Chapter 5

TAXONOMY, BIOSTRATIGRAPHY, AND PHYLOGENY OF EOCENE CATAPSYDRAX, GLOBOROTALOIDES, GUEMBELITRIOIDES, PARAGLOBOROTALIA, PARASUBBOTINA, AND PSEUDOGLOBIGERINELLA N. GEN.

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Abstract

The taxonomy, phylogeny, and biostratigraphy of Eocene Catapsydrax, Globorotaloides, Guembelitrioides, Paragloborotalia, Parasubbotina, and Pseudoglobigerinella Olsson and Pearson n. gen. are reviewed. A total of 17 species are recognized as distinct, namely Catapsydrax africanus (Blow and Banner), Catapsydrax dissimilis (Cushman and Bermúdez), Catapsydrax globiformis (Blow and Banner), Catapsydrax howei (Blow and Banner), Catapsydrax unicavus Bolli, Loeblich, and Tappan, Globorotaloides quadrocameratus Olsson, Pearson, and Huber n. sp., Guembelitrioides nuttalli (Hamilton), Paragloborotalia griffinoides Olsson and Pearson n. sp., Paragloborotalia nana (Bolli), Parasubbotina eoclasva Coxall, Huber, and Pearson, Parasubbotina griffinae (Blow), Parasubbotina inaequispira (Subbotina), Parasubbotina prebetica (Martinez-Gallego and Cremades), Parasubbotina pseudowilsoni Olsson and Pearson n. sp., Parasubbotina varianta (Subbotina), and Pseudoglobigerinella bolivariana (Petters).

INTRODUCTION

In this chapter we discuss a diverse series of genera that according to our researches were descended from the Paleocene species Parasubbotina varianta. All these genera are characterized by a cancellate spinose wall texture and are included in the Family Globigerinidae. Other members of the Family are discussed by Olsson and others (Chapter 6, this volume) and Premoli Silva and others (Chapter 7, this volume). The species level range-chart and phylogeny is presented in Figure 5.1. The group of taxa considered in this chapter is paraphyletic, in that the Family Hantkeninidae is descended from it (Coxall and others, 2003; Coxall and Pearson, Chapter 8, this volume). Several of the genera (Paragloborotalia, Globorotaloides, and Catapsydrax) persist into Oligo-Miocene strata. One new genus, Pseudoglobigerinella Olsson and Pearson n. gen., is described here for the first time, as well as several new species.

The taxonomy is hampered to some extent by the relative simplicity of the test morphology of these
genera, the large extent of variation between individuals that is generally encountered, and the fact that many of them seem to have evolved an ecological preference for cool and/or high productivity settings of which there are few thick and continuous stratigraphical records. Eocene parasubbotinids, paragloborotaliids and their relatives can occur in floods in such environments but are often rare and inconspicuous in deep-sea oligotrophic settings.

SYSTEMATIC TAXONOMY

**Order FORAMINIFERIDA Eichwald, 1830**

**Superfamily GLOBIGERINACEAE Carpenter, Parker and Jones, 1862**

**Family GLOBIGERINIDAE Carpenter, Parker and Jones, 1862**

**Genus Catapsydrax Bolli, Loeblich, and Tappan, 1957**

**TYPE SPECIES.** — *Globigerina dissimilis* Cushman and Bermúdez, 1937.

**DESCRIPTION.**

*Type of wall:* Coarsely cancellate, probably spinose in life, with tendency to develop a thick crust in some species.

*Test morphology:* Globular, lobulate, typically with 4 chambers in the final whorl. Chambers moderately inflated, appressed, with an umbilical bulla with one or more infralaminal apertures in the adult stage. The apertures are bordered by a continuous, narrow lip that may be thickened by gametogenetic calcification.

**DISTINGUISHING FEATURES.** — Distinguished from *Globorotaloides* by the more compact, radially compressed morphology, with appressed inflated chambers in the final whorl, and the coarse cancellate *ruber/sacculifer*-type wall texture (as opposed to the *sacculifer* type wall in *Globorotaloides*). Most *Globorotaloides* lack the obligate bulla with a uniform continuous lip or rim bordering the infralaminal aperture(s) which is characteristic of *Catapsydrax.* Distinguished from *Subbotina* and *Globoturborotalita* by the obligate bulla with infralaminal aperture(s).

**DISCUSSION.** — *Catapsydrax* was erected by Bolli, Loeblich and Tappan (1957, p. 36) to encompass several species that are characterized in the adult stage by an umbilical bulla with at least one accessory infralaminal aperture. Most of the included species were Miocene forms, but the holotype of the type species, *C. dissimilis* (Cushman and Bermúdez), is from the upper Eocene of Cuba. As described by Bolli, Loeblich and Tappan, this specimen, which is figured here in SEM for the first time (Plate 5.3, Figs. 18-20), has more than one infralaminal aperture around the bulla. *Catapsydrax dissimilis* is common in the Oligocene and ranges into the lower Miocene, where its highest occurrence datum is an important biostratigraphic marker horizon (Kennett and Srinivasan, 1983; Bolli and Saunders, 1985; Berggren and others, 1995).

The earliest species of *Catapsydrax*, *C. unicavus*, has a low, slightly inflated bulla covering the umbilicus with a single low arched infralaminal aperture. Subsequent species of *Catapsydrax*, *C. dissimilis* and *C. stainforthi*, developed two or more infralaminal apertural openings beneath a slightly inflated bulla. The infralaminal apertures, which are generally centered over the suture lines, are bordered by a continuous narrow thickened lip or rim in adult forms. Blow and Banner (1962) described a group of three species (which they placed in *Globigerinita*), from the upper Eocene (Zone E14) of Tanzania, namely *G. africanus*, *G. globiformis*, and *G. howei*. These taxa cannot be placed in *Globigerinita* because that genus is a microperforate taxon whereas Blow and Banner’s species have a cancellate wall texture. The species are all characterized by having a bulla with multiple infralaminar apertures and are here placed in *Catapsydrax.*

In our taxonomy, the first species of *Catapsydrax* is *C. unicavus*, which first appears in the lower Eocene. We take a broad concept of this taxon, including several species in synonymy with it, but at the same time we recognize that further work may reveal more taxonomic complexity that would justify splitting the species.

FIGURE 5.1. Stratigraphic ranges and inferred phylogenetic relationships of Eocene species of *Catapsydrax*, *Globorotaloides*, *Guembelitrioides*, *Paragloborotalia*, *Parasubbotina*, and *Pseudoglobigerinella* discussed in this chapter.
Several stable isotope studies (discussed below) have indicated that *Catapsydrax unicavus* and *C. dissimilis* are deep-dwelling species, consistently registering the most positive (coldest) $\delta^{18}O$ values of the assemblages in which they are found. The upper Eocene species described by Blow and Banner (1962) exhibit a range of morphologies that may indicate an evolutionary radiation into different parts of the water column, but this has yet to be tested.

*Catapsydrax africanus* (Blow and Banner, 1962)

**PLATE 5.1, FIGURES 1-14**

(Pl. 5.1, Figs. 1-3, new SEMs of holotype of *Globigerinita africana* Blow and Banner)


*Globigerinita echinata africana* Blow and Banner.—Blow, 1979: pl. 24: figs. 1 and 4; pl. 240: fig. 8 [Zone E14, Lindi, Tanzania].

?*Catapsydrax africana* (Blow and Banner).—Warraich and Ogasawara, 2001:43, fig. 12: 1-3 [Zone E10/11, Kirthar Fm., Sulaiman Range, Pakistan].

*Globigerinita echinata echinata* Bolli.—Blow, 1979: pl. 240: fig. 7 [Zone E14, Lindi, Tanzania]. [Not Bolli, 1957b.]

**DESCRIPTION.**

Type of wall: Cancellate, apparently spinose, ruber/sacculifer-type wall texture.

Test morphology: Low trochospiral, slightly lobate test with 3-4 chambers in the final whorl. Chambers inflated, globular, increasing moderately in size with a large inflated bulla covering the umbilicus; in spiral view 3-4 globular chambers increasing moderately in size, sutures straight, moderately depressed; in umbilical view dominated by a large inflated bulla with 3-4 semicircular, infralaminal apertures with a continuous, thickened imperforate rim opening onto each suture which is straight and moderately depressed; in edge view ovoid in shape with bulla showing one aperture opening onto the suture line.

Size: Maximum diameter of holotype 0.23 mm, thickness 0.22 mm.

**DISTINGUISHING FEATURES.** — *Catapsydrax africanus* is distinguished from *C. globiformis* by its less spherical test and by having a more inflated bulla that has larger, more open, infralaminal apertures. *Catapsydrax howei* is larger and has a larger, still more inflated bulla with large circular, infralaminal apertures.

**DISCUSSION.** — Blow and Banner (1962) originally placed *C. africanus* in *Globigerinita* but this genus is a microperforate taxon, hence it is here placed in *Catapsydrax*. The species name is changed to agree in gender with the genus *Catapsydrax* (ICZN, Art. 31.2). *Catapsydrax africanus* has a low, slightly inflated bulla covering the umbilicus with a single low arched aperture. The infralaminal aperture is bordered by a continuous narrow lip that becomes thickened with gametogenetic calcification. The wall texture of the ruber/sacculifer-type also becomes thickened by gametogenetic calcification. In *C. africanus* the bulla is more inflated and the infralaminal apertures are larger. Blow (1979) regarded *africanus* as a subspecies of *Catapsydrax echinatus* Bolli, but that species is regarded as an aberrant acarininid in this work (see Berggren and others, Chapter 9, this volume).

*Catapsydrax africanus* is a small form and has apparently been overlooked by many previous workers. We illustrate the holotype in SEM for the first time (Pl. 5.1, Figs. 1-3) as well as newly collected specimens from the type locality (Pl. 5.1, Figs. 4-7).

**PHYLOGENETIC RELATIONSHIPS.** — *Catapsydrax africanus* probably evolved from *C. howei* in the late middle Eocene by developing a less inflated bulla with smaller infralaminal apertures opening onto the sutures.

**STRATIGRAPHIC RANGE.** — Zone E13 (middle part; Abdel-Kireem, 1983) to Zone E15 (Blow and Banner, 1962).

**GEOGRAPHIC DISTRIBUTION.** — Known from tropical to mid latitude sites.

**STABLE ISOTOPE PALEOBIOLOGY.** — No data available.

**REPOSITORY.** — Holotype (P. 44553) deposited at the Natural History Museum, London.
**Catapsydrax dissimilis** (Cushman and Bermúdez, 1937)

*Plate 5.3, Figures 18-20*
(Pl. 5.3, Figs. 18-20, new SEMs of holotype of *Globigerinita dissimilis* Cushman and Bermúdez, 1937)

*n.b.* This is a commonly recognized species in the Oligocene and lower Miocene; here we present an abbreviated synonymy list.

*Globigerina dissimilis* Cushman and Bermúdez, 1937:25, pl. 3: figs. 4-6 [Eocene, Havana Province, Cuba].

*Catapsydrax dissimilis* (Cushman and Bermúdez).—Bolli, Loeblich, and Tappan, 1957:36, pl. 7: fig. 6a-c [reillustration of holotype], figs. 7a-8c [Oligocene-Miocene, Cipero Fm., Trinidad].—Kennett and Srivinasan, 1983:22, pl. 2: figs. 1, 3-8 [lower Miocene Zone N4, DSDP Site 206, Tasman Sea, South Pacific Ocean].

*Globigerinita dissimilis dissimilis* (Cushman and Bermúdez).—Blow and Banner, 1962:106, pl. 14: fig. D [middle Eocene *Truncorotaloides rohri* Zone, Lindi, Tanzania].

*Catapsydrax globiformis* (Blow and Banner, 1962)

*Plate 5.2, Figures 1-8*
(Pl. 5.2, Figs. 1-4: new SEMs of holotype of *Globigerinita globiformis* Blow and Banner)


*Catapsydrax globiformis* (Blow and Banner).—Fleisher, 1974:1016, pl. 4: fig. 6 [middle Eocene Zone E13, Site 219, Arabian Sea].—Warraich and Ogasawara, 2001:44, fig. 12: 7, 8 [Zone E10-13, Kirthar Fm., Sulaiman Range, Pakistan].

**DESCRIPTION.**

*Type of wall:* Cancellate, probably spinose, ruber/sacculifer-type wall texture.

