer, 1973, pl. 27, figs. 11-15 [lower Miocene Zone N4 and Zone N5, DSDP Site 18, South Atlantic Ocean].—

Jenkins, 1977:307, pl. 4, figs. 1, 2 [lower Miocene *G. trilobus trilobus* Zone, Sealab Trial Borehole, English Channel].—Jenkins, 1978, pl. 1, figs. 14-16 [lower Miocene *G. woodi connecta* Zone, DSDP Site 360, southeast Atlantic Ocean].—

Hoskins, 1984, figs. 7.7-12 [lower Miocene *G. trilobus trilobus* Zone, Awamoan Stage, New Zealand], figs. 8:5-6 [middle Miocene *P. glomerosa curva* Zone, Clifdenian Stage, New Zealand], figs. 8:7-9 [lower Miocene *G. woodi connecta* Zone, Otaian Stage, New Zealand].—

Jenkins and Srinivasan, 1986:813, pl. 5, figs. 2-4 [lower Oligocene *G. angiporoides* Zone, DSDP Site 593, Challenger Plateau, southwest Pacific Ocean].

Paragloborotalia pseudocontiniosa (Jenkins).—Cifelli and Scott, 1986, figs. 1d and 1h [lower Miocene, *G. (G.) woodi connecta* Zone, Otaian Stage, North Island, New Zealand].—

Spezzaferri and Premoli Silva, 1991:248, pl. XI, figs. 1a-c [lower Oligocene Subzone P21a, DSDP Hole 538A, Catoche Knoll, Gulf of Mexico], pl. XII, figs. 1a-c, 2a [lower Oligocene Zone P20, DSDP Hole 538A, Gulf of Mexico].—

Spezzaferri, 1994:54, pl. 20, figs. 1a-c [re-illustration of specimen from Spezzaferri and Premoli Silva, 1991, pl. XI, figs. 1a-c].—

Morgans and others, 2002, figs. 14M-O [lower Miocene *G. incognita* Zone, Altonian Stage, North Island, New Zealand].

Not *Paragloborotalia pseudocontiniosa* (Jenkins).—Li and others, 2003b:16, pl. 2, fig. 26 [lower Oligocene Zone P18-P19, ODP Hole 1134A, Great Australian Bight, Indian Ocean], pl. 2, figs. 27, 28 [upper Oligocene Zone P22, ODP Hole 1134A, Great Australian Bight, Indian Ocean] (= *P. semivera*).—

Wade and others, 2007:pl. II, figs. L, M [upper Oligocene Zone O5, ODP Hole 1218B, equatorial Pacific Ocean](= *P. opima*).

Not *Paragloborotalia pseudocontiniosa* (Jenkins).—Li and others, 2003b:16, pl. 2, fig. 26 [lower Oligocene Zone P18-P19, ODP Hole 1134A, Great Australian Bight, Indian Ocean], pl. 2, figs. 27, 28 [upper Oligocene Zone P22, ODP Hole 1134A, Great Australian Bight, Indian Ocean] (= *P. semivera*).—Wade and others, 2007:pl. II, figs. L, M [upper Oligocene Zone O5, ODP Hole 1218B, equatorial Pacific Ocean](= *P. opima*).

DESCRIPTION.

Type of wall: Normal perforate, coarsely cancellate, probably sparsely spinose in life, heavy game-

togenetic calcification is often present.

Test morphology: Test small to medium in size; low trochospiral, quadrate and lobulate in equatorial outline, chambers globular, inflated, embracing; some specimens may develop a kummerform final chamber; 4 chambers in ultimate whorl, increasing moderately to rapidly in size; in spiral view chambers moderately inflated, spherical, arranged in 2½-3 whorls, sutures slightly depressed, radial; in umbilical view chambers strongly inflated, sutures slightly depressed, radial, forming a cross, umbilicus narrow, moderately deep; aperture umbilical-extraumbilical, moderate to high loop-shaped arch, bordered by a narrow, often thickened, continuous lip; in edge view chambers spherical, spiral side slightly convex, periphery broadly rounded.

Size: Maximum diameter of holotype 0.23 mm (original measurement); 0.27 mm (remeasured this study); thickness of holotype 0.19 mm. Maximum diameter of illustrated paratype 0.28 mm, thickness 0.20 mm (this study).

DISTINGUISHING FEATURES.— *Paragloborotalia pseudocontinua* is characterized by its spherical chambers that increase moderately rapidly as added. It is differentiated from *P. continua* by its more umbilical-extraumbilical, high arched aperture with a thickened rim (although the paratype more closely resembles *continua*), and more spherical chambers. The aperture in the holotype of *pseudocontinua* is loop shaped and distinctly higher than in the holotype of *continua*; the aperture of *continua* is more extraumbilical in position. It is distinguished from *nana* in having a higher arched aperture, a faster rate of chamber expansion, a more ovate test, and lobulate equatorial profile, and from both *nana* and *opima* in having a high loop-shaped aperture and moderate spire. *Paragloborotalia pseudocontinua* is also smaller than *P. opima*.

It is differentiated from *incognita* by its greater spiral-side convexity, radial spiral sutures, and more spherical final chamber. The rate of chamber inflation in *P. pseudocontinua* is similar to *P. incognita* but greater than in *P. continua*; the final chamber of *pseudocontinua* and *incognita* is distinctly more inflated than in *continua*, which also has a more extraumbilical aperture than the latter two taxa. Basically, *incognita* is larger and has a flatter spiral side and slightly curved spiral sutures, while *continua* differs from *pseudocontinua* in having a more extraumbilical aperture; there are gradations between all of these end-members.

However, *P. pseudocontinua* has also previously been synonymised with *P. incognita* (e.g., Berggren and others, 1983; Kennett and Srinivasan, 1983; Li and others, 1992), indicating that there are subtle differences in the test morphology between these two taxa. Here we consider both to be valid taxa despite their similar morphologies. In addition, *pseudocontinua* ranges back to the early Oligocene, while *incognita* has its first occurrence in the earliest Miocene. The flatter spiral side and slightly curved sutures of *incognita* display advanced, transitional features between *P. pseudocontinua* and *Globoconella zealandica*.

Paragloborotalia pseudocontinua closely resembles *semivera*. Jenkins (1971) stated that most of the paratypes in the type sample of *semivera* have 4 chambers in the final whorl, which he classified as *G. (T) nana pseudocontinua* Jenkins (also Hoskins, 1984). Jenkins (1971) and Hoskins (1984) also noted a complete range of variation between the two (sub)species in this lower Miocene sample (Awamoan Stage, *G. trilobus trilobus* Zone). *Paragloborotalia pseudocontinua* is differentiated from *semivera* by its higher, almost circular aperture, and in possessing fewer chambers (4) in the final whorl. Some specimens of *pseudocontinua* may have a kummerform final chamber (Hoskins, 1984; figs. 7:10-12). *Paragloborotalia pseudocontinua* is distinguished from *acrostoma* by having only 4 chambers in the final whorl; we propose that *pseudocontinua* gave rise to *acrostoma* in the early Miocene.

DISCUSSION.— Jenkins (1960) described the occurrence of *Globorotalia opima* subsp. *continua* Blow in two distinct stratigraphic levels in the Lakes Entrance oil shaft of Victoria, in southeastern Australia. The lower occurrences are confined to the upper Oligocene-lower Miocene pre-*Globoquadrina dehiscens dehiscens* to *Globigerinoides triloba triloba* Zones, while the younger forms are limited to the upper Miocene *Globorotalia menardii miotumida* Zone. According to Jenkins (1960:366) these older forms “are a little larger” and the aperture is “a little larger” than the very similar younger forms. The two light microscope photomicrograph hypotypes illustrated by Jenkins and representing the two distinct levels, are indistinguishable. Jenkins (1967) went on to describe the older forms as a new subspecies: *Globorotalia nana pseudocontinua*. Jenkins (1967: 1076) concluded that the two taxa were homeomorphs; *G. mayeri continua* evolved from *Globorotalia mayeri mayeri* “well after the extinction of *G. nana pseudo-*

continua”.

Blow (1959) reported a range for *Globorotalia opima* subsp. *continua* from the lower Miocene *Catapsydrax stainforthi* Zone to the lower Pliocene *Sphaeroidinella seminulina* Zone. According to Jenkins (1967:1076), *pseudocontinua* and *continua* are very similar and “morphologically indistinguishable”. Hoskins (1984, figs. 8:1-4) illustrated specimens identified as *continua* from the middle Miocene *O. suturalis* Zone (Lillburnian Stage, New Zealand) that closely resemble *pseudocontinua* based on the large spherical final chamber. Further study may warrant synonymizing *pseudocontinua* with *continua*. However, for now, we will continue to recognize two distinct taxa (e.g., Jenkins, 1971; Spezzaferri, 1994); *P. pseudocontinua* is here considered to be the Oligocene morphotype characterized by a slightly convex spiral side and more umbilical aspect of the high arched aperture, while *P. continua* is a longer ranging Miocene morphotype characterized by its flat spiral side and more extraumbilical aspect of the moderately high, comma-shaped aperture.