*Test morphology:* Low trochospiral, nearly spherical test with 3-4 chambers in the final whorl. Chambers inflated, globular, increasing rapidly in size with a large bulla that covers the umbilicus and half of the surrounding chambers, walls thickened by gametogenetic calcification; in spiral view 3½-4 globular, embracing chambers increasing rapidly in size, sutures straight, slightly depressed; in umbilical view dominated by a large, low bulla with 3-4 small, semicircular, infralaminal apertures with a continuous, thickened imperforate rim opening onto each suture which is straight and slightly depressed; in edge view nearly circular in shape with large, slightly inflated bulla showing one small aperture opening onto the suture line.

*Size:* Holotype maximum diameter 0.23 mm, thickness 0.20 mm.

**DISTINGUISHING FEATURES.**—*Catapsydrax globiformis* is distinguished from *C. africanus* by its nearly spherical test with thickened walls, less inflated bulla, and smaller infralaminal apertures. *Catapsydrax howei* is larger and has large circular, infralaminal apertures around its strongly inflated bulla.

**DISCUSSION.**—This species is slightly smaller than *C. africanus* and has apparently been overlooked by most previous workers. Its thickened test suggests that it may have dwelled deeper in the water column than *C. africanus*. We illustrate the holotype in SEM for the first time (Pl. 5.2, Figs. 1-4).

**PHYLOGENETIC RELATIONSHIPS.**—*Catapsydrax globiformis* probably evolved from *C. unicavus* in the late Eocene by developing a more spherical test with a large low-lying, slightly inflated bulla with multiple infralaminal apertures opening onto the suture lines.

**STRATIGRAPHIC RANGE.**—Zone E12 to E15.

**GEOGRAPHIC DISTRIBUTION.**—Known from tropical to mid latitude sites.

**STABLE ISOTOPE PALEOBIOLOGY.**—No data available.
REPOSITORY.— Holotype (P. 44551) deposited at the Natural History Museum, London.

**Catapsydrax howei (Blow and Banner, 1962)**

**PLATE 5.2, FIGURES 9-16**  
(Pl. 5.2, Figs. 9-12: new SEMs of holotype of *Globigerinita howei* Blow and Banner.)


*Catapsydrax golicynensis* Menkes, 1975: 281-282, pl. 1: figs. 1-2 [upper Eocene zone of large globigerinids, Borehole 1, Golitsyn depression, Black Sea].

Not *Catapsydrax howei* (Blow and Banner).—Warraich and Ogasawara, 2001: 44, fig. 12: 4-6.

**DESCRIPTION.**

*Type of wall:* Cancellate, probably spinose in life, *rubera/sacculifer*-type wall texture.

*Test morphology:* Low trochospiral, lobulate test with generally 3 chambers, somewhat loosely coiled, in the final whorl. Chambers inflated, globular increasing rapidly in size with a large globular, inflated bulla covering the umbilicus; in spiral view 3 globular chambers increasing rapidly in size, sutures straight to slightly curved, moderately depressed; in umbilical view dominated by a large inflated bulla with 3 large circular, infralaminal apertures with a continuous, thickened imperforate rim facing each suture; sutures straight, somewhat strongly depressed; in edge view globular in shape with bulla showing one infralaminal aperture opening onto the suture line.

*Size:* Holotype maximum diameter 0.54 mm, thickness 0.53 mm.

**DISTINGUISHING FEATURES.**— *Catapsydrax howei* is distinguished from *C. africanaus* by its larger, more loosely coiled test, large globular bulla with large, circular, infralaminal apertures. *Catapsydrax globiformis* is smaller, has a spherical-shaped test with a low slightly inflated bulla with small circular, infralaminal apertures.

**DISCUSSION.**— The loosely coiled test with large circular, infralaminal apertures of *Catapsydrax howei* somewhat resembles Recent *Globigerinoides*, suggesting a shallow habitat in the water column. We illustrate the holotype in SEM for the first time (Pl. 5.2, Figs. 9-12) along with newly collected specimens from the type locality (Pl. 5.2, Figs. 13-16). *Catapsydrax golicynensis* Menkes from the upper Eocene of the Black Sea exhibits the large arched aperture of this species and is a probable synonym. The specimen figured by Warraich and Ogasawara (2001) is a five-chambered form that does not match the morphology of *C. howei*.

**PHYLOGENETIC RELATIONSHIPS.**— *Catapsydrax howei* probably evolved from *C. unicavus* in the middle Eocene by becoming larger and more loosely coiled, and developing a large, globular, inflated bulla with large circular, infralaminal apertures.

**STRATIGRAPHIC RANGE.**— Zone E9 to E16.

**GEOGRAPHIC DISTRIBUTION.**— Known from tropical to mid latitude sites.

**STABLE ISOTOPE PALEOBIOLOGY.**— No data available.

**REPOSITORY.**— Holotype (P. 44550) deposited at the Natural History Museum, London.
PLATE 5.1 Catapsydrax africanus (Blow and Banner, 1962)
PLATE 5.2 *Catapsydrax globiformis* (Blow and Banner, 1962), *Catapsydrax howei* (Blow and Banner, 1962)
Catapsydrax unicavus Bolli, Loeblich, and Tappan, 1957

**PLATE 5.3, FIGURES 1-17**

(Pl. 5.3, Figs. 1-3: new SEMs of holotype of *Catapsydrax unicavus* Bolli)

(Pl. 5.3, Figs. 5-7: new SEMs of holotype of *Globigerina taroubaensis* Brönnimann)

(Pl. 5.3, Figs. 9-11: new SEMs of holotype of *Globorotaloides suteri* Bolli)

?Globigerina taroubaensis* Brönnimann, 1952:18, pl. 2: figs. 16-18 [lower Eocene Ramdat Marl, Trinidad].

*Catapsydrax unicavus* Bolli, Loeblich, and Tappan 1957: 37, pl. 7: fig. 9a-c [upper Oligocene, Cipero Fm., Trinidad], pl. 37: fig. 7a, b [middle Eocene *Truncorotaloides rohri* Zone, Navet Fm., Trinidad].—Stainforth and others, 1975:328, fig. 149-1, 2, 4 [upper Oligocene *Globigerina ciperoensis* Zone, Cipero Fm., Trinidad], fig. 149-5a-c [holotype re-illustrated], fig. 149-3a,b [re-illustration of Blow and Banner, 1962, pl. XIV, fig. M, N].—Kennett and Srivinasan, 1983:26, pl. XIII: figs. N-P [Zone O1, Lindi, Tanzania].

*Globigerina unicavus unicavus* (Bolli), Blow and Banner, 1962:109, pl. 14: figs. M, N [lower Oligocene *Globigerina ampliapertura* Zone, Cipero Fm., Trinidad].


*Globigerina isahayensis* Asano, 1962:55, pl. 21: fig. 9a-c [Eocene, Kyushu, Japan].


DESCRIPTION.

Type of wall: Cancellate, apparently spinose, rubber/sacculifer-type wall texture, generally with heavy gametogenetic calcification.

Test morphology: Low trochospiral, lobulate test with 4 chambers in the final whorl. Chambers globular, embracing, increasing rapidly in size with a small globular, slightly inflated bulla extending over the umbilicus; wall thickened by gametogenetic calcite in adult specimens; in spiral view 4 globular chambers increasing rapidly in size; sutures straight to slightly curved, moderately depressed; in umbilical view 4 globular chambers, with a slightly inflated bulla that has one infralaminal aperture with a continuous, thickened imperforate rim, sutures straight, moderately depressed; in edge view ovoid in shape with small bulla.

Size: Holotype maximum diameter 0.22 mm, thickness 0.17 mm.

DISTINGUISHING FEATURES.—*Catapsydrax unicavus* is distinguished from *C. africanus* by its less inflated bulla with only one infralaminal aperture and from *Catapsydrax dissimilis* by its small compact test and bulla with just one infralaminal aperture. *Catapsydrax globiformis* has a spherical-shaped test.
with a low, slightly inflated bulla with small circular, infralaminal apertures.

**DISCUSSION.**— The type specimen of *unicavus* (which is illustrated in SEM for the first time on Pl. 5.3, Figs. 1-3) is from the lower Miocene Cipero Formation of Trinidad. It is a compact form with a flat inner whorl. Bolli (1957b, p. 116) recorded the stratigraphic range of *unicavus* as beginning in the lower Oligocene *Globigerina ampliapertura* Zone. Bolli (1957b, p. 117) went on to describe the genus *Globorotaloides* for forms that traverse the supposedly characteristic morphologies of three genera in their ontogeny, namely a *Globorotalia*-like inner whorl, followed by a *Globigerina*-like stage where the aperture becomes umbilical, and finally a *Catapsydrax*-like stage with an umbilical bulla.

Comparisons of the respective holotypes of *unicavus* and *suteri* (Pl. 5.3, Figs. 1-3, 9-11) reveal many similarities. Both are compact forms with a relatively flat inner whorl and a similar, cancellate wall texture, although neither is very well preserved. The two species differ mainly in the fact that *suteri* has a more inflated bulla. However we do not consider this an important characteristic, as it is very variable in populations, and conclude that the two specimens are conspecific, with *suteri* (Bolli) being a junior synonym of *Catapsydrax unicavus*. The status of specimens of true *Globorotalia*-like forms that have been described as *suteri* in the literature are discussed under that genus, below.

Brönnimann (1952) described a small compact bullate species as *Globigerina taroubaensis* from the lower Eocene Navet Formation of Trinidad. The holotype is illustrated for the first time in SEM in Pl. 5.3, Figs. 5-7. It is very similar to the holotype of *unicavus* and we regard it as a possible senior synonym. However because *taroubaensis* has rarely been described by subsequent workers (with the notable exception of Blow, 1979, p. 1346) we recommend continuance of the *unicavus* name until such time as the respective taxa can be researched in more detail in their type sections. It may well be that *taroubaensis* will ultimately be recognized as specifically distinct, as argued by Blow (1979).

Finlay (1939) described (without illustrating) *Globigerina linaperta* var. *turgida*. Jenkins selected and illustrated a lectotype in 1964. Blow (1969) considered the taxon valid, placing it in *Globigerinina* which is a microperforate genus in contrast to the normal perforate *turgida*. Fleisher (1974) and Krasheninnikov and Basov (1983) assigned *turgida* to *Globorotaloides* following Jenkins (1964). In our opinion the taxon is best placed in *Catapsydrax* due to its bulla with a single aperture. We have chosen to regard *turgida* and *unicavus* as conspecific and since *unicavus* was first illustrated and is a well understood taxon we prefer to use this name for nomenclatural stability.

Specimens of *Catapsydrax unicavus* are consistently present in middle and upper Eocene planktonic foraminiferal assemblages, but only as a minor component. Stable isotope studies (e.g. Poore and Matthews, 1984) suggest that they occupied a deep-dwelling planktonic habitat, in which population sizes were never large. We have observed considerable variability in the degree of chamber appression and bulla morphology. However, we acknowledge that future studies may well reveal more than one valid taxon within our broad concept of *unicavus*, especially as regards the larger, more loosely coiled morphotypes; but with the present level of understanding we can suggest no consistent way to subdivide them.

**PHYLOGENETIC RELATIONSHIPS.**— *Catapsydrax unicavus* is probably derived from a subbotinid in the early Eocene by developing a bulla that extends over the umbilicus.

**STRATIGRAPHIC RANGE.**— Zone E2 to N6.

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**Owall, Pearson, and Huber**

Plate 5.3, 1-17, *Catapsydrax unicavus* Bolli, 1957; 18-20, *Catapsydrax dissimilis* (Cushman and Bermúdez, 1937)

1-4, 14, 16 (1-3, holotype, USNM 4216, *Globigerina ciperoensis* Zone, Cipero Fm. Trinidad), Zone E11, Guayabal Fm, Tampico, Mexico; 5-7 *Globigerina taroubaensis* Brönnimann, 1952, holotype (USNM 370087), lower Eocene, Ramdat Marl, Trinidad; 8, 15, Zone E7, Aragon Fm, Mexico; 9-11 *Globorotaloides suteri* Bolli, 1957, holotype (USNM P5654), *Globigerina ampliapertura* Zone, Cipero Fm, Trinidad; 12, Zone AE6/7, ODP Hole 1138A/38R/e, Kerguelen Plateau, southern Indian Ocean; 13, Zone E8, TDP Site 2/18/1, 20-26 cm, Kilwa, Tanzania; 17, Zone E10/11?, ODP Hole 761B/8H/5, Wombat Plateau, eastern Indian Ocean; 18-20 *Catapsydrax dissimilis* (Cushman and Bermúdez, 1937), holotype (USNM 23430), upper Eocene, Cuba. Scale bar: 1-20 = 100 µm.
Plate 5.3 Catapsydrax unicavus Bolli, Catapsydrax dissimilis (Cushman and Bermúdez, 1937)
PLATE 5.4 *Globorotaloides eovariabilis* Huber and Pearson n. sp.
Chapter 5 - Catapsydrax, etc.

GEOGRAPHIC DISTRIBUTION.— Global.

STABLE ISOTOPE PALEOBIOLOGY.— Stable isotope studies (Poore and Matthews, 1984) suggest that C. unicavus occupied a deep-dwelling planktonic habitat in which population sizes were never large.

REPOSITORY.— Holotype (USNM 4216) Smithsonian Museum of Natural History, Washington, D.C.

Genus Globorotaloides Bolli, 1957

TYPE SPECIES.— Globorotaloides variabilis Bolli, 1957.

DESCRIPTION.

Type of wall: Spinose, normal perforate, coarsely cancellate, sacculifer-type to ruber/sacculifer-type wall texture.

Test morphology: Globular, lobulate, with 4-6 chambers in the final whorl; in spiral view the inner whorl has a Globorotalia-like flattened coil; chambers become globular and more loosely coiled in the ultimate whorl; in umbilical view the ultimate chamber may be cantilevered towards the umbilicus, aperture extrumbilical bordered by thin continuous lip; in edge view chambers globular, near spherical, aperture a circular opening bordered by a continuous lip.

DISTINGUISHING FEATURES.— Distinguished from other Globigerinacea by Globorotalia-like flattened inner coil of chambers, and the outer coil of globigerine chambers and coarsely cancellate wall texture. Parasubbotina lacks the flattened inner coil of chambers and in general the wall texture is not as coarsely cancellate.

DISCUSSION.— Globorotaloides was described from the upper Miocene of Trinidad. It is a distinctive form that is easily recognized although we here exclude one species that has commonly been included in the genus and to which Eocene forms have generally been referred, namely suteri Bolli (here regarded as a junior synonym of Catapsydrax unicavus; see above). Globorotaloides maintains a low diversity throughout its geologic range, with seldom more than two species present at any one level. It apparently evolved in the early Eocene Zone E2 and ranges to the Recent. In the Eocene it had a wide geographic distribution from low to high latitudes, but it is most common and stratigraphically useful in the high latitudes.

Globorotaloides eovariabilis Huber and Pearson new species

PLATE 5.4, FIGURES 1-17

Clavigerinella ?columbiana (Petters).—McKeel and Lipps, 1975:258, pl.3: fig. 8a-c (partim; not pl. 4: fig. 6a, b = Parasubbotina eoclava Coxall, Huber, and Pearson) [lower middle Eocene, Elkton Siltstone, Coast Ranges, Oregon]. [Not Petters, 1954.]


Globorotalia munda Jenkins.—Krasheninnikov and Basov, 1983:841 (partim), pl. 10: fig. 101 [lower Eocene, DSDP Site 511, Falkland Plateau, South Atlantic]. [Not Jenkins, 1966.]


Plate 5.4 Globorotaloides eovariabilis Huber and Pearson n. sp.

1-3, 5-11 (1-3, holotype, USNM 523429; 5-8, paratype, USNM 523430a; 9, 10 paratype, USNM 523430b), Zone E10-E11, ODP Site 647/50R/5, 101 cm, Labrador Basin, North Atlantic Ocean; 4, Zone AE7, ODP Hole 690B/12H/2, 63-77, Maud Rise, southern Indian Ocean; 12, 13, 17, Zone AE2, ODP Hole 738C/6R/1, 84-89 cm, Kerguelen Plateau, southern Indian Ocean (same specimen); 14-16, Zone AO1, ODP Hole 738B/4H/5, 90-95 cm, Kerguelen Plateau, southern Indian Ocean (same specimen). Scale bar: 1-7, 9-17 = 40 µm; 8 = 10 µm.

Globorotaloides aff. suteri Bolli.—Nocchi and others, 1991:268, pl. 4: figs. 4, 5 [lower middle Eocene Zone E8-E9, ODP Site 699, southern South Atlantic]. [Not Bolli, 1957b.]

Globorotaloides suteri Bolli.—Berggren, 1992:564, pl. 4: fig. 4 [upper Eocene G. suteri Zone ODP Hole 748B, Kerguelen Plateau, southern Indian Ocean]. [Not Bolli, 1957b.]

Globorotaloides sp. 1, Berggren, 1992: 568, pl. 4: fig. 11 [upper Eocene G. suteri Zone, ODP Hole 748B, Kerguelen Plateau, southern Indian Ocean].

DESCRIPTION.

Type of wall: Normal perforate, coarsely cancellate, sacculifer-type wall texture, often with corroded interpore ridges resulting in a remnant wall texture consisting of distinct ‘rosettes’ around the pores.

Test morphology: Test outline lobate, subcircular in axial view, axial periphery rounded to very slightly compressed, biconvex, oval to egg-shaped in edge view; 3-3½ whorls of slightly inflated chambers arranged in a flattened to slightly elevated trochospire; 14-15 chambers in adult tests, 4½-6 in the final whorl increasing moderately in size; umbilicus shallow to moderately deep and narrow; umbilical sutures moderately depressed, radial; spiral initially indistinct, later weakly depressed, radial; aperture a low umbilical-extraumbilical arch extending one-third towards peripheral margin, surrounded by a broad lip that extends into the umbilical area.

Size: Holotype (USNM 523429) maximum diameter 0.18 mm, breadth 0.10 mm; paratype a (USNM 523430) maximum diameter 0.13 mm, breadth 0.80 mm; paratype b (USNM 523430) maximum diameter 0.15 m, breadth 0.93 mm.

ETYMOLOGY.—Named as “dawn” variabilis because of its superficial resemblance to the much younger species Globorotaloides variabilis Bolli.

DISTINGUISHING FEATURES.—Differs from Globorotaloides quadrocameratus n. sp. by having 4½ to 6, rather than 4-4½, final whorl chambers that are less inflated and increase more gradually in size; differs from Globorotaloides variabilis by its smaller size and less flat inner whorl.

DISCUSSION.—This form has been widely recognized at high latitude sites using various species names and open nomenclature. It is included in Globorotaloides because of its coarsely cancellate wall texture and low, sometimes flattened spiral coil. Specimens frequently exhibit corroded interpore ridges with a remnant surface texture consisting of a distinct rosette pattern (Pl. 5.4, Figs. 4, 13-15). A high latitude form from the lower Eocene of Site 690 (Maud Rise) that may be related to this species was designated by Stott and Kennett (1990, pl. 5, figs. 3-4) as “Tenuitella” reissi (Loeblich and Tappan). This morphotype has a similar coarsely reticulate wall texture but it is higher spired and the equatorial margin is more compressed.

PHYLOGENETIC RELATIONSHIPS.—Descended from Globorotaloides quadrocameratus n. sp. during the early Eocene. Intermediate morphologies can be found (e.g., Pl. 5.5, Figs. 13-15).

STRATIGRAPHIC RANGE.—Lower Eocene-lower Oligocene, Zone E7 to Zone O1 at low latitudes, and Zone AE4-AO1 at high latitudes.

GEOGRAPHIC DISTRIBUTION.—Found at deep-sea sites in southern and northern high latitudes but not at middle or low latitudes.

Plate 5.5 Globorotaloides quadrocameratus Olsson, Pearson, and Huber n. sp.

1-8, 12, 16 (1-3, holotype, USNM 521865; 5-7, paratype, USNM 521866), Zone E11, Guayabal Formation, Tampico, Mexico, type locality (8 = wall texture view of fig. 4, 16 = wall texture view); 9-11, Zone E7, TDP Site 2/10/CC, Kilwa Masoka, Tanzania (same specimen); 13-15 (specimen showing transition to Globorotaloides eovariabilis), Zone AE6/7, ODP Hole 738B/15X/CC, Kerguelen Plateau, southern Indian Ocean. Scale bar: 1-7, 9-15 = 100 µm; 8 = 10 µm; 16 = 20 µm.
PLATE 5.5 Globorotaloides quadrocameratus Olsson, Pearson, and Huber n. sp.
PLATE 5.6 Guembelitrioides nuttalli (Hamilton, 1953)
STABLE ISOTOPIC PALEOBIOLOGY.— No data available.

TYPE LOCALITY.— The holotype and paratypes are from the middle Eocene of ODP Hole 647A (Sample 647A-50R-5, 101 cm) in the Labrador Basin, which was assigned to calcareous nannofossil Zone NP16 by Firth (1989).

REPOSITORY.— Holotype (USNM 523429) and paratypes (USNM 523430a, 523430b) deposited at the Smithsonian Museum of Natural History, Washington, D.C.

Globorotaloides quadrocameratus, Olsson, Pearson, and Huber new species

PLATE 5.5, FIGURES 1-16

Globigerina sp. McKeel and Lipps, 1972:90, pl. 3: fig. 4a-c (partim; not pl. 2: fig. 2a-c) [upper Eocene, Alsea Siltstone, Coast Ranges, Oregon].

DESCRIPTION.

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

Test morphology: Test very low trochospiral, lobulate in outline, chambers globular; in spiral view 4-4½ globular, slightly embracing chambers in ultimate whorl, increasing rapidly in size, ultimate chamber may be reduced in size, sutures moderately depressed, straight; in umbilical view 4 globular, slightly embracing chambers, increasing rapidly in size, ultimate chamber often reduced and directed towards and over the umbilicus, sutures moderately depressed, straight, umbilicus small and often covered by ultimate chamber, aperture umbilical in adult specimens, a low opening bordered by narrow thickened lip; in edge view chambers globular in shape, slightly embracing.

Size: Maximum diameter of holotype 0.27 mm, minimum diameter 0.25 mm, maximum width 0.13 mm.

ETYMOLOGY.— Named after the four chambers in the final whorl, by which it is distinguished from Globorotaloides eovariabilis n. sp.

DISTINGUISHING FEATURES.— Globorotaloides quadrocameratus n. sp. is characterized by its small, lobulate test, 4-4½ chambers in the ultimate whorl, the umbilically directed ultimate chamber, and the sacculifer-type wall texture.

DISCUSSION.— Globorotaloides quadrocameratus n. sp. appears to be the first species of Globorotaloides. It may have evolved in the basal Eocene from a parasubbotinid ancestor by flattening of the coil and developing a coarsely cancellate test, which is typical of the genus. The species is more typical of low latitude localities than later species of Globorotaloides, but also occurs in mid and higher latitudes.

PHYLOGENETIC RELATIONSHIPS.— The origin of Globorotaloides quadrocameratus is unknown. It is possibly derived from Parasubbotina varianta with which it shares some morphologic features, principally in the sacculifer wall texture on parts of the test, rapidly enlarging chambers, and low trochospiral test. It also gave rise to Globorotaloides eovariabilis n. sp.

STRATIGRAPHIC RANGE.— E2 to E16.

GEOGRAPHIC DISTRIBUTION.— This species is known from tropical and high latitude sites.

STABLE ISOTOPE PALEOBIOLOGY.— No data available.

Plate 5.6 Guembelitrioides nuttalli (Hamilton, 1953)

1 (holotype, USNM 688704), middle Eocene, Horizon Guyot, Pacific Ocean; 2, Zone E9, ODP Hole 865B/7H/3, 60-62 cm; 5, 7, 8, 13, Zone E9, ODP Hole 865C/7H/1, 110-112 cm; 6, 9, 10, Zone E9, ODP Hole 865B/6H/1, 89-91 cm, 12, Zone E9, ODP Hole 865B/7H/3, 60-62 cm, Allison Guyot, equatorial Pacific Ocean; 3, 4, 11, 16, Zone E7, Aragon Fm, Tampico, Mexico; 14 (reillustration of pl. 1, fig. 15, Pearson and others, 2004), Zone E8, TDP Site 2/18/1, 20-26 cm, Kilwa Tanzania; 15 (reillustration of pl. 1, fig. 16, Pearson and others, 2004), Zone E8, TDP Site 2/9/CC, Kilwa, Tanzania; 17-19 (holotype, Globigerinoides higginsi Bolli, 1957, USNM P5720), middle Eocene, core sample 120-122 cm, western North Atlantic Ocean; 20, Zone E9, TDP Site 13/16/2, 30-40 cm, Mkazambo, Tanzania. Scale bar: 1-20 = 100 µm.
REPOSITORY.— Holotype (USNM 521865) and paratype (USNM 521866) deposited at the Smithsonian Museum of Natural History, Washington, D.C.