PHYLOGENETIC RELATIONSHIPS.— *Paragloborotalia pseudocontinua* was likely derived from *nana* in the mid-Oligocene (Zone O4). Jenkins and Srinivasan (1986) report the lowest occurrences of 5 chambered forms, attributed to *semivera*, at about the same stratigraphic level as the lowest occurrences of *pseudocontinua*. Based on the close similarity of the two taxa discussed above, we propose that 4 chambered *pseudocontinua* was the direct ancestor of the 5 chambered *semivera*. *Paragloborotalia pseudocontinua* also gave rise to *incognita* near the time of the Oligocene/Miocene boundary by becoming flatter on the spiral side, having slightly curved spiral sutures, and in having a subspherical final chamber that is slightly elongated in the direction of coiling. We propose that *pseudocontinua* gave rise to *acrostoma* in the early Miocene by increasing the number of chambers in the final whorl to 5.

TYPE LEVEL.— Lower Miocene *Globigerina woodi connecta* Zone, Pareora Series, Otaian Stage, Pargarenga Harbour section, New Zealand.

STRATIGRAPHIC RANGE.— Zone O2 to Zone M5. The species spans the Oligocene and ranges into the middle Miocene (Spezzaferri, 1994), however there

are very few studies in which *P. pseudocontinua* is a common component of Miocene material. Jenkins (1967) states that *Globorotalia nana pseudocontinua* (= *P. pseudocontinua*) ranges from the mid-Oligocene (Whaingaroan Stage, *G. euapertura* Zone) to lower middle Miocene (lower Lillburnian Stage, *O. suturalis* Zone) and does not overlap with middle Miocene *G. mayeri continua* (= *P. continua*). In the southeast Atlantic Ocean, the last occurrence of *P. pseudocontinua* is in the lower Miocene *Globigerinoides trilobus trilobus* Zone of DSDP Sites 360 and 362, whereas *G. mayeri continua* is reported to occur from the middle Miocene *G. mayeri mayeri* through the upper Miocene *G. conomiozea* Zone (Jenkins, 1978). A similar stratigraphic range for *Globorotalia (Turborotalia) pseudocontinua* is reported for DSDP Sites 279, 281, and 282 in the southwest Pacific (Jenkins, 1975). Poore (1984) recorded a lowest occurrence of *pseudocontinua* within lower Oligocene Zone OL2 (= ~O2) at DSDP Site 522 in the southeast Atlantic Ocean, and a highest occurrence in the lowermost Miocene Subzone M1a. Spezzaferri (1994) reported a range from lower Oligocene Subzone P21a (= O3/4) to within the middle Miocene based on her detailed study of numerous deep sea sites. Jenkins and Srinivasan (1986) also report a first occurrence of *pseudocontinua* in lower Oligocene Subzone P21a from the southwest Pacific Ocean. In a review paper of southern mid- and high latitude planktonic foraminiferal biostratigraphy and chronostratigraphy, Jenkins (1993) reported a lowest occurrence in lower Oligocene Zone P19.

GEOGRAPHIC DISTRIBUTION.— Cosmopolitan with recorded occurrences in the southwest Pacific Ocean (DSDP Leg 29; Jenkins, 1975); southeast Atlantic Ocean (DSDP Leg 40, Jenkins, 1978; DSDP Leg 73, Poore, 1984); English Channel, and type Aquitani-Burdigalian (Jenkins, 1966, 1977).

STABLE ISOTOPE PALEOBIOLOGY.— No data available. Specimens analyzed by Wade and others (2007) are now considered *P. opima*.

REPOSITORY.— New Zealand Geological Survey, Holotype (TF 1530) and 3 paratypes.

***Paragloborotalia pseudokugleri* (Blow, 1969)**

PLATE 5.9, FIGURES 1-16

(Pl. 5.9, Figs. 1-3: new SEMs of holotype of *Globorotalia* (*Turborotalia*) *pseudokugleri* Blow)*Globorotalia* sp. cf. *G. kugleri* Bolli, 1957, pl. 28, figs. 7a-c. [*Globorotalia kugleri* Zone, Ciperio Fm., Trinidad].*Globorotalia* (*Turborotalia*) *pseudokugleri* Blow, 1969:391, pl. 10, figs. 4-6 [reproduced from Bolli, 1957, pl. 28, figs. 7a-c], pl. 39, figs. 5, 6 [*Globorotalia kugleri* Zone, Mosquito Creek, Ciperio Fm., Trinidad].—Brönnimann and Resig, 1971:1314, pl. 39, fig. 2 [upper Oligocene Zone N3, DSDP Hole 64.1, Ontong Java Plateau, western equatorial Pacific Ocean].—Quilty, 1976:646, pl. 13, figs. 16, 17 [lower Miocene Zone N4, DSDP Site 320, south-eastern Pacific Ocean].—Blow, 1979:193, pl. 10, figs. 4-6 [reproduced from Bolli, 1957, pl. 28, figs. 7a-c], pl. 39, figs. 5, 6 [reproduced from Blow, 1969, pl. 39, figs. 5-6].*Globorotalia* cf. *pseudokugleri* Blow.—Jenkins and Orr, 1972:1103, pl. 31, figs. 2, 3 [reworked into the Pliocene *G. fistulosus* Zone, DSDP Site 76, eastern Pacific Ocean].*Globorotalia pseudokugleri* Blow.—Krasheninnikov and Pflaumann, 1978:593, pl. 6, figs. 4-6 ["Oligocene", DSDP Site 366, eastern equatorial Atlantic Ocean].—Poore, 1979:471, pl. 10, fig. 6 [upper Oligocene Zone P22, DSDP Site 407, North Atlantic Ocean].—Poore, 1984:444, pl. 2, figs. 8, 9 [upper Oligocene Zone OL6, DSDP Site 522, southern Angola Basin, South Atlantic Ocean].—Vincent and Toumarkine, 1990:803, pl. 3, figs. 6, 7 [lower Miocene Zone N4, ODP Site 707, Mascarene Plateau, western equatorial Indian Ocean].*Globorotalia* (*Fohsella*) *kugleri pseudokugleri* Blow.—Chaproniere, 1981:126, pl. 12, figs. D, E [upper Oligocene to lower Miocene Cartier beds, Ashmore Reef No. 1 well, northwest Australia]."*Globorotalia*" *pseudokugleri* Blow.—Premoli Silva and Spezzaferri, 1990:303, pl. 3, fig. 1a-c [upper Oligocene Zone P22, ODP Hole 709B, Madingley Rise, equatorial Indian Ocean].*Paragloborotalia pseudokugleri* (Blow).—Spezzaferri and Premoli Silva, 1991:248-253, pl. XI, fig. 7a-c [upper Oligocene Zone P22, DSDP Hole 538A, Gulf of Mexico].—Spezzaferri, 1991:315, pl. 1, figs. 3a-d [reproduced from Premoli Silva and Spezzaferri, 1990, pl. 3, fig. 1a-c],

figs. 2a-3d [upper Oligocene Zone P22, ODP Hole 709C, Madingley Rise, western equatorial Indian Ocean].—Leckie and others, 1993:125 (partim), pl. 8, figs. 6-10, 14-16 [upper Oligocene Zone P22, ODP Hole 803D, Ontong Java Plateau, western equatorial Pacific Ocean], pl. 8, figs. 11-13 [upper Oligocene Zone P22, ODP Hole 628A, Little Bahama Bank, western North Atlantic Ocean].—Spezzaferri, 1994:56, pl. 23, figs. 1a-c [reproduced from Premoli Silva and Spezzaferri, 1990:303, pl. 3, fig. 1a-c], 2a-3b [reproduced from Spezzaferri, 1991, pl. 1, figs. 2a-3c].—Rögl, 1996:151-153, pl. 1, figs. 10-12 [lower Miocene, Rigoroso Fm., Piedmont Basin, Italy], pl. 2, figs. 3, 9 [Ciperio Fm, Trinidad].—Pearson and Chaisson, 1997:63, pl. 2, fig. 16 [upper Oligocene Zone P22, ODP Hole 926B, Ceara Rise, western equatorial Atlantic Ocean].

"*Paragloborotalia*" *pseudokugleri* (Blow).—Pearson and Wade, 2009:208, pl. 6, figs. 4-7 [upper Oligocene Zone O6 (=Zone O7), Ciperio Fm., Trinidad].?*Paragloborotalia pseudokugleri* (Blow).—Li and others, 2005:19, pl. 3, figs. 11-16 [upper Oligocene Zone P22, ODP Site 1148, South China Sea], 17-20 [lower Miocene Subzone N4a, ODP Site 1148, South China Sea].*Globorotalia kugleri* Bolli, 1957.—Postuma, 1971:134, pl. on p. 135 [*Globorotalia kugleri* Zone, San Fernando, Trinidad].—Stainforth and Lamb, 1981:26 (partim), pl. 7, figs. 4a-c [upper Oligocene *Globigerina ciperiensis* Zone, Atlantic Slope Project corehole 5B, western North Atlantic Ocean].—Poore, 1984:444, pl. 2, fig. 10 [upper Oligocene Zone OL6, DSDP Site 522, southern Angola Basin, South Atlantic Ocean] (note, specimen shown only in spiral view; stratigraphic position suggests it is *P. pseudokugleri*).—Bolli and Saunders, 1985:203 (partim), fig. 26.3a-c [reproduction of holotype drawing from Bolli, 1957, pl. 28, figs. 7a-c]. [Not Bolli, 1957.]*Globorotalia* (*Turborotalia*) *mendacis* Blow.—Brönnimann and Resig, 1971:1314, pl. 39, figs. 6-8 [lower Miocene Zone N4, DSDP Hole 64.1, Ontong Java Plateau, western equatorial Pacific Ocean].—Quilty, 1976:646, pl. 12, figs. 21, 22 [lower Miocene Zone N4, DSDP Site 320, southeastern Pacific Ocean]. [Not Blow, 1969.]Not "*Globorotalia*" *pseudokugleri* Blow.—Premoli Silva and Spezzaferri, 1990, pl. 3, fig. 3a-c [upper Oligocene Zone P22, ODP Hole 709B, Madingley Rise, western equatorial Indian Ocean] (= *Paragloborotalia kugleri*).Plate 5.9 *Paragloborotalia pseudokugleri* (Blow, 1969)**1-3** (holotype, USNM P5665), *Globorotalia kugleri* Zone, Ciperio Fm., Trinidad; **4, 8** (same specimen), Zone O7, ASP 5B/16/29-35" western North Atlantic Slope; **5-7** (same specimen), Zone M1, ODP Site 904/34/4, 139", New Jersey slope, North Atlantic Ocean; **9-11** (Premoli Silva and Spezzaferri, 1990; pl. 3, fig. 1a-c), Zone P22, ODP Hole 709B, Madingley Rise, equatorial Indian Ocean; **12, 16** (same specimen), ODP Hole 803D/35/6, 25-27 cm; **13-15** (same specimen), Zone M1, ODP Site 904/34/4, 139", New Jersey slope, North Atlantic Ocean. Scale bar: **1-7, 9-16** = 100 µm, **8** = 10 µm.

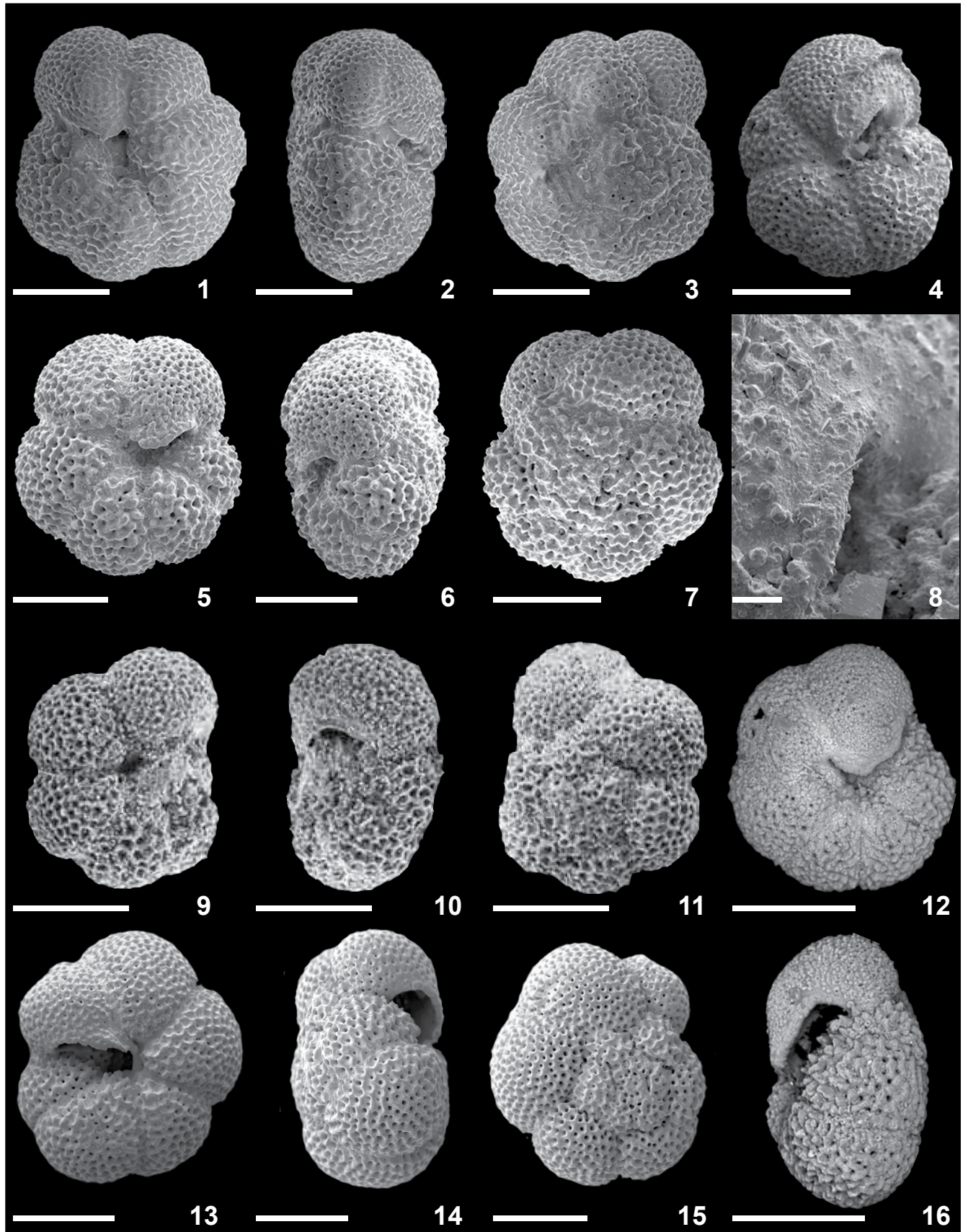


PLATE 5.9 *Paragloborotalia pseudokugleri* (Blow, 1969)

DESCRIPTION.

Type of wall: Normal perforate, coarsely cancellate, sparsely spinose in life, heavy gametogenetic calcification is often present.

Test morphology: Test small to medium in size; low trochospiral, moderately lobulate in equatorial outline, chambers wedge-shaped, moderately inflated, embracing; 5-7 chambers in the ultimate whorl, increasing slowly in size; in spiral view chambers arranged in 2½-3 whorls, sutures slightly depressed, radial to moderately curved, occasionally strongly curved; in umbilical view chambers wedge-shaped and moderately appressed, sutures slightly depressed, radial, umbilicus narrow, moderately deep; aperture umbilical-extraumbilical, a low slit or very low arch, bordered by a lip; in edge view chambers sub-spherical, spiral side flat to slightly convex, umbilical side slightly convex, periphery broadly rounded.

Size: Maximum diameter of holotype 0.31 mm (original measurement); 0.27 mm (remeasured this study); thickness 0.17 mm (this study).

DISTINGUISHING FEATURES.— A mosaic of characters separate *P. pseudokugleri* from *P. kugleri* (see the extended discussion under *P. kugleri* for means of distinguishing the two species). The most important feature, as described by Blow (1969:391), is that the test is “smoothly rounded, broad, not subacute peripheral margin”, a view that is supported here. Also the chambers are more inflated and less tightly appressed, the outline is more lobulate and circular, and the spiral side sutures are usually either straight or less strongly curved than is typical in *kugleri*. Earliest forms have straight and radial spiral sutures while later forms have a tendency for curvature, which can be quite marked (e.g., Spezzaferri and Premoli Silva, 1991, pl. 11, fig. 7a-c). *Paragloborotalia pseudokugleri* is distinguished from its likely ancestor *P. nana* by having 5 or more chambers in the final whorl (typically 6-7) and by having somewhat less inflated chambers. Early specimens of *P. pseudokugleri* are distinctly smaller than later Oligocene forms (Leckie and others, 1993; Spezzaferri, 1994). A 5½ chambered specimen, transitional between *nana* and *pseudokugleri* is shown on Plate 5.7, Figures 14-16.

DISCUSSION.— This species is discussed extensively under *P. kugleri*, above. The holotype chosen by Blow (1969) was originally a paratype of *kugleri*, as figured by Bolli (1957, pl. 28, fig. 7), from the same locality and

level (lower Miocene) as the holotype. Blow (1969) also figured two paratypes. We have also investigated with SEM (not shown) two of Blow’s unfigured paratypes (Natural History Museum, London, Nos P49740 and P49741). The second of these shows slight pinching of the periphery and strongly curved spiral sutures such that we would now assign it to *P. kugleri*.

There is considerable morphological evolution within the range of *P. pseudokugleri*, beginning with smaller (<150 µm) ‘primitive’ forms with 5-6 chambers in the final whorl and radial spiral sutures to larger (>150 µm) more ‘advanced’ forms, like the holotype, with up to 7 chambers in the final whorl and moderately curved spiral sutures (e.g., Spezzaferri, 1994). Even specimens with quite strongly curved spiral sutures are assigned to this morphospecies if they show a rounded periphery in edge view. A rounded periphery is the key feature of *pseudokugleri* s.s.