Genus Guembelitrioides El Naggar, 1971


TYPE SPECIES.— “Globigerinoides” higginsi Bolli, 1957; junior synonym of “Globigerinoides” nuttalli Hamilton, 1953.

DESCRIPTION.
Type of wall: Spinose, high porosity cancellate sacculifer type wall texture, pore diameter 5 µm.

Test morphology: Test trochospiral, globigeriniform, high spired becoming helicospiral with ontogeny; chambers subspherical, loosely attached in final whorl(s); sutures radial, moderately to strongly depressed; periphery distinctly lobate; primary aperture arched, umbilical, at least one supplementary aperture is usually present on the spiral side of the final whorl.

DISTINGUISHING FEATURES.— Guembelitrioides is distinguished from the high-spired Subbotina gortani group by the presence of supplementary sutural apertures in most specimens. The two are also separated by a gap in their stratigraphic ranges. As described by Blow (1979), in both general morphology and wall ultrastructure Guembelitrioides is closely similar to the modern genus Globigerinoides but is an unrelated homeomorph.

DISCUSSION.— El-Naggar (1971, p. 450) in his classification of Globigerinacea stated that, in his view, “highly turreted Globigerinoides” species, such as Globigerinoides higginsi Bolli, 1957, are in fact Guembelitrias with developed supplementary apertures. They are related to Guembelitria in the same way as Globigerinoides is related to Globigerina”. However, Guembelitrioides bears no relation to Guembelitria, which is a microperforate nonspinose genus. On the other hand, Bolli (1957b) in describing his species clearly stated that his Globigerinoides higginsi (= nuttalli) had no relationship with Neogene Globigerinoides even though they both shared supplementary apertures. Nevertheless it is useful to recognize the nuttalli (= higginsi) morphology as distinct at the generic level, so El Naggar’s name stands. The genus is monospecific.

Loeblich and Tappan (1961, 1988) included the genus Guembelitriodes in the Family Catapsydracidae. Here we include it in the Family Globigerinidae.

Guembelitrioides nuttalli (Hamilton, 1953)

PLATE 5.6, FIGURES 1-20
(Pl. 5.6, Fig. 1, new SEM of holotype of Globigerinoides nuttalli Hamilton)
(Pl. 5.6, Figs. 17-19, new SEMs of holotype of “Globigerinoides” higginsi Bolli)

Globigerinoides nuttalli Hamilton, 1953:224-225, pl. 32: fig. 23 (holotype), figs. 22, 24 [middle Eocene Hantkenina aragonensis Zone, Horizon Guyot, Pacific Ocean].

Guembelitrioides nuttalli (Hamilton).—Pearson and others, 2004:36, pl. 1: figs. 15, 16 [middle Eocene, Tanzania].

“Globigerinoides” higginsi Bolli, 1957b:164, pl. 36: figs. 11a-c (holotype) [lower middle Eocene, from an unnamed core, western North Atlantic Ocean], figs. 12a-13b paratypes [middle Eocene Hantkenina aragonensis Zone, Navet Fm., Trinidad].— Toumarkine, 1983:118, pl. 9: figs. 14a-b (refigured holotype), figs. 15-16 [middle Eocene Globorotalia lehneri Zone, DSDP Site 313, mid-Pacific Ocean].
Plate 5.7 Paraglobochone griffinoides Olsson and Pearson, n. sp.
Paragloborotalia nana (Bolli, 1957), Paragloborotalia opima (Bolli, 1957)
**Globigerinoides higginsi** Bolli.—Samanta, 1970:194, pl.2: fig.15 [middle Eocene Zone E12, Lakhpat, Cutch, India].—Toumarkine, 1975:742, pl. 1, figs. 16-17 [middle Eocene *Globorotalia lehneri* Zone, DSDP Site 313, mid-Pacific Ocean].

**Globigerina higginsi** (Bolli).—Stainforth and others, 1975:189, fig. 52-1a-3a (reillustration of holotype and paratypes); fig. 52-5?, 6-7, 8? [middle Eocene *Hantkenina aragonensis* Zone, Navet Fm., Trinidad].


**Guembelitrioides higginsi** (Bolli).—Pearson and others, 1993:128, pl. 2: figs. 10-12 [middle Eocene, DSDP Site 523, South Atlantic Ocean].

Not *Globigerina higginsi* (Bolli).—Pujol, 1983, pl. 7, fig. 7 [DSDP Hole 516F, Rio Grande Rise, South Atlantic Ocean = *Subbotina gortanii*?].

Not *Subbotina higginsi* (Bolli).—Nocchi and others, 1991, pl. 2: fig. 17 [= *Praemurica lozanoi*].

Not *Globigerina higginsi* Bolli.—Warraich and Ogasawara, 2001:45, fig. 17: 12, 13.

**DESCRIPTION.**

*Type of wall:* Cancellate, spinose, sacculifer-type, cancellate wall.

*Test morphology:* Test trochospiral, initially moderately high spired to helicospiral late in ontogeny; chambers globigeriniform, mainly spherical, increasing rather rapidly in size as added, the last one often somewhat ovate, 9-10 to occasionally 15, arranged in 2½-3 loosely coiled whorls; periphery of the last whorls strongly lobate; sutures radial, ranging from moderately depressed in the initial spire to strongly depressed in the adult; umbilicus narrow and deep sometimes covered by a bulla of variable size; primary aperture a medium high arch, umbilical in position; one to more supplementary apertures may be present along the sutures on the spiral side of the final whorl(s).

**Size:** Holotype height 0.48 mm, width 0.45 mm; largest diameter of *higginsi* holotype 0.55 mm.

**DISTINGUISHING FEATURES.**—The very high spire, lobate periphery, globular chambers and supplementary apertures typically characterize this species. Moreover, Hamilton (1953) clearly described the wall surface with typically hexagonal pore structures. Specimens from Tanzania show spine holes and spines embedded in the wall, indicating that it was spinose in life (Pearson and others, 2004; Premoli Silva and others, Chapter 7, this volume).

**DISCUSSION.**—*Guembelitrioides nuttalli* is a common constituent of middle Eocene assemblages but has generally been described under the name *Globigerinoides higginsi* Bolli. This species displays some morphological variability of the number of chambers and height of the spire, the range of which is well exemplified by both *nuttalli* and *higginsi* holotypes. Other variable features are the possible presence of more than one supplementary aperture, the size of the last chamber and the primary aperture and possible presence of a bulla-like final chamber. Stainforth and others (1975) included *higginsi* in the genus *Globigerina* as they did not consider the presence of secondary sutural apertures of generic importance. Pujol (1983) illustrated a high-spired specimen as *Globigerina higginsi*, which is not conspecific with *G. nuttalli* and resembles *Subbotina gortanii*. Warraich and Ogasawara (2001) also figured a high-spired specimen that also resembles *S. gortanii*.

**PHYLOGENETIC RELATIONSHIPS.**—Hillebrandt (1976) considered Bolli’s types of *G. higginsi* as conspecific with *Globigerina lozanoi* Colom, but he later

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**Plate 5.8, 1-12, Paragloborotalia nana** (Bolli, 1957), 13-16, *Paragloborotalia opima* (Bolli, 1957)

*Paragloborotalia nana* 1-4 (1-3, holotype, USNM P5661), Zone O5, *Globorotalia opima opima* Zone Cipero Fm, Trinidad; 5, 11, 12, Zone E7, TDP Site 25/CC, Tanzania (11, 12, transitional to *Paragloborotalia griffioides*); 6-8, Middle Eocene, ODP Hole 960A/14R/CC, Ivory Coast, eastern South Atlantic Ocean; 9, 10, Zone E9, TDP Site 2/10/CC Kilwa Masoko, Tanzania. *Paragloborotalia opima* 13-16 (13-15, holotype, new SEMs, USNM P5659), Zone O5, *Globorotalia opima opima* Zone Cipero Formation, Trinidad. Scale bar: 1-16 = 100 μm.
(1976) stated that G. higginisi (= G. nuttalli) was descended from lozanoi. Further, Blow (1979, p. 863) suggested that there are transitional forms between lozanoi and higginisi (= nuttalli). According to him, “both taxa are very similar in dorsal morphology” and the “trends involved are merely confined to a simple increase in the height of the trochospire and the acquisition of supplementary apertures on spiral side” with both lozanoi and higginisi (= nuttalli) morphotypes coexisting in Zone P9 (= E7). However, we disagree that G. nuttalli is derived from lozanoi. It is difficult to see the derivation of the 4-chambered, spinose, highly lobulate nuttalli from the 6-chambered, nonspinose, slightly lobulate lozanoi. Furthermore, G. nuttalli has a high porosity, cancellate sacculifer-type wall that also occurs in Parasubbotina inaequispira, which is a highly lobulate taxon. We believe that P. inaequispira is a more likely ancestor of Guembelitrioides, but intermediate forms have yet to be found. Subbotina yeguaensis is also a possible ancestral taxon since it has a lobulate test with a moderately elevated initial spire, although it is not as lobulate as P. inaequispira.

Blow (1979) also suggested that higginisi (= nuttalli) may be ancestral to Globigerinatheka mexicana (= Porticaulaphera in Blow 1979). This relationship, however, is rejected here, as transitional forms between G. nuttalli and G. mexicana have not been observed. Nevertheless G. nuttalli is regarded by us as the most likely ancestor of the Globigerinatheka group (see Premoli Silva and others, Chapter 7, this volume).

STRATIGRAPHIC RANGE.— Base E8 to top E10.

GEOGRAPHIC DISTRIBUTION.— Mid to low latitudes.

STABLE ISOTOPE PALEOBIOLOGY.— Guembelitrioides nuttalli has carbon and oxygen stable isotopic characters intermediate between the muricate species and the subbotinids, suggesting an intermediate depth habitat (Pearson and others, 1993).

REPOSITORY.— Holotype (USNM 688704) deposited at the Smithsonian Natural History Museum, Washington, D.C.

Genus Paragloborotalia Cifelli, 1982

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

DESCRIPTION.

Type of wall: Normal perforate, coarsely cancellate, sacculifer-type wall texture, spinose (Cifelli, 1982).

Test morphology: Very low trochospiral, globular, compact, subquadrate to quadrate in outline, chambers globular, much embracing; in spiral view, 4-5 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 4-5 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.

DISTINGUISHING FEATURES.— The genus is distinguished by the very low trochospiral test and low-arched umbilical-extraumbilical aperture with a thick lip of constant thickness. There are 4-5 chambers in the ultimate whorl, and a coarsely cancellate, sacculifer-type wall.
Plate 5.9 Parasubbotina eoclava Coxall, Huber, and Pearson, 2003
OLSSON, PEARSON, AND HUBER

Plate 5.10 Parasubbotina griffinae (Blow, 1979)
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 non-spinose genus *Globorotalia*. However, in an early application of wall texture-based taxonomy, Cifelli (1982) showed that *opima* possesses a cancellate wall and, based on observed spine holes, must originally have been spinose. *Paragloborotalia opima* is descended from the closely related species *P. nana*, which was initially traced down to the lower Oligocene of the Cipero Formation, Trinidad by Bolli (1957b) and subsequently into the upper Eocene by Blow (1979). We have now traced it as low as Zone E7 in cores from Tanzania, although these earliest morphotypes show some transitional features to *P. griffinoides* n. sp. Our researches show that *P. nana* is part of a conservative lineage of low-trochospiral species that is rooted in the genus *Parasubbotina*.

*Parasubbotina* is a more loosely coiled genus with less embracing chambers, and its species tend to be more variable in morphology in chamber arrangement and shape, size, and wall texture; whereas *Paragloborotalia* has a very conservative, generalized morphology, and less variable test morphology. From its origin from *Parasubbotina* in Zone E1, it is represented by only two Eocene species, *P. nana* and *P. griffinoides* n. sp. These are both characterized by (typically) having only 4 chambers in the ultimate whorl, an umbilical-extraumbilical aperture with a thick lip of constant thickness around the aperture, and small test size.

*Paragloborotalia griffinoides* Olsson and Pearson, new species

Plate 5.7, Figures 1-19
(Pl. 5.7, Figs. 4-6: reillustration of paratypes of *Globorotalia (Turborotalia) griffinae* Blow)

*Globorotalia bolivariana* Petters, Bolli 1957a: 169, pl. 37: fig. 14a-16 [*Porticulasphaera mexicana* Zone, Navet Fm., Trinidad]. [Not Petters, 1954.]

*Subbotina bolivariana* (Petters).—McKeel and Lipps, 1972:85, pl. 1, fig. 1a-c [middle Eocene, Tulee Fm., Coast Ranges, Oregon]. [Not Petters, 1954.]