The nature of the wall has been the subject of some debate, with Spezzaferri (1991) and Rögl (1996) arguing that it is spinose and Pearson and Wade (2009; pl. 6, figs. 6a-f) arguing for a nonspinose wall, having illustrated some well-preserved forms with fused and aligned inner pore ridges which are more typical of the cancellate nonspinose wall. This debate affects the generic designation of the *pseudokugleri* – *kugleri* group. The issue was conclusively solved by the discovery of true spines projecting from a well-preserved specimen (Pl. 5.9, Fig. 8).

Li and others (2005) illustrated a suite of very small specimens from the South China Sea. Because of the small size we include these in questionable synonymy, noting that there may be confusion with *P. birnageae* and heavily encrusted *Turborotalita quinqueloba*. *Paragloborotalia pseudokugleri* is distinguished from *P. birnageae* by its more deeply depressed sutures and lobulate equatorial outline, broadly rounded peripheral margin, and higher aperture with smaller lip (*P. pseudokugleri* lacks an appressed final chamber with flap-like flange or apertural plate).

PHYLOGENETIC RELATIONSHIPS.— According to its author this species was a descendant of *Globorotalia mendacis* Blow, but that species is regarded by us as a synonym of *P. birnageae* and likely evolved from *P. pseudokugleri*. The ancestry of this species has been the subject of uncertainty because it is very rare near the base of its stratigraphic range and debate about the nature of the wall. Aze and others (2011) suggested that

it may have evolved from a nonspinose group. However, the spinose wall texture confirms that it is a true paragloborotaliid and probably evolved from *P. nana* by an increase in the number of chambers in the final whorl and in development of a more lobulate periphery. Rare intermediate morphologies have been observed near the beginning of the stratigraphic range (Pl. 5.7, Figs. 14-16; Premoli Silva and Spezzaferri, 1990; Leckie and others, 1993; Spezzaferri, 1994). The species gave rise to *P. kugleri* by gradual transition (see discussion under that species).

TYPE LEVEL.— Lower Miocene *Globorotalia kugleri* Zone ‘type locality’ sensu Bolli, 1957, Cipero Formation, Trinidad (equivalent to Zone M1). This is from the same sample as the holotype of *kugleri*. Blow’s figured paratype is from the *Globorotalia kugleri* Zone ‘co-type locality’, Mosquito Creek, Cipero Fm., Trinidad (equivalent to Zone M1). This locality was re-collected by Pearson and Wade (2009) where it is assigned to uppermost Oligocene Zone O6 (=O7 of this work) and hence is apparently slightly older than Bolli’s locality.

STRATIGRAPHIC RANGE.— The lowest occurrence of *P. pseudokugleri* has been observed in mid Zone P22 (Spezzaferri and Premoli Silva, 1991; Leckie and others, 1993; Spezzaferri, 1994) and was used to define the base of Zone O7 by Wade and others (2011), a datum that is supported by this study. The highest occurrence was reported by Blow (1969) as being about half way within the range of *P. kugleri* (i.e., within Zone M1), but subsequent authors have found it extending to near the top of the range (e.g., at Rio Grande Rise by Pujol, 1983; Ontong Java Plateau by Chaisson and Leckie, 1993; and at Ceara Rise by Pearson and Chaisson, 1997). Recent observations from IODP Site U1337 suggest a ~400 kyr offset between the extinction of *P. pseudokugleri* and *P. kugleri* (King and Wade, pers. comm., 2016).

GEOGRAPHIC DISTRIBUTION.— Cosmopolitan, most common at low and mid-latitudes, but in fact it has been found nearly as far north as the Reykjanes Ridge and east Greenland margin in the North Atlantic Ocean (Poore, 1979; Spezzaferri, 1998).

STABLE ISOTOPE PALEOBIOLOGY.— Poore and Matthews (1984), Pearson and others (1997), and Pearson and Wade (2009) all record this species as a mixed-layer dwelling form. Pearson and others (1997)

analyzed this species from a series of consecutive samples through several climate cycles across the Oligocene-Miocene transition, alongside four other species including “*Paragloborotalia mayeri*” (which would now be assigned to *P. siakensis*; see discussion under that taxon). *Paragloborotalia pseudokugleri* had similar oxygen isotope ratios to that species, consistent with a mixed-layer habitat for both taxa, but carbon isotope ratios are distinctly more positive than *P. siakensis*. This may be evidence of symbiotic association in *pseudokugleri* but not in *siakensis*; increasing $\delta^{13}\text{C}$ with size supports this suggestion (Pearson and Wade, 2009).

REPOSITORY.— Holotype (USNM P5665) deposited at the Smithsonian Museum of Natural History, Washington, D.C.

Paragloborotalia semivera (Hornibrook, 1961)

PLATE 5.10, FIGURES 1-16

(Pl. 5.10, Figs. 1-3: new SEMs of holotype of *Globigerina semivera* Hornibrook)

(Pl. 5.10, Figs. 15, 16: new SEMs of paratype of *Globigerina semivera* Hornibrook)

Globigerina semivera Hornibrook, 1961:149-150, pl. 23, figs. 455-457 [lower Miocene *G. trilobus trilobus* Zone, Rifle Butts Fm., Awamoan Stage, Campbells Beach, South Island, New Zealand].

Globorotalia (Turborotalia) nana semivera (Hornibrook).— Jenkins, 1971:125-127, pl. 12, figs. 342-344 [holotype re-illustrated from Hornibrook, 1961, pl. 23, figs. 455-457].

Globorotalia semivera (Hornibrook).—Berggren and Amdur, 1973, pl. 27, figs. 16-19 [lower Miocene Zone N4 and Zone N5, DSDP Site 18, South Atlantic Ocean].—Jenkins, 1977:308, pl. 4, figs. 5-7 [lower Miocene *G. trilobus trilobus* Zone, English Channel].—Jenkins, 1978, pl. 1, figs. 23, 24 [lower Miocene *G. trilobus trilobus* Zone, DSDP Site 360, eastern South Atlantic Ocean].—Berggren and others, 1983, pl. 3, figs. 4, 5, pl. 4, fig. 1 [lower Miocene Zone N5 and Zone N6, DSDP Site 516, Rio Grande Rise, western South Atlantic Ocean].—Hoskins, 1984, figs. 7:1-6 [lower Miocene *G. trilobus trilobus* Zone, Awamoan Stage, New Zealand].

Globorotalia (Jenkinsella) semivera (Hornibrook).—Kennett and Srinivasan, 1983:172, pl. 42, figs. 3-5 [lower Miocene *Globorotalia miozea* Zone, DSDP Site 206, New Caledonia Basin, western South Pacific Ocean].

Paragloborotalia semivera (Hornibrook).—Premoli Silva and Spezzaferri, 1990:304, pl. 3, figs. 8a-c [lower Miocene

Zone N4, ODP Hole 709B, Madingley Rise, western equatorial Indian Ocean].—Spezzaferri, 1994:55-56, pl. 20, figs. 6a-c [upper Oligocene Subzone P21b, ODP Hole 709B, Madingley Rise, western equatorial Indian Ocean], pl. 22, figs. 1a-c [lower Miocene Zone N5, DSDP Hole 526A, Walvis Ridge, eastern South Atlantic Ocean].—Morgans and others, 2002, fig. 14P [lower Miocene *P. incognita* Zone, Altonian Stage, North Island, New Zealand].—Li and others, 2003a:23, pl. 1, fig. 23 [lower Miocene Zone SAN2, ODP Hole 1134B, Great Australian Bight, Indian Ocean], pl. 1, fig. 24 [lower Miocene Zone SAN3, ODP Hole 1134A, Great Australian Bight, Indian Ocean].—Li and others, 2003b:16, pl. 2, fig. 24 [upper Oligocene Subzone P21b, ODP Hole 1134A, Great Australian Bight, Indian Ocean], pl. 2, fig. 25 [upper Oligocene Zone P22, ODP Hole 1134A, Great Australian Bight, Indian Ocean].

Paragloborotalia semivera (Hornibrook) – *Paragloborotalia acrostoma* (Wezel).—Spezzaferri, 1994, pl. 22, figs. 2a-c [lower Miocene Zone N5, DSDP Hole 526A, Walvis Ridge, eastern South Atlantic Ocean].

Paragloborotalia mayeri s.l. (Cushman and Ellisor).—Chaisson and Leckie, 1993:164-165, pl. 8 (partim), figs. 16, 17 [lower Miocene Subzone N4b, ODP Hole 806B, western equatorial Pacific Ocean]. [Not Cushman and Ellisor, 1939.]

Paragloborotalia pseudocontinua (Jenkins).—Li and others, 2003b:16, pl. 2, fig. 26 [lower Oligocene Zone P18-P19, ODP Hole 1134A, Great Australian Bight, Indian Ocean], pl. 2, figs. 27, 28 [upper Oligocene Zone P22, ODP Hole 1134A, Great Australian Bight, Indian Ocean]. [Not Jenkins, 1967.]

DESCRIPTION.

Type of wall: Normal perforate, coarsely cancellate, probably sparsely spinose in life, heavy game-genetic calcification is often present.

Test morphology: Test large in size; low trochospiral, moderately lobulate in equatorial outline, chambers globular, inflated, embracing; 4½-5 chambers in ultimate whorl, increasing rapidly in size in initial whorl and slowly in the final whorl; in spiral view chambers subspherical, arranged in 2½-3 whorls, sutures

depressed, radial to slightly curved; in umbilical view chambers spherical to subspherical, sutures depressed, radial, umbilicus very narrow to nearly closed, moderately deep; aperture umbilical-extraumbilical, moderately high arch bordered by a thickened, continuous rim or lip; in edge view chambers spherical, spiral side slightly convex, umbilical side equally convex, periphery broadly rounded.

Size: Maximum diameter of holotype 0.41 mm (original measurement); 0.39 mm (remeasured this study); thickness of holotype 0.28 mm (this study).

DISTINGUISHING FEATURES.—Hornibrook (1961) described *semivera* as having a relatively flat spiral side, three whorls with 4-4½ chambers in the final whorl, radial sutures and a wide umbilical to extraumbilical aperture bordered by a lip. However, Jenkins (1971) and Spezzaferri (1994) used a taxonomic concept based on 4½-5 chambers in the final whorl, with radial to slightly curved sutures on both the spiral and umbilical side. Specimens with 4-4½ chambers in the final whorl closely resemble *pseudocontinua*. Jenkins (1971) stated that most of the paratypes in the original type sample have 4 chambers in the final whorl, which he classified as *G. (T.) nana pseudocontinua* Jenkins. Jenkins (1971) also noted a complete range of variation between the two (sub)species in the type sample, an observation also made by examining *semivera* topotypes at the Natural History Museum in London (this study). *Paragloborotalia semivera* is differentiated from *P. pseudocontinua* by its somewhat larger size and in possessing more chambers within the final whorl. Both taxa are gradational throughout their ranges. *Paragloborotalia semivera* differs from *opima* in having a high loop-shaped aperture and moderate spire.

Paragloborotalia semivera is distinguished from *acrostoma* by its more compact, embracing chambers, higher spiral-side convexity, and by its lower arched aperture. It is differentiated from both *siakensis* and *mayeri* by having a higher, more convex spiral

Plate 5.10 *Paragloborotalia semivera* (Hornibrook, 1961)

1-3 (holotype, NPC 1430), lower Miocene *G. trilobus trilobus* Zone, Awamoan Stage, Campbells Beach, South Island, New Zealand; **4, 8** (Chaisson and Leckie, 1993; pl. 8, figs. 16, 17), Subzone N4b, ODP Hole 806B, Ontong Java Plateau, western equatorial Pacific Ocean; **5-7** (Spezzaferri, 1994; pl. 22, figs. 2a-c), Zone N5, ODP Hole 526A, Walvis Ridge, eastern South Atlantic Ocean; **9-11** (Spezzaferri, 1994; pl. 20, figs. 6a-c), Subzone P21b, ODP Hole 709B, Madingley Rise, equatorial Indian Ocean; **12**, Subzone N4b, ODP Hole 806B, Ontong Java Plateau, western equatorial Pacific Ocean; **13-14** (Spezzaferri, 1994; pl. 22, figs. 1b-c), Zone N5, ODP Hole 526A, Walvis Ridge, eastern South Atlantic Ocean; **15-16** (paratype, Basal collection), lower Miocene *G. trilobus trilobus* Zone, Awamoan Stage, Campbells Beach, South Island, New Zealand. Scale bar: **1-15** = 100 µm (scale bars estimated for **4, 8**); **16** = 50 µm.

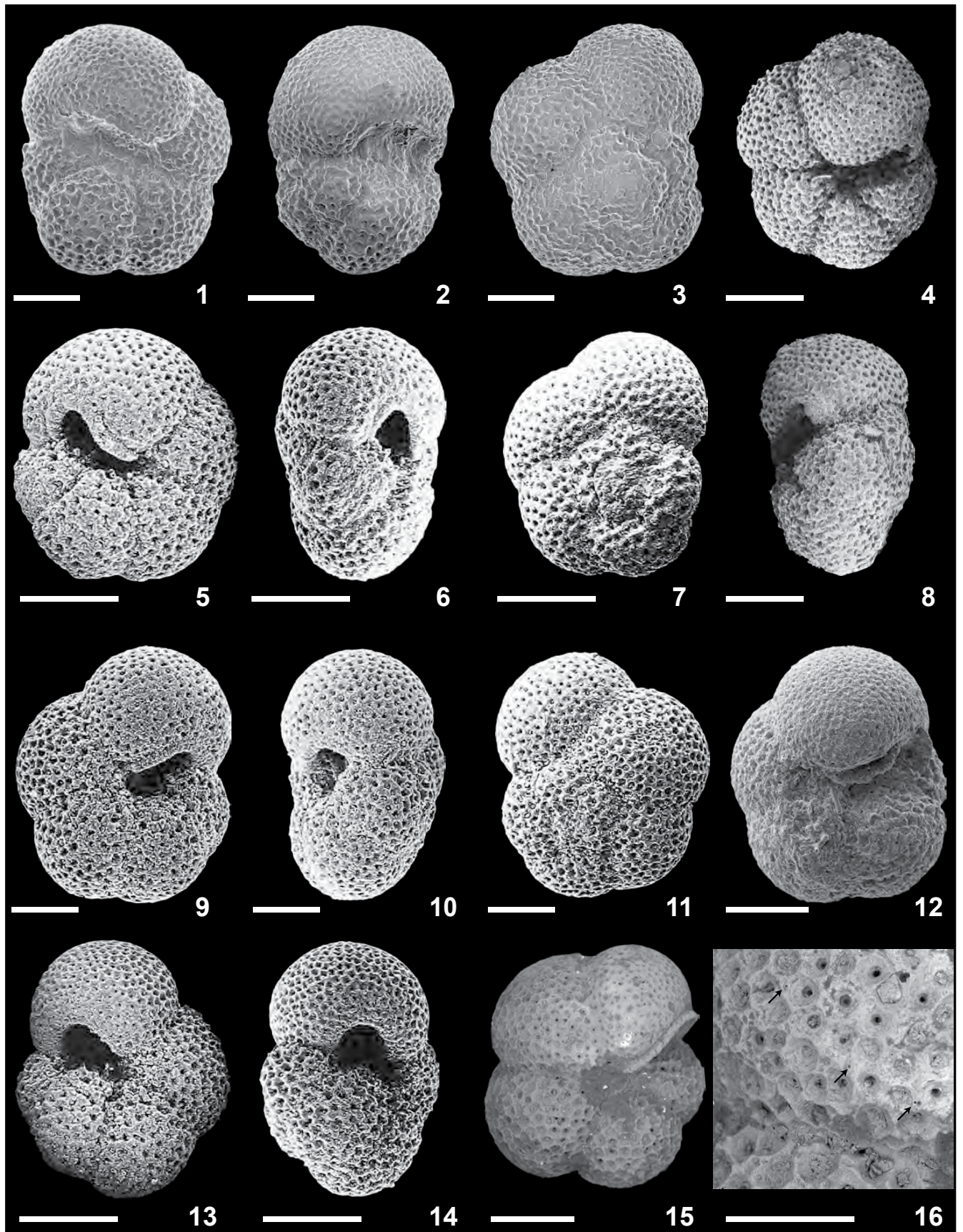


PLATE 5.10 *Paragloborotalia semivera* (Hornibrook, 1961)

side, subcircular, less ovate equatorial outline, and a more compact test with more embracing chambers and a narrow, closed umbilicus. It is further differentiated from *siakensis* by having more embracing chambers and a less lobulate test and a higher arched aperture, and from *mayeri* in having less recurved sutures on the spiral side and fewer (typically 5 compared with 5½-6) chambers in the final whorl. In some cases *P. semivera* had been included within the taxonomic concept of *mayeri* and/or *siakensis* (Leckie and others, 1993; Chaisson and Leckie, 1993; Pearson and Wade, 2009) and *pseudocontinua* (Jenkins and Srinivasan, 1986).

DISCUSSION.—Hornibrook (1961) originally placed *semivera* in *Globigerina* on account of the umbilical tendency of the aperture. Jenkins (1967:1070) had stated that “*G. siakensis* is very close in morphology to *G. nana semivera* and may prove to be synonymous with it.”, but we recognize a clear distinction between *siakensis* and *semivera*. Chaisson and Leckie (1993) and Leckie and others (1993) had lumped *P. semivera* into a broader concept of *P. mayeri* s.l.; the ‘*semivera*’ form is restricted to the upper Oligocene of ODP Hole 803D and basal Miocene of Hole 806B. Jenkins (1977) suggested that *acrostoma* is a junior synonym of *semivera*, but we consider the two taxa to be unique and not directly related.

PHYLOGENETIC RELATIONSHIPS.—Derived from *pseudocontinua* by an additional chamber in the final whorl and larger size.

TYPE LEVEL.—Lower Miocene *G. trilobus trilobus* Zone, Awamoan Stage, Rifle Butts Formation, Campbells Beach, All Day Bay, South Island, New Zealand.