*Globorotaloides wilsoni* Cole.—Poore and Brabb, 1977:263, pl. 2: figs. 10-13 [middle Eocene Zone E13, Twobar Shale Member, San Lorenzo Fm., Santa Cruz mountains, California]. [Not Cole, 1927.]

*Globorotalia (Turborotalia) griffinae* Blow, 1979:1072 (partim), pl. 157: fig. 7 [Zone E8, KANE 9-Core 42, Endeavour seamount, equatorial Atlantic Ocean]; pl. 162, figs. 8-9 [Zone E8, KANE 9-Core 42, Endeavour seamount, equatorial Atlantic Ocean]; pl. 165, figs. 1-3 [Zone E8, KANE 9-C piston core, Endeavour seamount, equatorial Atlantic Ocean]. [Not Blow, 1979.]

*Turborotalia griffinae* (Blow).—Toumarkine and Luterbacher, 1985:127, fig. 27:18 (reillustration of Blow 1979, pl. 165, fig. 2); fig. 27:19-23 [Middle Eocene, Bou Arada, Tunisia]. [Not Blow, 1979.].—Warraich and Ogasawara, 2001:23, fig. 5: 13, 14, 18 [Zone E10-12, Kirthar Fm., Sulaiman Range, Pakistan]. [Not Blow, 1979.]

*Globorotalia nana* Bolli.—Poore and Bybell, 1988:18, pl. 5: fig. 9 [upper Eocene, Core ACGS # 4, New Jersey Coastal Plain]. [Not Bolli, 1957b.]

DESCRIPTION.

Type of wall: Normal perforate, coarsely cancellate, 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
opening, sometimes closed off by surrounding chambers;
aperture umbilical-extrumbilical, bordered by a narrow,
often thickened, continuous, lip; ultimate chamber may
be slightly reduced in size; in edge view chambers
globular, periphery rounded, aperture a high arch
extending midway onto the peripheral edge, bordered
by a thickened lip.

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

ETYMOLOGY.— Named because it is like, but not
identical to, Parasubbotina griffinae (Blow).

DISTINGUISHING FEATURES.— P. griffinoides is
distinguished by its small, very low trochospiral,
compact, subquadrate test, coarsely cancellate wall, and
aperture with a thickened continuous lip. 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. Parasubbotina
griffinae differs from Paragloborotalia griffinoides in
its generally larger test size, greater number of chambers
in the ultimate whorl, and high porosity, reticulate wall.

DISCUSSION.— When Blow (1979) described
Globorotalia (Turborotalia) griffinae (=Parasubbotina
griffinae) he selected the holotype and some paratypes
from the same sample (KANE 9 Core 42, 200 cm) from
which he also illustrated Hastigerina? bolivariana (= Pseudoglobigerinella bolivariana). His case for
regarding griffinae as ancestral to bolivariana is clear
from the SEM illustrations of the two species (his pl.
150, figs. 1-9) as they both share a sacculifer-type
reticulate wall texture. The illustration of paratypes from
other levels in KANE 9 Core 42 (his pl. 157, fig. 7, from
95 cm; pl. 162, figs. 8, 9, from 42 cm; pl. 165, figs. 1-3,
from 15 cm), however, clearly differ from the holotype
and paratypes of the species illustrated from the type
level of the holotype. These paratypes differ in having
a more coarsely cancellate, non-reticulate wall texture
and a thickened, continuous apertural lip. The test is
more compact and subquadrate in shape, in contrast to
P. griffinoides. These morphotypes are the basis for the
new species, Paragloborotalia griffinoides. Toumarkine
and Luterbacher (1985) and Warraich and Ogasawara
(2001) also included morphotypes like these in griffinae
(which were placed by them in Turborotalia, fig. 27:19-
23 and fig. 5: 13, 14, 18, respectively). P. griffinoides is
a common and widespread form in the Eocene and its
stratigraphic range is from lower to upper Eocene.

PHYLOGENETIC RELATIONSHIPS.— The genus
Paragloborotalia arose through the development of P.
griffinoides from Parasubbotina varianta in Zone P5.
The close relationship of P. griffinoides and P. varianta
is clearly seen in specimens from Zone E1 in the Bass
River Borehole, New Jersey (Pls. 5.7 and 5.13). The
two species are linked by transitional morphotypes that
show a range of test morphology from the inflated,
compact, subquadrate test of P. griffinoides to the more
loosely coiled, less inflated test of P. varianta.

STRATIGRAPHIC RANGE.— Zone E1 to Zone E16.

GEOGRAPHIC DISTRIBUTION.— P. griffinoides
seems to have preferred cold-water high productivity
environments and is generally absent from deep-sea
oligotrophic settings.

STABLE ISOTOPE PALEOBIOLOGY.— Recorded
(as P. wilsoni) by Pearson and others (2001) with

Plate 5.11, 1-15, Parasubbotina inaequispira (Subbotina, 1953); 16-18, Parasubbotina prebetica (Martínez-Gallego and Cremades,
1978)

1-3 Parasubbotina inaequispira (holotype, VNIGRI No. 3069), lower/middle Eocene, Zone of Conical Globorotalia, Kuban River, northern
Caucasus; 4, 6, 7, lower/middle Eocene, bed 11, Khieu River, northern Caucasus; 5, 10 (10 reillustration of pl. 1, fig. 13, Pearson and
others, 2004), Zone E6/7, TDP Site 2/25/CC, Kilwa, Tanzania; 8, 9, 11-15, Zone E1, Bass River Borehole, ODP 174AX: 1171.0-.6 feet (15 =
wall texture view of fig. 14). 16-18 Parasubbotina prebetica (holotype), lower Eocene, Villafranqueza, Rincon de Santana hills, Spain.
Scale bar: 1-14 = 100 μm; 15 = 4 μm.
Parasubbotina inaequispira (Subbotina, 1953), Parasubbotina prebetica (Martínez-Gallego and Cremades, 1979)

Plate 5.11 Parasubbotina inaequispira (Subbotina, 1953), Parasubbotina prebetica (Martínez-Gallego and Cremades, 1979)
OLSSON, PEARSON, AND HUBER

PLATE 5.12 Parasubbotina pseudowilsoni Olsson and Pearson, n. sp.
consistently positive $\delta^{18}$O and strongly depleted $\delta^{13}$C indicating a deep planktonic habitat.

REPOSITORY.—Holotype (USNM 523424) deposited at the Smithsonian Museum of Natural History, Washington, D.C.

*Paragloborotalia nana* (Bolli, 1957)

**Plate 5.8, Figures 1-16**
(Pl. 5.8, Figs. 1-3: new SEMs of holotype of *Globorotalia opima nana* Bolli)

*Globorotalia opima nana* Bolli 1957b:118, pl. 28: fig. 3a-c [Oligocene *Globorotalia opima opima* Zone, Cipero Fm., Trinidad].—Bolli and Saunders, 1985:202, fig. 26:16a-c (holotype reillustrated), fig. 26:15, 17-20 (paratypes) [Oligocene *Globorotalia opima opima* Zone, Cipero Fm., Trinidad].—Toumarkine 1978:714, pl. 8: figs. 3-4 [Oligocene *Globorotalia opima opima* Zone, DSDP Site 360, southeast Atlantic Ocean].

*Globorotalia* (Turborotalia) *opima nana* Bolli.—Blow, 1969:154, pl. 39: fig. 1 [lower Oligocene Zone P20, Cipero Fm., Trinidad].


*Jenkinsella opima nana* (Bolli).—Poag and Commeau, 1995:149, pl. 6: figs. 21, 22 [Oligocene, Hammond Well, Maryland].

*Paragloborotalia nana* (Bolli).—Pearson and others, 2004:36, pl. 1: fig. 21 [middle Eocene Zone P11, Tanzania].

**DESCRIPTION.**

Type of wall: Normal perforate, coarsely cancellate, *sacculifer*-type, spinose in life, heavy gametogenetic calcification is often present.

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

Size: Maximum diameter of holotype 0.25 mm, minimum diameter 0.23 mm, maximum width 0.28 mm.

**DISTINGUISHING FEATURES.**—*Paragloborotalia nana* is a small species, as the name suggests, and tends to be very conservative in morphology. A prominent lip is always present, which often nearly obscures the primary aperture. *Paragloborotalia nana* usually has 4 chambers in the final whorl. The slowly enlarging chambers in the final whorl give the test a compact, quadrangular appearance. The tight coiling, much inflated, embracing chambers, and very narrow umbilicus combined with straight radial sutures means that the sutures make out a cross pattern in both spiral and umbilical views in four-chambered specimens. *P. nana* is distinguished from *P. griffinoidea* in having a quadrate-shaped, more compact test. In *P. nana*, the chambers in the ultimate whorl increase more slowly in size with the ultimate chamber nearly equal in size to the penultimate chamber, thus developing a quadrate shape.
PHYLOGENETIC RELATIONSHIPS.— *P. nana* evolved from *P. griffiooides* in the middle Eocene by developing more inflated, embracing chambers, and a slower rate of chamber size increase in the ultimate whorl. It was ancestral to *P. opima* in the Oligocene.

STRATIGRAPHIC RANGE.— According to Blow (1979) and Toumarkine and Luterbacher (1985), *P. nana* first appeared in upper Eocene Zone E13. However, forms transitional from *P. griffiooides* occur as low as Zone E7 in Tanzania (Pearson and others, 2004). It persisted until the lower Miocene.

GEOGRAPHIC DISTRIBUTION.— Worldwide in the low and mid-latitudes.

STABLE ISOTOPE PALEOBIOLOGY.— Douglas and Savin (1978) and Poore and Matthews (1984) recorded distinctly positive δ¹⁸O for this species indicating a deep planktonic habitat.

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

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

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

DESCRIPTION.

*Type of wall:* Normal perforate, cancellate, spinose.

*Test morphology:* Test very low trochospiral, globular, lobulate in outline, chambers globular; in spiral view 4-5 globular, somewhat embracing chambers in ultimate whorl, increasing rapidly in size; in umbilical view 4-5 globular, somewhat embracing chambers, umbilicus a small sized opening, enclosed by surrounding chambers, aperture umbilical-extrumbilical.

DISTINGUISHING FEATURES.— Genus distinguished by low trochospiral test, chambers increasing rapidly in size in ultimate whorl, and high-arched umbilical-extrumbilical aperture with lip of variable thickness, sometimes dentate. Wall cancellate, originally spinose.

DISCUSSION.— The genus was originally erected by Olsson and others (1992) to encompass two Danian species, *P. pseudobulloides* and *P. varianta*, which are united by a low trochospiral test, high arched aperture and cancellate spinose wall texture. Although they are similar in overall test morphology to closely related *Praemurica inconstans* and similar forms, their spinose wall texture was considered as being of high taxonomic status, such that *Parasubbotina* was included in the Family Globigerinidae and *Praemurica* in the Globorotaliidae. Olsson and others (1992) noted that *Parasubbotina* ranges at least as high as Zone P4, but the topmost occurrence of *P. varianta* was not firmly established by them. Thus, initial investigations by the Paleogene Working Group indicated that *Parasubbotina* might be a short-lived genus restricted to the Paleocene, with the bulk of the Cenozoic spinose radiation stemming from *Eoglobigerina* (Pearson, 1993).

*Parasubbotina* was reviewed by Olsson and others (1999). In that work, the stratigraphic range of *P. varianta* was found to extend at least to the lower Eocene. Further investigations reported here shows that *varianta*-like morphologies extend as high as the middle Eocene (confirming the original suggestion of Subbotina, 1953) and it now appears that this species was the root of a substantial evolutionary radiation. The new observations
Plate 5.13 Parasubbotina varianta (Subbotina, 1953)
Plate 5.14 Pseudoglobigerinella bolivariana (Petters, 1954)
indicate that Parasubbotina is closely related to Paragloborotalia, with which it shares the spinose wall, generally low-trochospiral coiling mode and high-arched aperture. The latter genus is distinguished, however, by the thick, continuous lip that rims the aperture and in having a generally slower rate of chamber enlargement, a tighter coiling mode, and more embracing chambers, which tends to result in a quadrate-shaped, more compact test as is typical, for example, in Paragloborotalia nana (Bolli). The number of chambers in the ultimate whorl is usually 4.

A prominent feature of the taxonomy presented here is the inclusion of the frequently decribed species Globigerina inaequispira Subbotina in Parasubbotina, rather than in Subbotina where it has often been placed (e.g., Blow, 1979). This assignment has been made after detailed study of type material on the basis of its coiling mode and the fact that P. inaequispira has been observed to intergrade with other parasubbotinids in high productivity assemblages.