STRATIGRAPHIC RANGE.—Lower Oligocene Zone O4 to lower Miocene Zone M5. In New Zealand, Hornibrook (1961) records a range from the upper Oligocene (lower Miocene?) Waitakian Stage to the lower middle Miocene Lillburnian Stage. Jenkins (1971) recorded the

range from the upper Oligocene upper Whaingaroan Stage, *Globigerina (G.) euapertura* Zone, to the upper lower Miocene Clifdenian Stage, *Praeorbulina glomerosa* Zone (Zone N8/M5; Wade and others, 2011). In the southeast Atlantic Ocean, Jenkins (1978) reported a range of uppermost Oligocene *G. euapertura* Zone through the middle part of the lower Miocene *G. triloba triloba* Zone at DSDP Sites 360 and 362. In her detailed study of many DSDP sites from around the world ocean, Spezzaferri (1994) reported a lowest occurrence within lower Oligocene Subzone P21a (= O3/O4).

GEOGRAPHIC DISTRIBUTION.—Cosmopolitan; reported from the southwest Pacific Ocean (DSDP Leg 29; Jenkins, 1975), the southeast Atlantic Ocean (DSDP Leg 40; Jenkins, 1978), the English Channel, type Aquitanian-Burdigalian (Jenkins, 1966, 1977), and the Caribbean (Chaisson and D’Hondt, 2000). Berggren (ODP Leg 120; 1992) recorded *semivera* on the Kerguelen Plateau in the southern Indian Ocean. Kennett and Srinivasan (1983) reported a warm subtropical to temperate distribution.

STABLE ISOTOPE PALEOBIOLOGY.—No data available.

REPOSITORY.—GNS Science National Paleontological Collection (NPC), Register No. 1430 (holotype).

Paragloborotalia siakensis (LeRoy, 1939)

PLATE 5.11, FIGURES 1-16

Globorotalia siakensis LeRoy, 1939:262, pl. 4, figs. 20-22 [Miocene?, Rokan-Tapanoeli region, central Sumatra].—Berggren and Amdurer, 1973, pl. 28, figs. 6, 7 [lower Miocene Zone N4, DSDP Site 14, South Atlantic Ocean], fig. 8 [upper Oligocene Subzone P21b, DSDP Site 17B, South Atlantic Ocean].—Kennett, 1973, pl. 14, figs. 1, 2 [middle Miocene *G. mayeri* Zone, DSDP Site 206, New Caledonia Basin, western South Pacific Ocean].—Stainforth and others, 1975:317, 320, fig.

Plate 5.11 *Paragloborotalia siakensis* (LeRoy, 1939)

1-3 (holotype, No. P.S. 1075a; Zachariasse and Sudijono, 2012; pl. 5, fig. 1a-c) Miocene?, Rokan-Tapanoeli region, central Sumatra; 4, 8, 12 (same specimen), Zone N5 (=M2/M3), NHM slide BP1566, Trinidad; 5-7 (same specimen), 9-11 (same specimen), Zone O7, ODP Hole 628A/16/5, 100-102 cm, Little Bahama Bank, western North Atlantic Ocean; 13, 14, Zone O7, Atlantic Slope Project corehole 5B/16B/29-35”, western Atlantic Ocean; 15, 16, Zone M3/M4, ODP Hole 871A/12H/2, 59-61 cm, Limalok Guyot, western equatorial Pacific Ocean. Scale bar: 1-13, 15, 16 = 100 µm, 14 = 10 µm.

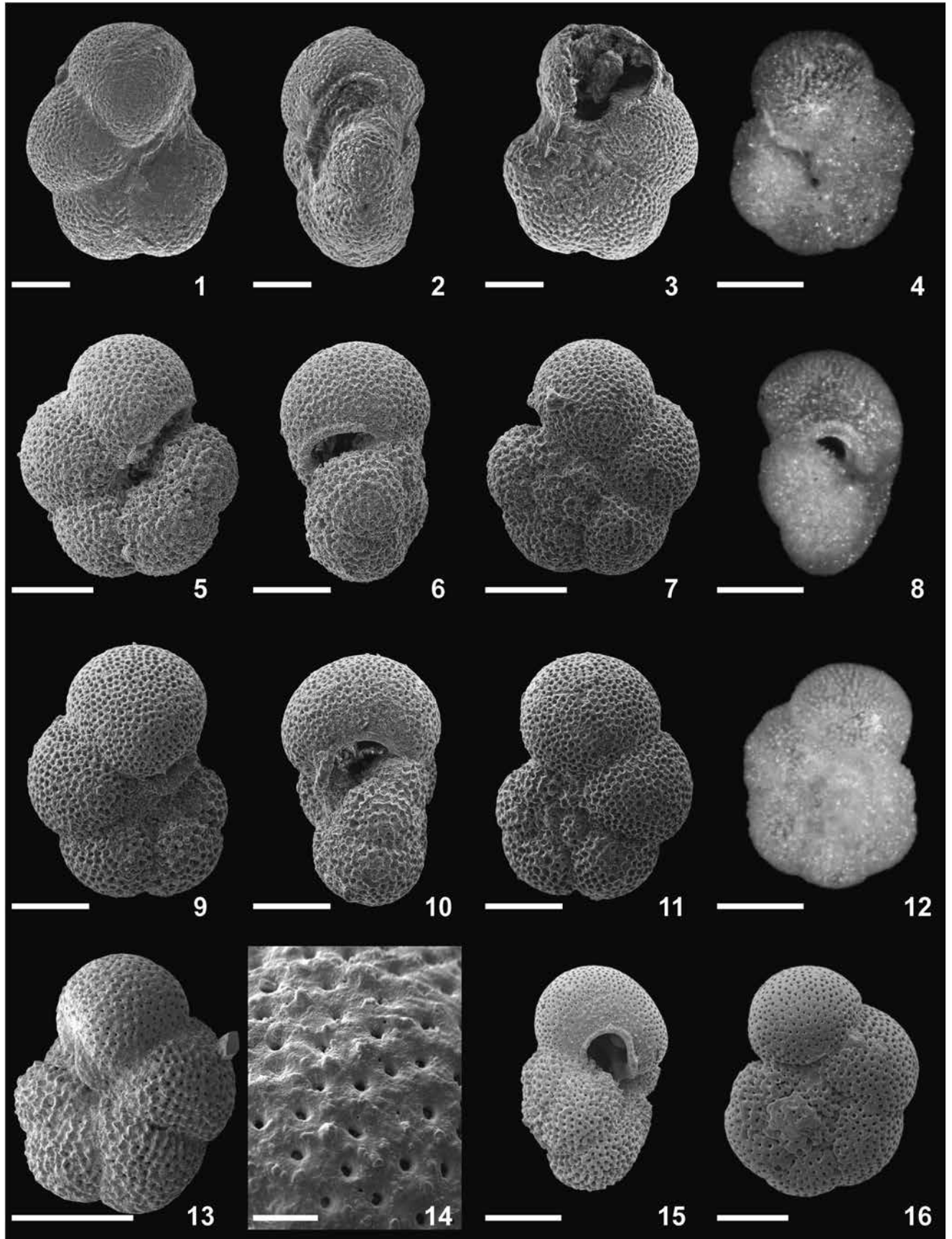


PLATE 5.11 *Paragloborotalia siakensis* (LeRoy, 1939)

143.1, 2 [lower Miocene *Catapsydrax dissimilis* Zone, Cipero Fm., Trinidad]; fig. 143.3 (holotype drawing reproduced); fig. 143.4, 5 [middle Miocene *Globorotalia fohsi fohsi* Zone, corehole, Gulf of Mexico].—Iaccarino and Salvatorini, 1979, pl. 3, figs. 10, 14 [middle Miocene Zone N12, DSDP Site 398, Vigo Seamount, eastern North Atlantic Ocean].—Berggren and others, 1983, pl. 3, figs. 8-10 [lower Miocene Zone N5, DSDP Site 516, Rio Grande Rise, western South Atlantic Ocean].

Globorotalia (Turborotalia) siakensis LeRoy.—Quilty, 1976:647, pl. 14, figs. 5, 6 [mid Miocene Zone N10/N11, DSDP Site 319, southeastern Pacific Ocean].—Molina, 1979:239-241, pl. 28, figs. 1A-C [lower Miocene *G. primordius* Zone, Levigado NA-4, Spain].

Globorotalia (Jenkinsella) siakensis LeRoy.—Kennett and Srinivasan, 1983:172, pl. 42, figs. 1, 6-8 [middle Miocene Zone N9, DSDP Site 289, Ontong Java Plateau, western equatorial Pacific Ocean].

Paragloborotalia siakensis (LeRoy).—Spezzaferri and Premoli Silva, 1991:253, pl. XI, figs. 2a-c [upper Oligocene Zone P22, DSDP Hole 538A, Catoche Knoll, Gulf of Mexico].—Spezzaferri, 1994:55, pl. 21, figs. 1a-c [reproduced from Premoli Silva and Spezzaferri, 1991, pl. 11, figs. 2a-c], figs. 2a-c [upper Oligocene Zone P22, DSDP Hole 667A, Sierra Leone Rise, equatorial Atlantic Ocean].—Fox and Wade, 2013:401, fig. 15.1-5, fig. 21 [middle Miocene Zone M6, IODP Hole U1338C, eastern equatorial Pacific Ocean].—Sanchez and others, 2014:116-117, pl. 11, figs. 1-8 [lower Miocene *Catapsydrax dissimilis* Zone, Cipero Fm., Trinidad], pl. 11, figs. 9-16 [lower Miocene *Globorotalia fohsi peripheroronda* Zone, Carapita Fm., eastern Venezuela Basin].