**Parasubbotina eoclava** Coxall, Huber, and Pearson, 2003

PLATE 5.9, FIGURES 1-16
(Pl. 5.9, Figs. 1-10: reillustration of holotype and paratypes of Parasubbotina eoclava Coxall, Huber and Pearson)

Subbotina inaequispira Subbotina.—Blow, 1979:1272 (partim), pl. 163: figs. 9-10 [Zone E8, Kane 9-Core 42, Endeavour seamount, eastern North Atlantic Ocean]. [Not Subbotina, 1953.]

Clavigerinella ?columbiana Petters.—McKeel and Lipps, 1975:258, pl. 4: fig. 6a, b (partim; not pl. 3: fig. 8a-c = Globorotaloides eovariabilis Huber and Pearson n. sp.) [lower middle Eocene Tyee Fm., Coast Ranges, Oregon]. [Not Petters, 1954.]

Parasubbotina eoclava Coxall, Huber and Pearson, 2003:256, pl. 8: figs. 1-3 holotype, 4-11 paratypes [middle Eocene Zone E8, ODP Hole 865B, Allison Guyot, equatorial Pacific Ocean].—Pearson and others, 2004:36, pl.1:fig. 14 [middle Eocene Zone E6/7, Tanzania].

**DESCRIPTION.**

*Type of wall:* Reticulate Clavigerinella-type wall texture, spinose in life.

*Test morphology:* Very low trochospiral, somewhat laterally compressed, lobulate-petaloid in outline, chambers globular and well separated with a tendency for the final chamber to become slightly radially elongated; in spiral view surface flattened so that chambers of inner whorl are distinguishable; sutures straight, slightly depressed; in umbilical view 4 chambers in the final whorl, increasing rapidly in size, umbilicus moderately small, narrow and deep, sutures straight and slightly depressed; in edge view primary aperture a moderately high arch, interiomarginal, umbilical-extraumbilical, bordered by a well developed, asymmetrical flaring lip that extends from the umbilicus to the equatorial margin.

**Size:** Holotype maximum diameter 0.48 mm, thickness 0.26 mm.

**DISTINGUISHING FEATURES.—** Parasubbotina eoclava is characterized by its low trochospiral coiling, Clavigerinella-type reticulate wall texture, an interiomarginal umbilical-extraumbilical aperture bordered by a broad, flaring apertural lip, and a tendency toward radial extension of the last one or two chambers which anticipates the clavate morphology of Clavigerinella (from which it gets its name). It differs from Parasubbotina inaequispira (Subbotina) in possession of a distinctive flaring lip, more compressed morphology and in the more rapid increase in chamber size through the final whorl. It differs from Clavigerinella eocanica in consistently showing low
trochospiral rather than planispiral coiling, having less-proounced clavate chambers, a more asymmetrical, and lower arched aperture and a less-well developed apertural lip. It is distinguished from *Parasubbotina prebetica* in having lower trochospiral coiling, a flat spiral side, 4-4½ rather than 4½-5 chambers in the final whorl, chambers increasing gradually in size in the final whorl that are considerable less bulbous than in *P. prebetica*, a small umbilicus and a more equatorial position and higher arch-morphology of the aperture.

**DISCUSSION.**—Blow (1979, p. 1198-1199) remarked that the genus *Clavigerinella* appears in the record “without any transitional forms in terms of apertural characteristics” but nevertheless “some specimens of early forms included in the taxon *Subbotina inaequispira* (Subbotina)... show some degree of radial elongation of the chambers combined with an aperture which is markedly asymmetrically placed with respect to the umbilicus”, and he suggested that such forms might be ancestral. Toumarkine and Luterbacher (1985, fig. 22.19) illustrated a so-called “*G. inaequispira* – *C. eocanica eocanica* transition” which appears to be a sub-adult specimen of *C. eocanica*. Coxall and others (2003) erected the species *Parasubbotina eoclava* to include some forms previously included in *P. inaequispira* that they considered as distinct from the holotype morphology of that taxon and show some transitional features toward *Clavigerinella*, particularly the strongly asymmetrical aperture with its broad lip, the low trochospiral coiling, and the tendency for radially extended chambers.

**PHYLOGENETIC RELATIONSHIPS.**— *Parasubbotina eoclava* evolved from *P. inaequispira* in the latest early Eocene and was ancestral to *Clavigerinella eocaenica* (Coxall and others, 2003).

**STRATIGRAPHIC RANGE.**—Zone E7 to E9 (Coxall and others, 2003).

**GEOGRAPHIC DISTRIBUTION.**— *Parasubbotina eoclava* is known from relatively high productivity environments in the low to mid-latitudes, where it often co-occurs with *Clavigerinella* spp. (Coxall and others, 2003).

**STABLE ISOTOPE PALEOBIOLOGY.**—This species was recorded with more positive δ¹⁸O and more negative δ¹³C than coexisting *Turborotalia frontosa*, indicating a cold water sub-thermocline or upwelling environment (Coxall and others, 2003).

**REPOSITORY.**—Holotype (USNM 517714) and paratypes (USNM 517715-517716) deposited at the Smithsonian Museum of Natural History, Washington DC.

*Parasubbotina griffinae* (Blow, 1979)

**PLATE 5.10, FIGURES 1-15**

(Pl. 5.10, Figs. 1-4: reillustration of holotype and paratypes of *Globorotalia* (*Turborotalia*) *griffinae* Blow)

?*Globigerina micropora* de Klasz, Le Calvez and Rerat, 1969:278, pl. 2: fig. 5a-c [lower middle Eocene Amiba Fm., Gabon].

*Globorotalia* (*Turborotalia*) *griffinae* Blow, 1979:1072, pl. 96: figs. 5-9 (fig. 8 = holotype) (partim; not pl. 157, fig. 7; pl. 162, figs. 8, 9; pl. 165, figs. 1-3 = *Paragloborotalia griffinoides* Olsson and Pearson, n. sp.) [lower Eocene Zone E7, KANE 9-Core 42, Endeavour Seamount, equatorial Atlantic Ocean].

*Turborotalia griffinae* (Blow).—Toumarkine and Luterbacher, 1985:127, fig. 27:13-17 (partim; not fig. 27:18-23.) [reillustration of holotype and paratypes].

**DESCRIPTION.**

*Type of wall:* Normal perforate, high porosity, reticulated *Clavigerinella*-type, spinose.

*Test morphology:* Very low trochospiral, globular, lobulate in outline, chambers globular, much inflated; in spiral view 4-5 globular, somewhat embracing chambers in ultimate whorl, increasing moderately in size, inner whorl of chambers partly overlapped by the ultimate whorl, sutures moderately depressed, straight, penultimate and ultimate chamber may be reduced in size relative to preceeding chambers; in umbilical view 4-5 globular, somewhat embracing chambers, increasing moderately in size, sutures moderately depressed, straight, umbilicus a small sized opening, enclosed by surrounding chambers, aperture umbilical-extraumbilical, bordered by a narrow continuous, lip or thickened rim; in edge view chambers globular in shape, aperture a low arch extending midway
onto the peripheral edge, bordered by a narrow lip or thickened rim.

Size: Maximum diameter of holotype 0.41 mm, thickness 0.29 mm.

DISTINGUISHING FEATURES.— *Parasubbotina griffinae* is distinguished by its very low trochospiral, globular test with strongly inflated chambers, with the inner whorls partially overlapped by the ultimate whorl, and the high porosity, reticulated *Clavigerinella*-type wall texture.

DISCUSSION.— When Blow (1979) described *Globorotalia (Turborotalia) griffinae (=Parasubbotina griffinae)*, he selected the holotype and some paratypes from the same sample (KANE 9 Core 42, 200 cm) from which he also illustrated hypotypic specimens of *Pseudoglobigerinella bolivariana* (Petters). His case for regarding *griffinae* as ancestral to *bolivariana* is clear from the SEM illustrations of the two species (his pl. 150, figs. 1-9) as they both share a *Clavigerinella*-type reticulate wall texture. Blow also illustrated paratypes of *P. griffinae* from other levels in KANE 9 Core 42 (his pl. 157, fig. 7, from 95 cm; pl. 162, figs. 8, 9, from 42 cm; pl. 165, figs. 1-3, from 15 cm) that clearly differ from the holotype and paratypes of the species illustrated from the type level. These paratypes have a more coarsely cancellate, non-reticulate wall texture and a thickened, continuous apertural lip. Toumarkine and Luterbacher (1985) included morphotypes like these in *griffinae* (their fig. 27:19-23). We place all these in *Paragloborotalia griffinoidea* n. sp. (see discussion under that species).

Although not readily recognized by previous workers, *P. griffinae* appears in the stratigraphic record shortly before the development of *Pseudoglobigerinella bolivariana* and can be considered an intermediate morphotype linking *P. inaequispira* and *P. bolivariana*. We have also found specimens attributable to *P. griffinae* as high as Zone E14 in Java (Pl. 5.10, Figs. 9-11) although we recognize that detailed stratigraphic investigations may reveal these forms, which are less inflated than the holotype, not to be conspecific.

*Globigerina micropora* de Klasz, Le Calvez and Rerat appears from the type illustration to have the gross test morphology of *griffinae* but the character of the aperture and wall texture cannot be determined.

PHYLOGENETIC RELATIONSHIPS.— *Parasubbotina griffinae* evolved from *P. inaequispira* and rapidly gave rise to *Pseudoglobigerinella bolivariana*.

STRATIGRAPHIC RANGE.— Zone E7 to Zone E14.

GEOGRAPHIC DISTRIBUTION.— Global in low to mid latitudes, *P. griffinae* is a common constituent of relatively high productivity environments in the Eocene.

STABLE ISOTOPIC PALEOBIOLOGY.— Relatively heavy $\delta^{18}$O indicating cool water (H. K. Coxall, unpublished data).

REPOSITORY.— Holotype and paratypes deposited in the British Museum of Natural History, London.

**Parasubbotina inaequispira** (Subbotina, 1953)

*Plate 5.11, Figures 1-15*

(Pl. 5.11, Figs. 1-3: new SEMs of holotype of *Globigerina inaequispira* Subbotina)

*Globigerina inaequispira* Subbotina, 1953: 84, pl. 6: figs. 1a-c (holotype), 4a-c [lower / middle Eocene Zone of conical *Globorotalia*, Kuban River, northern Caucasus], pl. 6: figs. 2a-3c [lower / middle Eocene Zone of conical *Globorotalia*, Foraminiferal layer, Series F, (bottom), Kuban River, northern Caucasus].—Stainforth and others, 1975:191, fig. 54-1a-c [from Subbotina, 1953], fig. 54-2a-c [reillustration of holotype], fig. 54-3-5 [middle Eocene, no locality given].—Toumarkine and Luterbacher, 1985: 117, fig. 19-5a-c [reillustration of holotype].

*Subbotina inaequispira* (Subbotina).—Blow, 1979:1272 (partim), pl. 151: fig. 5-7 [lower Eocene Zone E7, KANE 9-Core 42, Endeavour Seamount, eastern North Atlantic Ocean]; pl. 163: figs. 4-8 [middle Eocene Zone E8, KANE 9-Core 42, Endeavour Seamount, eastern North Atlantic Ocean]; pl. 180: figs. 1, 4-7 [middle Eocene Zone E9, DSDP Hole 21A, Gulf of Mexico]; pl. 191: fig. 7 [middle Eocene Zone E12, Sample RS.311, Kilwa area, Tanzania].—Warraich and others, 2000:299 fig. 18: 6-8 [Dungan Fm., Sulaiman Range, Pakistan].—Warraich and Ogasawara, 2001:48, fig. 13: 17-19 [Zone E5, Dungan Fm., Sulaiman Range, Pakistan].

*Parasubbotina inaequispira* (Subbotina).—Pearson, and others, 2004:36, pl. 1: fig. 13 [lower Eocene Zone E6/7, Tanzania].

*Globigerina achtschacujmensis* Khalilov, 1956:238, pl. 2: figs. 2a-c [“middle Eocene”, Maly Caucasus, Azebaidzhan].
Globigerina inaequispis\textsuperscript{a} Subbotina var. \textit{transversa} Khalilov, 1956:241, pl. 2: fig. 4a-c. [“middle Eocene”, Maly Caucasus, Azebadzhazan].

\textit{Globigerina baylissi} Samanta, 1973:436, pl. 2: figs. 4-6 [middle Eocene Truncorotaloides rohri Zone, Rakhi Nala section, Pakistan].