Globorotalia cf. mayeri Cushman and Ellisor.—Keller, 1981:125-127, pl. 2, 7 figures [upper Oligocene Zone P22, DSDP Site 292, Benham Rise, western North Pacific Ocean].

Globorotalia mayeri Cushman and Ellisor.—Bolli and Saunders, 1982a, pl. 1, figs. 25, 26, 30, 36, 38; pl. 2, figs. 1-6, 8, 9, 14-17, 21-31, 36, 38, 43-45; pl. 3, 1-6, 13-18, 22-29, 32-43 [upper Oligocene to middle Miocene, *Globigerina ciperoensis ciperoensis* Zone to *Globorotalia mayeri* Zone, Cipero Fm., Trinidad].

Paragloborotalia semivera (Hornibrook)/*Paragloborotalia mayeri* (Cushman and Ellisor) group.—Leckie and others, 1993:125, pl. 7, figs. 5-8, 10-14 [upper Oligocene Zone P22, ODP Hole 803D, Ontong Java Plateau, western equatorial Pacific Ocean; upper Oligocene Zone P22, ODP Hole 628A, Little Bahama Bank, western North Atlantic Ocean].

Not *Globorotalia siakensis* LeRoy.—Jenkins, 1960:366, 368, pl. 5, figs. 7a-c [lower Miocene *Globigerinoides trilobus trilobus* Zone, Lakes Entrance Oil Shaft, Victoria, Aus-

tralia] (= *Globorotalia bella*).—Postuma, 1971:358, pl. on p. 359 [Trinidad] (= *P. mayeri*).

DESCRIPTION.

Type of wall: Normal perforate, coarsely cancellate, sparsely spinose in life (Hilgen and others, 2000; Zachariasse and Sudijono, 2012; Sanchez and others, 2014), heavy gametogenetic calcification is often present.

Test morphology: Test large in size; low trochospiral, strongly lobulate in equatorial outline, chambers globular, inflated, slightly embracing; some specimens may develop a kummerform final chamber; 4½-5½ chambers in the ultimate whorl of mid- to late Oligocene forms, up to 6-7 chambers in latest Oligocene to middle Miocene forms, increasing rapidly in size in initial whorl and slowly in the final whorl; in spiral view chambers subspherical, arranged in 2½-3 whorls, sutures depressed, radial; in umbilical view chambers spherical to subspherical, sutures depressed, radial, umbilicus narrow moderately deep; aperture umbilical-extraumbilical, low to moderately high arch, bordered by a prominent lip; in edge view chambers spherical, spiral side flat to slightly convex, umbilical side slightly convex, periphery broadly rounded.

Size: Maximum diameter of holotype 0.40 mm, maximum thickness 0.28 mm (original measurements); maximum diameter 0.41 mm, thickness 0.25 mm (remeasured this study).

DISTINGUISHING FEATURES.—*Paragloborotalia siakensis* is distinguished from *opima* in always having at least 5 chambers in the final whorl, a more ovate, and lobulate equatorial outline due to greater chamber expansion, less embracing chambers, and more open umbilicus. The holotype of *P. siakensis* is slightly larger than the holotype of *P. mayeri*; the arched aperture of *siakensis* is not as high as the *mayeri* holotype; the holotype of *siakensis* has a prominent lip bordering the aperture, while the holotype of *mayeri* has an imperforate band and lacks a lip. *Paragloborotalia siakensis* is further distinguished from *mayeri* in having radial rather than slightly curved spiral-side sutures. This radial suture pattern is the more primitive condition, giving rise to the derived curved sutures in the latest Oligocene, a pattern that repeats itself in other early Miocene ‘globorotaliid’ lineages. Both taxa have similarly variable apertural characteristics, stratigraphic trend of increasing

chamber number, paleobiogeographic distribution, and highest occurrence.

Paragloborotalia siakensis is distinguished from *pseudokugleri* by having a more rapid chamber expansion rate and more ovate equatorial outline, and in having a higher arched aperture. In addition, *pseudokugleri* commonly has slightly curved spiral sutures. Distinguished from *P. birnageae* by having a more rapid chamber expansion rate and more ovate equatorial outline, by having depressed sutures and more inflated, less embracing chambers, and a distinctly higher arched aperture. Distinguished from *Fohsella? peripheroronda* in having a broadly rounded periphery due to more spherical chambers, radial rather than curved spiral-side sutures, and a higher arched aperture.

DISCUSSION.— Bolli and Saunders (1982a) argued that *siakensis* is synonymous with *P. mayeri*, but many workers differentiate the two forms based on the radial spiral sutures and lower arched aperture in *siakensis*, and the slightly curved spiral sutures and higher-arched aperture in *mayeri* (e.g., Kennett and Srinivasan, 1983; Spezzaferri and Premoli Silva, 1991; Spezzaferri, 1994; Pearson and Wade, 2009). Other than these subtle differences, the two taxa are very similar and share a highest occurrence in the early late Miocene (top of Zone M11/N14; Wade and others, 2011). *Paragloborotalia siakensis* is the ‘primitive’ form, initially very small with 5 chambers in the final whorl and radial spiral sutures in the early to mid-Oligocene, increasing in size and giving rise to *P. mayeri* s.s. with 5 chambers in the final whorl and slightly curved spiral sutures in the latest Oligocene; both taxa then increase to 6-7 chambers in the early to middle Miocene. According to Spezzaferri and Premoli Silva (1991), small specimens of *P. siakensis* (<150 μm) first appear in the lower Oligocene, in the lower part of Zone P19 in both the Indian Ocean and Gulf of Mexico. Larger specimens (>150 μm) appear in Subzone P21a of the Gulf of Mexico, while even larger specimens (>250 μm) appear within Zone P22 in the Indian Ocean.

In the near topotype material discussed and illustrated by Zachariasse and Sudijono (2012), specimens of *P. siakensis* generally have 5 chambers in the final whorl with a range of 4½-6½ chambers. They note that kummerform chambers are common, including one of the two specimens illustrated by LeRoy (1944). The aperture is variable from low to moderately high arch, with well-developed lip; some specimens lack a

well-developed lip and instead have an imperforate rim around the aperture (e.g., Pearson and Wade, 2009).

PHYLOGENETIC RELATIONSHIPS.— *Paragloborotalia siakensis* was probably derived from *nana* by the addition of another chamber in the final whorl, less embracing chambers, more rapid rate of chamber expansion, and a higher arched aperture. Alternatively, *siakensis* may have been derived from *opima* based on many of the same morphological changes, but the earliest forms of *siakensis* were small suggesting that *nana* was the more likely ancestor. *Paragloborotalia mayeri* is most likely descended from *siakensis* in the latest Oligocene (Kennett and Srinivasan, 1983; Premoli Silva and Spezzaferri, 1991; Spezzaferri, 1994).

TYPE LEVEL.— Miocene?, locality Ho-528, Tapoeng Kiri area, Rokan-Tapaneoli Region, Central Sumatra, Indonesia.

STRATIGRAPHIC RANGE.— Lower Oligocene Zone O3 to upper Miocene Zone M11 (Spezzaferri and Premoli Silva, 1991; Spezzaferri, 1994; Wade and others, 2011).

GEOGRAPHIC DISTRIBUTION.— According to Kennett and Srinivasan (1983), *siakensis* is more common in equatorial and warm subtropical locations, while *mayeri* is more common in temperate locations. Spezzaferri (1994) reports a cosmopolitan distribution for *siakensis*.

STABLE ISOTOPE PALEOBIOLOGY.— Late Oligocene *P. siakensis* from Trinidad suggest an upper thermocline depth of calcification with no photosymbionts (Pearson and Wade, 2009). Matsui and others (2016) interpreted a lower mixed-layer habitat for the late Oligocene *siakensis* group (including *mayeri* and *semivera*) from the equatorial Pacific Ocean. Gasperi and Kennett (1993) reported consistently low $\delta^{18}\text{O}$ values through the lower and middle Miocene of DSDP Site 289 in the western equatorial Pacific suggesting a mixed-layer habitat.

REPOSITORY.— No. P.S. 1075a, Government Geological Museum, Bandoeng, Indonesia.

Genus *Parasubbotina* Olsson, Hemleben, Berggren, and Liu, 1992

TYPE SPECIES.— *Globigerina pseudobulloides* Plummer, 1926.

DISTINGUISHING FEATURES.— “Test very low trochospiral with 10-12 chambers, and with 4-5 chambers in the ultimate whorl. The chambers which are inflated globular and slightly ovoid in shape increase rapidly in size. The aperture is interiomarginal, umbilical to extra-umbilical, a high rounded arch which is bordered by a narrow lip. The umbilicus is narrow, deep and open to the previous chambers. The wall is weakly to strongly cancellate and spinose. Spine holes are numerous and located at the juncture of and along the cancellate ridges. They may be obscured by gametogenetic and/or diagenetic calcification” (Olsson and others, 1992).