**DESCRIPTION.**

\textbf{Type of wall:} Symmetrically to asymmetrically cancellate (initially \textit{rubber/sacculifer}-type wall texture but becoming high porosity, reticulated \textit{sacculifer}-type in adult morphology and particularly in stratigraphically younger morphotypes \textit{Clavigerinella}-type with surface thickening), normal perforate, spinose.

\textbf{Test morphology:} Test very low trochospiral, globular, lobulate in outline, chambers globular; in spiral view 4-4/\textit{g} globular, well separated chambers in final whorl, increasing moderately in size, sutures moderately depressed, straight, final chamber may be slightly reduced in size relative to the penultimate chamber; in umbilical view 4-4/\textit{g} globular, well separated chambers, increasing moderately in size, sutures moderately depressed, straight, umbilicus a moderate sized opening, enclosed by surrounding chambers, aperture umbilical to somewhat extraumbilical and directed towards the anterior side of the test, bordered by a narrow continuous, lip, ultimate chamber may be slightly reduced in size relative to the penultimate chamber; in edge view chambers globular in shape, well separated, aperture visible as a low arch, bordered by a narrow lip.

\textbf{Size:} Maximum diameter of holotype 0.42 mm, thickness 0.28 mm.

**DISTINGUISHING FEATURES.**— Subbotina (1953) alluded to the “\textit{Globigerinella}-like” coiling style of her species and the small size of the inner whorl in comparison to the outer whorl, the latter feature lending the taxon its name. These features arise from the rapid rate of chamber expansion and their low and slightly irregular trochospiral arrangement, characters that help assign the species to the genus \textit{Parasubbotina}. The species is distinguished by its lobulate, very low trochospiral test with 4-4/\textit{g} chambers in the final whorl and its anteriorly directed umbilical-extraumbilical aperture.

The species has been widely identified in previous literature, but often incorrectly so. \textit{Parasubbotina inaequispis}\textsuperscript{a} is distinguished from \textit{P. varianta} by being more openly coiled and having less closely appressed chambers. It differs from \textit{Paragloborotalia griffinoides} n. sp. principally in having much less dorso-ventral expansion and lacking the thick, prominent lip of that taxon. It differs from \textit{P. eolavla} in lacking radially elongate chambers and a thick, flaring lip.

**DISCUSSION.**— The holotype of \textit{Parasubbotina inaequispis} (Subbotina) is illustrated here in SEM for the first time (Pl. 5.11, Figs. 1-3). Blow (1979, p. 1259) regarded \textit{P. inaequispis} as ancestral to \textit{Subbotina crociapertura} because of the tendency in \textit{P. inaequispis} “to produce apertural systems with a slightly expanded to very slightly hooked distal part”, which he believed led to the distinctive hook-shaped aperture in \textit{S. crociapertura}. However, the majority of specimens he illustrated to demonstrate this feature cannot be placed in \textit{P. inaequispis}. In fact, Blow’s images of \textit{inaequispis} show different types of wall texture that suggests mixing of separate species. The specimens of \textit{S. crociapertura} from Tanzania illustrated by Blow, which includes the holotype, have a \textit{bulloides}-type wall texture whereas \textit{P. inaequispis} has a \textit{rubber/sacculifer}-type wall texture. Some specimens of \textit{P. inaequispis} illustrated by Blow (his pl. 177, fig. 3; pl. 180, figs. 2, 3; pl. 185, fig. 9) have a \textit{bulloides}-type wall texture and may be morphotypes of \textit{S. crociapertura}.

Of particular interest are Blow’s images of \textit{P. inaequispis} from Zones E7 and E8 from the Endeavour Seamount in the North Atlantic Ocean (his pl. 151, figs. 5-7; pl. 163, figs. 4-10). These specimens show a fully developed, high porosity, reticulated, \textit{sacculifer}-type wall texture that is characteristic of the genus \textit{Clavigerinella}, which apparently first developed in \textit{P. inaequispis}. Some of the specimens illustrated (his pl. 151, figs. 9 and 10) are placed in the intermediate species \textit{Parasubbotina eolavla} Coxall, Huber, and Pearson that evolved from \textit{P. inaequispis} and is believed to be directly ancestral to \textit{Clavigerinella}.

The type material of \textit{Globigerina achshacujmensis} Khalilov and \textit{Globigerina inaequispis} var. \textit{transversa} Khalilov has been viewed by WAB and, despite the poor preservation, both are clearly synonyms of \textit{P. inaequispis}. The holotype and three paratypes of \textit{Globigerina baylissi} Samanta were viewed by PNP. Samanta distinguished his taxon from \textit{inaequispis} by the supposed radial elongation of the final chamber, but this feature is poorly developed and falls within the range of variation here permitted to \textit{P.}}
inaequispira. More markedly radially elongate parasubbotinids are assigned to *P. eoклава* Coxall, Huber and Pearson.

**PHYLOGENETIC RELATIONSHIPS.**— *Para-
subbotina inaequispira* appears to have developed from *P. varianta* (Subbotina) in the earliest Eocene. In turn it gave rise to *P. eoклава* and *P. griffinae* in the latest early Eocene.

**STRATIGRAPHIC RANGE.**— Zone E1 to Zone E8.

**GEOGRAPHIC DISTRIBUTION.**— Global in low to mid latitudes. *Parasubbotina inaequispira* is a common constituent of relatively high productivity environments in the Eocene.

**STABLE ISOTOPIC PALEOBIOLOGY.**— Relatively heavy δ¹⁸O indicating cool water (H. K. Coxall, unpublished data).

**REPOSITORY.**— Holotype (No. 3069) and paratypes (Nos. 4016-4018) deposited in the VNIGRI collections, St. Petersburg, Russia.

**Parasubbotina prebetica** (Martínez-Gallego and Cremades, 1978)

*Plate 5.11, Figures 16-18*  
(Pl. 5.11, Figs. 16-18: reillustration of holotype of *Globigerina prebetica* Martínez-Gallego and Cremades)

*Globigerina prebetica* Martínez-Gallego and Cremades, 1978, pl. 1, figs. 1-3 (holotype); figs. 4-6 (paratype) [lower Eocene *Globorotalia aragonensis* Zone, Rincón de Santana hills, Prebética Mountains, Spain].

**DESCRIPTION.**

*Type of wall:* Cancellate, normal perforate, high porosity, reticulated *Clavigerinella*-type wall texture.

*Test morphology:* Very low trochospiral, highly lobulate, 4-4½ chambered symmetrical test with elongate, globular to cylindrical chambers; in spiral view 4-4½ globular/cylindrical chambers, the last 4 of almost equal size, forming a pinwheel shape of 4 opposing chambers; in umbilical view identical to the spiral view in arrangement of ultimate whorl chambers, umbilicus small, shallow, aperture a low umbilical-extraumbilical arch, bordered by broad lip; in edge view compressed, parallel sided, chambers spherical in shape.

*Size:* No information available.

**DISTINGUISHING FEATURES.**— Identified by the symmetrical, compressed test with elongate, globular to cylindrical chambers. The radially elongate chambers are reminiscent of *Clavigerinella*, but this species is distinguished from that genus by the trochospiral coiling mode.

**DISCUSSION.**— This species has only one known occurrence. Its high porosity, reticulated *sacculifer*-type wall texture indicates that is a member of *Parasubbotina* and is apparently an early evolutionary offshoot from *P. inaequispira* with a short stratigraphic range.

**PHYLOGENETIC RELATIONSHIPS.**— *Para-
subbotina prebetica* appears to have developed from *P. inaequispira* in Lower Eocene Zone E5.

**STRATIGRAPHIC RANGE.**— Upper part of Zone E5.

**GEOGRAPHIC DISTRIBUTION.**— Known only from Spain. The morphology is convergent with other cold water high productivity species.

**STABLE ISOTOPIC PALEOBIOLOGY.**— No data available.

**REPOSITORY.**— Holotype (MC-25) and paratype (MC-26) deposited in the collections of the Museum of the Departamento de Paleontología, Universidad de Granada, Spain.

**Parasubbotina pseudowilsoni** Olsson and Pearson  
*new species*

*Plate 5.12, Figures 1-16*  
(*Turborotalia wilsoni* Cole.—Toumarkine and Luterbacher, 1985:125, fig. 27:2-3 [middle Eocene Zone E10/11, Guayabal Fm., type locality, Tampico, Mexico]. [Not Cole, 1927.])

**DESCRIPTION.**

*Type of wall:* Cancellate, normal perforate, spinose, *ruber-sacculifer* type wall texture.
Test morphology: Test small, very low trochospiral, globular, lobulate in outline, chambers globular; in spiral view 5 globular, moderately embracing chambers in ultimate whorl, increasing moderately in size, sutures moderately depressed, ultimate chamber usually slightly reduced in size relative to the penultimate chamber; in umbilical view 5 globular, moderately embracing chambers, increasing moderately in size, sutures moderately depressed, straight; umbilicus a moderate sized opening, enclosed by surrounding chambers; aperture umbilical to somewhat extraumbilical, bordered by a continuous lip, which varies in its width from narrow to broad; in edge view chambers globular in shape, moderately embracing, aperture visible as a low arch, bordered by a narrow to broad lip.

Size: Maximum diameter of holotype 0.25 mm, thickness 0.15 mm.

ETYMOLOGY.— Named after its resemblance to Globigerina wilsoni Cole which is referred to Globoturborotalita carcoselleensis in this work.

DISTINGUISHING FEATURES.— Parasubbotina pseudowilsoni n. sp. is a small form with a compact, very low trochospiral test that typically has 5 chambers in the final whorl, as seen in dorsal view. Parasubbotina varianta is larger and has a more lobulate test with 4 chambers in the ultimate whorl.

DISCUSSION.— Toumarkine and Luterbacher (1985) reillustrated the line drawing of the holotype of Globigerina wilsoni along with three SEM images they identified to that species from the type Guayabal Formation, from where G. wilsoni was originally described. New SEM images of the holotype of G. wilsoni (Chapter 6, Pl. 6.23, Figs. 15-17), although poorly preserved, show that it differs from the hypotypes illustrated by Toumarkine and Luterbacher in that the ultimate chamber is more flattened and extends towards and over the umbilicus. In this respect, the holotype appears much more like Globorotaloides carcoselleensis Toumarkine and Bolli (=Turborotalita carcoselleensis), which is common in the Guayabal Formation. However, the poor state of preservation does not allow an accurate identification, and we place wilsoni in questionable synonymy with carcoselleensis. Parasubbotina pseudowilsoni n. sp. is also a common form in the Guayabal Formation and occurs as a relatively inconspicuous component in many other Eocene localities.

PHYLOGENETIC RELATIONSHIPS.— Parasubbotina pseudowilsoni n. sp. appears to have developed from P. varianta (Subbotina) in the uppermost Lower Eocene.

STRATIGRAPHIC RANGE.— Upper Zone E7 to Zone E11.

GEOGRAPHIC DISTRIBUTION.— Cosmopolitan in low to mid latitudes.

STABLE ISOTOPIC PALEOBIOLOGY.— No data available.

REPOSITORY.— Holotype (USNM 521869) and paratype USNM 521870 deposited at the Smithsonian Museum of Natural History, Washington, D.C.

Parasubbotina varianta (Subbotina, 1953)

DISCUSSION.— P. varianta is characterized primarily by its low trochospiral coiling and 4 very rapidly expanding chambers in the final whorl. Subbotina’s holotype is a poorly preserved specimen but nevertheless shows the cancellate wall and inflated, closely appressed chambers that characterize the Parasubbotina clade. The holotype is about 0.2 mm in maximum diameter, but much larger specimens up to 0.5 mm have been reported (Subbotina, 1953; Olsson and others, 1999). The aperture of the holotype is difficult to discern because of adhering sediment, but the range of lower Danian hypotypes selected by Olsson and others (1999) show arched apertures bordered by a generally thin lip that in some specimens jut into the umbilicus as a poorly developed tooth-like structure.

It is very difficult to place clear morphological bounds on the taxon as specimens differ widely in chamber arrangement and apertural characteristics. This was noted by Subbotina (1953) in her original description.
and probably accounts for the species name. *Parasubbotina varianta* is distinguished from *P. inaequispira* by its more closely appressed chambers, and from *Parasubbotina griffinae* by having less strongly inflated, less embracing chambers and a coarsely cancellate wall texture in contrast to the reticulate wall texture in *P. griffinae*. *Paragloborotalia griffinoides* n. sp. has a more quadrate, tightly coiled, compact test, and a thick continuous lip that borders the aperture.