DISCUSSION.— *Parasubbotina* is distinguished from *Paragloborotalia* by its more rapid rate of chamber growth and generally greater chamber inflation, with a more lobulate equatorial outline. See Olsson and others (2006) for additional discussion of the genus.

PHYLOGENETIC RELATIONSHIPS.— *Parasubbotina* evolved from *Hedbergella monmouthensis* in Zone P0 (Olsson and others, 1999).

STRATIGRAPHIC RANGE.— Zone P0 to Zone O1.

GEOGRAPHIC DISTRIBUTION.— Global in low to high latitudes in northern and southern hemispheres.

***Parasubbotina hagni* (Gohrbandt, 1967)**

Globigerina eocaena Gümbel.—Subbotina, 1953:63-64, pl. 6, fig. 5a-c; pl. 7, fig. 1a-c [upper Eocene *Acarinina* Zone (upper part), Kuban River, northern Caucasus]. [Not Gümbel, 1868.]

Globigerina hagni Gohrbandt, 1967:324-326, pl.1, figs. 1-9 (1-3 = holotype, 4-9 = paratypes) [middle Eocene, Helvetikum, Salzburg, Austria].

Parasubbotina hagni (Gohrbandt).—Rögl and Egger, 2012:44, pl.2, figs. 22-27 (25 paratype) [middle Eocene Zone E8, Holzhäusl section north-east of Mattsee, Austria].

DISCUSSION.— *Globigerina hagni* Gohrbandt (1967) was previously assigned to *Subbotina* by various authors including Poore and Brabb (1977) and Olsson and others (2006). Rögl and Egger (2012) re-examined and illustrated the type specimens described by Gohrbandt and concluded that *hagni* belonged in the genus *Parasubbotina*. Olsson and others (2006) restricted *P. hagni* to the Eocene. However, Wade and Pearson (2008) recorded specimens from Tanzania (as *Subbotina hagni*), with a stratigraphic range that extends into lower Oligocene Zone O1 (Figure 5.1). A discussion and plate of *hagni* including SEMs from Gohrbandt type samples is given in Olsson and others (2006).

***Parasubbotina varianta* (Subbotina, 1953)**

PLATE 5.12, FIGURES 1-16

Globigerina varianta Subbotina, 1953:63-64, pl. 3, fig. 5a-c [lower Paleocene zone of Rotaliform *Globorotalia*, Kuban River, northern Caucasus].

Globorotalia opima nana Bolli.—Stainforth and Lamb, 1981:25, pl. 4, fig. 1a-c [upper Eocene, Atlantic Slope Project corehole 5B, western North Atlantic Ocean]. [Not Bolli, 1957.]

See Olsson and others (1999) for further synonymy of this species.

DESCRIPTION.

Type of wall: Normal perforate, coarsely cancellate, *ruber/sacculifer*-type, spinose.

Test morphology: Test very low trochospiral, globular, subquadrate in outline, chambers globular, much inflated, embracing; in spiral view 4, occasionally 4½ globular, embracing chambers in ultimate whorl, increasing rapidly in size, sutures slightly depressed, straight, last 4 chambers make up about three quarters of the test, ultimate chamber may be slightly reduced in size; in umbilical view 4, occasionally 4½ globular, embracing chambers, increasing rapidly in size, sutures slightly depressed, straight, umbilicus very small sized opening, sometimes closed off by surrounding chambers, aperture a high arch, umbilical-extraumbilical, bordered by a narrow, often thickened, continuous, lip, ultimate chamber may be slightly reduced in size; in edge view chambers globular, periphery rounded.

Plate 5.12 *Parasubbotina varianta* (Subbotina, 1953)

1-16, Zone O1, AGS 66, 9A-1A, Shubuta Fm., Alabama. Scale bar: 1-6, 8-15 = 100 µm; 7, 16 = 10 µm.

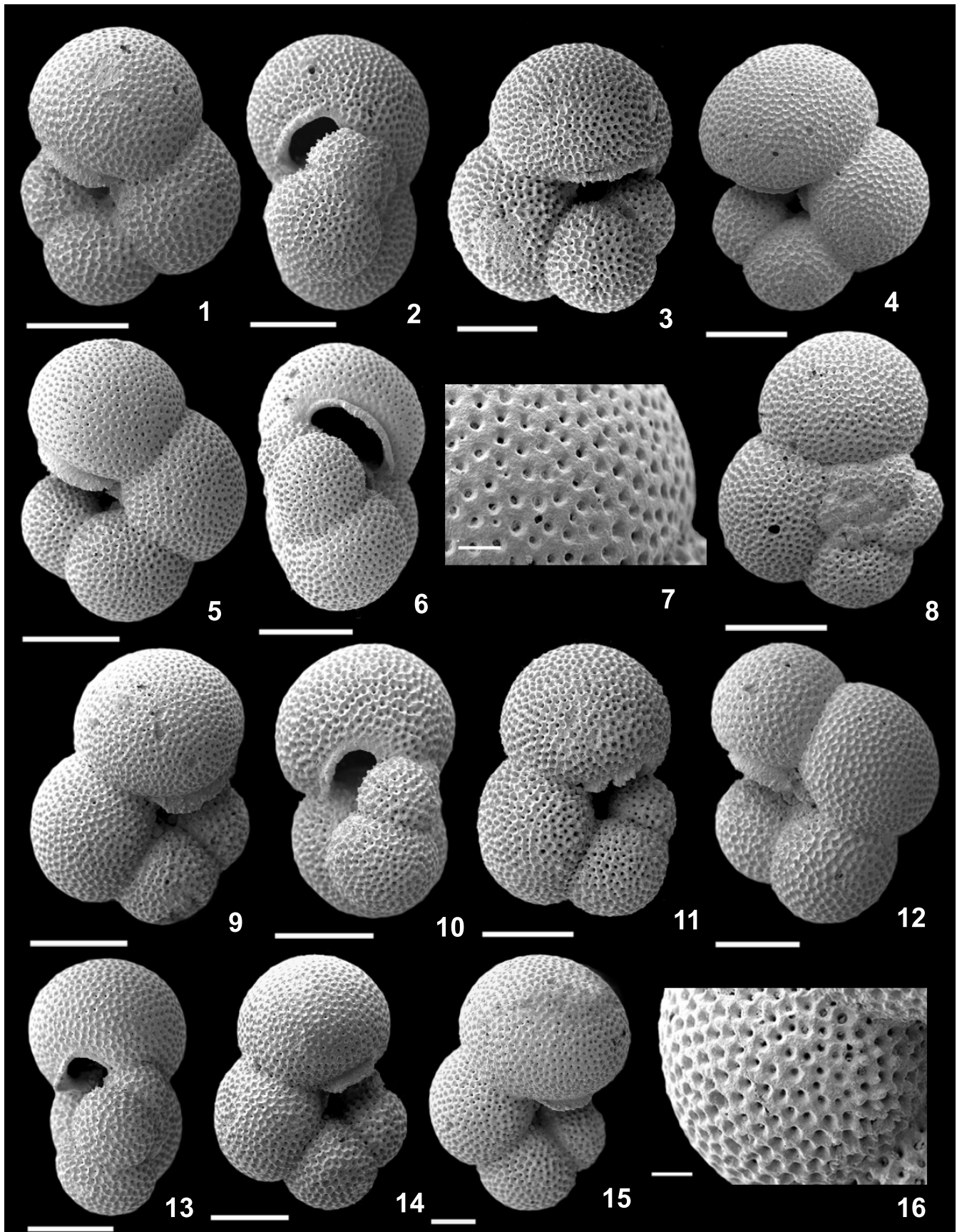


PLATE 5.12 *Parasubbotina varianta* (Subbotina, 1953)

Size: Maximum diameter of holotype 0.41 mm, minimum diameter 0.39 mm, maximum width 0.29 mm.

DISTINGUISHING FEATURES.— *Parasubbotina varianta* is more loosely coiled and its chambers are less embracing than in *P. griffinoides*, leading to a more lobulate test. In *P. griffinoides*, the apertural lip is more uniform and constant in thickness than in *P. varianta* and other species of *Parasubbotina*.

DISCUSSION.— See Olsson and others (2006) for other plate images and discussion of this species.

PHYLOGENETIC RELATIONSHIPS.— *Parasubbotina varianta* evolved from *P. pseudobulloides* (Olsson and others, 1999).

TYPE LEVEL.— Zone of rotaliiform *Globorotalia*, Elburgan Fm., Kuban River section, northern Caucasus.

STRATIGRAPHIC RANGE.— *Parasubbotina varianta* is a long ranging taxon that evolved in the Danian. We have identified this species from Zone O1 in records from the equatorial Pacific Ocean and US Gulf Coast Plain, thus extending its recorded range into the lowermost Oligocene.

GEOGRAPHIC DISTRIBUTION.— Widespread in low and middle latitudes.

STABLE ISOTOPE PALEOBIOLOGY.— No data available.

REPOSITORY.— Holotype (No. 3994) and paratypes (Nos. 3995-4003) deposited in the VNIGRI collections (378/20), St Petersburg, Russia.

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