**PHYLOGENETIC RELATIONSHIPS.**— The *Parasubbotina varianta* plexus arose from *P. pseudobulloides* in the Danian (Olsson and others, 1999). It seems to have been the source of a major radiation in the upper Paleocene - lower Eocene, when it gave rise to *Globorotaloides quadrocameratus*, *P. inaequispira*, and *Paragloborotalia griffinoides*.

**STRATIGRAPHIC RANGE.**— Zone P1c to Zone E10. The Working Group initially considered the species to be restricted to the Paleocene and lowermost Eocene (Olsson and others, 1999). However, similar morphologies have now been observed as high as middle Eocene Zone E10 in more poorly preserved material from the Indian Ocean.

**GEOGRAPHIC DISTRIBUTION.**— Widespread in low and middle latitudes.

**STABLE ISOTOPIC PALEOBIOLOGY.**— See Olsson and others (1999). Eocene specimens have yet to be analysed.

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

**Genus Pseudoglobigerinella Olsson and Pearson**

**new genus**

**TYPE SPECIES.**— *Globigerina wilsoni bolivariana* Petters, 1954.

**DESCRIPTION.**

*Type of wall*: Normal perforate, spinose, high porosity, reticulate, *Clavigerinella*-type wall structure, covered by a thick crust in adult stage.

*Test morphology*: Globular, nearly involute, asymmetrically planispiral in adult stage (juvenile stage very low trochispiral), slightly lobulate in outline, chambers globular; 4-5 globular, embracing chambers in final whorl, increasing rapidly in size, ultimate chamber much inflated, sutures moderately depressed, straight, umbilicus small and often covered by ultimate chamber; in edge view chambers globular in shape, slightly embracing, aperture asymmetrically equatorial, varying from a low arch to a high distinctive arch, bordered by an imperforate rim and sometimes by a narrow lip that broadens on both sides towards the center of the coil.

*Size*: Maximum diameter of type species 0.52 mm, thickness 0.40 mm.

**ETYMOLOGY.**— Named for its resemblance to modern *Globigerinella*.

**DISTINGUISHING FEATURES.**— *Pseudoglobigerinella* n. gen. is identified by its inflated, nearly involute, globular test, asymmetrical equatorial aperture, and the reticulate, *Clavigerinella*-type wall texture and thickened crust. A tendency towards uncoiling occurs in some morphotypes of the genus.

**DISCUSSION.**— The inflated, involute test of *Pseudoglobigerinella bolivariana*, which becomes planispiral in the final whorl, is unlike any other Paleogene species. Its homeomorphy (in terms of gross morphology) with the Neogene species *Hastigerina (Hastigerina) siphonifera* (= *Globigerinella siphonifera*) led Blow (1979) to questionably place it in *Hastigerina* although he recognized that future study might provide criteria whereby *bolivariana* could be placed in a new genus. In fact, the wall textures of *bolivariana* and *siphonifera* are quite different from one another (see Olsson and Hemleben, this volume). *Globigerinella siphonifera* has a *bulloides*-type wall, and seems to have shared a common ancestor with *Globigerina* in the upper Oligocene. *Pseudoglobigerinella bolivariana*, on the other hand, has a highly porous, reticulate *Clavigerinella*-type wall that develops a thickened crust. Furthermore, there is no known phylogenetic linkage between the two species; *bolivariana* is unknown in levels above the middle Eocene, whereas *siphonifera* evolved from *G. praesiphonifera* in the upper Miocene.

Hillebrandt (1976) first proposed that "Subbotina inaequispira" (= *Parasubbotina inaequispira*) was the ancestral species to *Pseudohastigerina globulosa* Hillebrandt (=*Pseudo-
globigerinella bolivariana). Blow (1979) also regarded *inaequispira* as the ancestral species of the lineage, leading to *bolivariana* through *Globorotalia* (Turborotalia) *griffinae* Blow (= *Parasubbotina griffinae*). Both Blow (1979) and Toumarkine and Luterbacher (1985) made the interesting observation that *inaequispira* also gave rise to the *Clavigerinella* lineage at about the same time (i.e., Biochron E7). The high porosity, reticulate, *Clavigerinella*-type wall texture of both *Clavigerinella* and *Pseudoglobigerinella* n. gen. is shared with *P. inaequispira*, in which it apparently first developed.

**Pseudoglobigerinella bolivariana** (Petters, 1954)

**PLATE 5.14, FIGURES 1-22**

(Pl. 5.14, Figs. 1-3: new SEMs of holotype of *Globigerina wilsoni bolivariana* Petters)


*Globigerina wilsoni bolivariana* Petters, 1954:39, pl. 8: fig. 9 a-c [middle Eocene *Asterigerina crassaformis* Zone, Carreto Fm., Colombia].—Weiss, 1955:309, pl. 2: figs. 6-8 [middle Eocene, lower Talara shales, northwestern Peru].


*Hastigerina? bolivariana* (Petters).—Toumarkine and Luterbacher, 1985:127, fig. 27.24a-c (reillustration of holotype), fig. 27.25-29 [early Middle Eocene, El Datil Fm., Punta Mosquito, Venezuela].

*Globigerinella alexi* Haque, 1956:177, pl. 27: fig. 7a, b. [Eocene, Pakistan].


*Pseudohastigerina sphaeroidalis* Hillebrandt, 1978:337 [new name for *Pseudohastigerina globulosa* Hillebrandt; see above].

**DESCRIPTION.**

Type of wall: Normal perforate, spinose, high porosity, reticulate, *Clavigerinella*-type wall structure, covered by a thick crust in adult stage.

Test morphology: Test globular, nearly involute, asymmetrically planispiral in adult stage (juvenile stage very low trochospirally), slightly lobulate in outline, chambers globular; in spiral view generally 4 globular, embracing chambers in ultimate whorl, increasing rapidly in size, in terminal stage ultimate chamber overlaps the spiral coil, sutures moderately depressed, straight; in umbilical view 4-5 globular, embracing chambers, increasing rapidly in size, ultimate chamber much inflated, sutures moderately depressed, straight, umbilicus small and often covered by ultimate chamber; in edge view chambers globular in shape, slightly embracing, aperture asymmetrically equatorial, varying from a low arch to a high distinctive arch, bordered by an imperforate rim and sometimes by a narrow lip that broadens on both sides towards the center of the coil.

Size: Maximum diameter of holotype 0.52 mm, thickness 0.40 mm.

**DISTINGUISHING FEATURES.** — *Pseudoglobigerinella bolivariana* is identified by its compact, nearly involute, globular test, asymmetrical equatorial aperture, and the *Clavigerinella*-type reticulate wall texture and thickened crust. It is distinguished from *Parasubbotina griffinae* by having an aperture that extends on to the spiral side.

**DISCUSSION.** — *Pseudoglobigerinella bolivariana* has long been considered an enigmatic species due to its equatorial aperture. Blow (1979) was uncertain of its generic designation when he placed the species in ‘*Hastigerina!*’, emphasizing its homeomorphy with the Recent species ‘*Hastigerina siphonifera*’ (= *Globigerinella siphonifera*) which he regarded as derived from the trochospiral species *Globorotalia* (Turborotalia) *obesa* (Blow, 1979, p.1178). He regarded his new species, *Globorotalia* (Turborotalia) *griffinae* Blow 1979, as having an analogous ancestral relationship with *P. bolivariana* as *G. obesa* did with *H. siphonifera* (i.e., the derivation of planispiral coiling from a low trochospirally coiled morphotype). Toumarkine and Luterbacher (1985) followed Blow in placing *bolivariana* in ‘*Hastigerina!*’.

Blow selected the holotype and some paratypes for his new species *G. (T.) griffinae* from the same sample.
(KANE 9 Core 42, 200 cm) from which he also illustrated *bolivariana*. His case for regarding *griffinae* as ancestral to *bolivariana* is clear from the SEM illustrations of the two species (his pl. 150, figs. 1-9) as they both share a *Clavigerinella*-type reticulate wall texture (but see comments under *Paragloborotalia griffinoides* regarding other paratypes of *griffinae*). Blow also emphasized the general range of morphologic variation in his illustrations of *bolivariana* (Blow, 1979, p. 1178) in morphotypes that are more loosely coiled with 5 chambers in the ultimate whorl, to the tightly coiled morphotype with a large inflated ultimate chamber. Toumarkine and Luterbacher (1985) illustrated large inflated morphotypes (their fig. 27.25-28) similar to the holotype but also illustrated a form (their fig. 27.29) similar to the loosely coiled forms illustrated by Blow (his pl. 150, figs. 3, 4). Plate 5.14 (this chapter) shows some of the range of morphologic variation observed in this species. Of interest is the considerable variation in the size of the aperture, from a low arch to a highly elevated arch.

The derivation of the lineage leading to *Pseudoglobigerinella bolivariana* is uncertain, as the species has not been intensively studied in stratigraphic sections. Weiss (1955) noted the tendency in some morphotypes of *P. bolivariana* “towards *Globigerinella*-like uncoiling” (1955, p. 309) as did Toumarkine and Luterbacher (their fig. 27.29). Blow was struck by the close homeomorphy with the Recent species *Hastigerina siphonifera* (= *Globigerinella siphonifera*) and believed that “both the Neogene and Palæogene forms have the same basic globigerinacean wall structure” (Blow, 1979, p. 1176). However, subsequent studies show that *siphonifera* has a bulloides-type wall texture (Hemleben, and others, 1991) whereas *P. bolivariana* has a reticulate, *Clavigerinella*-type wall texture (this volume), much different from that of *siphonifera*. Thus, the two species exhibit only a gross homeomorphic similarity. Although Blow placed *bolivariana* questionably in *Hastigerina*, he believed that *bolivariana* should be placed in a new genus if it was demonstrated that the two species could be morphologically separated.

Hillebrandt (1976) considered *Globigerina inaequispira* Subbotina (= *Parasubbotina inaequispira*) as the ancestor of his new species *Pseudohastigerina sphaeroidalis* (here considered a junior synonym of *P. bolivariana*). Blow (1979, p. 749) also entertained a similar idea, in that he believed “that *Globorotalia (Turborotalia) griffinae* represents the derivation of an essentially turborotaliid type of coiling pattern...from the morphotypes included in *Subbotina inaequispira*”, from which he derived *P. bolivariana*. As discussed above, there are two sets of morphotypes that Blow included in his species *griffinae*. The first set (illustrated on his pl. 150) appears related to *bolivariana* in that it possesses a high porosity reticulate *Clavigerinella*-type wall texture like *bolivariana*. This type of wall texture also occurs in *Parasubbotina eoclova* Coxall, Huber, and Pearson, which is regarded as the ancestral species of the *Clavigerinella* lineage (Coxall and others, 2003) and also in *P. inaequispira*, particularly in the late early Eocene (see discussion under *P. inaequispira*). Thus, it appears that *P. inaequispira* gave rise to two planispiral genera in the late early Eocene, *Pseudoglobigerinella* and *Clavigerinella*.

*Pseudoglobigerinella bolivariana* is a rare species except in areas of high productivity, where it can dominate the planktonic foraminiferal assemblages.

The species was first described by Petters (1954) from the same sample as *Clavigerinella colombiana* (Petters), which is also considered by us as an indicator of high productivity. In Ecuador, Stainforth (1948) reported that *bolivariana* was frequently associated with radiolarian-rich shales, and Weiss (1955) recorded it in depauperate assemblages from Peru that were probably affected by upwelling. The *griffinae-bolivariana-colombiana* biofacies may prove of some use in delineating ancient areas of upwelling.

**PHYLOGENETIC RELATIONSHIPS.**— *Pseudoglobigerinella bolivariana* was derived from *Parasubbotina griffinae* by a more rapid increase in chamber size, the development of a nearly involute planispiral test, and an asymmetrical equatorial aperture.

**STRATIGRAPHIC RANGE.**— Assemblages with abundant *P. bolivariana* are usually difficult to correlate with the standard (sub)tropical biozonation because the more oligotrophic zone fossils are usually absent. *Pseudoglobigerinella* appears restricted to the uppermost part of the lower Eocene and the lower half of the middle Eocene (approximately correlative with Zones E7 to E10; Blow, 1979).

**GEOGRAPHIC DISTRIBUTION.**— Identified only in middle Eocene low latitude upwelling areas.
STABLE ISOTOPIC PALEOBIOLOGY.— No data available.

REPOSITORY.— Holotype (USNM 689637) deposited in the Cushman Collection, Smithsonian Museum of Natural History, Washington, D.C.

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