### **Chapter 9**

# TAXONOMY, BIOSTRATIGRAPHY, AND PHYLOGENY OF OLIGOCENE TO LOWER MIOCENE GLOBIGERINOIDES AND TRILOBATUS

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#### **ABSTRACT**

The taxonomy, phylogeny and biostratigraphy of late Oligocene and early Miocene Globigerinoides and Trilobatus is reviewed. Trilobatus and Globigerinoides are two long-ranging genera appearing in the late Oligocene and early Miocene, respectively. They diversified within the range interval of Paragloborotalia kugleri and are still present in modern oceans as some of the most abundant mixed-layer dwelling groups. The distinctive characteristic of the genera is the presence of one to several supplementary apertures on the spiral side. Globigerinoides species possess a ruber/sacculifer-type wall, Trilobatus possesses a sacculifer-type wall texture. The ruber-type wall texture

probably appeared in the late Miocene with the appearance of *G. ruber* s.s. The following species of *Globigerinoides* are recognized as valid: *G. altiaperturus* Bolli, *G. bollii* Blow, *G. italicus* Mosna and Vercesi, *G. joli* Spezzaferri n. sp., *G. neoparawoodi* Spezzaferri n. sp., *G. obliquus* Bolli, and *G. subquadratus* Brönnimann. The following species of *Trilobatus* are recognized as valid: *T. altospiralis* Spezzaferri n. sp., *T. immaturus* (LeRoy), *T. praeimmaturus* (Brönnimann and Resig), *T. primordius* (Blow and Banner), *T. quadrilobatus* (d'Orbigny), *T. subsacculifer* (Cita, Premoli Silva, and Rossi) and *T. trilobus* (Reuss).

#### INTRODUCTION

The late Oligocene and the Oligocene-Miocene transition are characterized by the appearance of planktonic foraminiferal forms characterized by the presence of one to several supplementary apertures on the spiral side (e.g., Bolli, 1966; Blow, 1969) and a spinose macroperforate and cancellate wall texture (e.g., Hemleben and others, 1989). These forms represent the most abundant group of planktonic foraminifera still present in the modern oceans. They were originally lumped into the genus "Globigerinoides" (quotation marks are here used to indicate the concept of the genus as formerly

understood, i.e. both *Globigerinoides* and *Trilobatus*), which includes several species that diversified around the Oligocene/Miocene boundary (Spezzaferri, 1994). However, the ancestry and early phylogeny of these forms has been unclear for a long time. Several authors have explained the large variety of "*Globigerinoides*" morphologies, the uncertain morphological limits between species, and the different types of wall textures, as a result of their polyphyletic origin (Takayanagi and Saito, 1962; Keller, 1981; Kennett and Srinivasan, 1983; Jenkins, 1985). Blow and Banner (1962) proposed "*Globigerinoides*" *primordius* as the first representative of the genus "*Globigerinoides*" evolving from *Globigerina* 

praebulloides occlusa. Takayanagi and Saito (1962) distinguished two different groups of "Globigerinoides" based on the position of the primary aperture: one with the aperture placed above the sutures between the three earlier chambers ("Globigerinoides" bollii, "G." conglobatus, "G." immaturus, "G". obliquus, "G." sacculifer and "G." trilobus) and the second with the aperture placed above the sutures between the penultimate and antepenultimate chambers ("G." elongatus, "G." cyclostomus and "G." ruber). These studies did not take into account wall textures but were based only on morphological features. Kennett and Srinivasan (1983) also described two groups of "Globigerinoides", one originated from Globigerina sensu stricto with a bulloides-type wall texture, and the second evolved from Zeaglobigerina woodi (now Globoturborotalita) with a spinose and cancellate wall texture. Kennett and Srinivasan (1983) stated that the observation of several species of "Globigerinoides" evolving from different ancestors demonstrates that the genus is polyphyletic and therefore "artificial". A similar conclusion was reached by Keller (1981), who identified three lineages, but again with different component species. One originated from Globigerina praebulloides, the second from Globigerina woodi (now Globoturborotalita), and the third from Globigerina connecta (now Globoturborotalita). A polyphyletic origin for this group was also proposed by Jenkins (1985), Spezzaferri and Premoli Silva (1991), and Spezzaferri (1994).

According to Hemleben and Olsson (2006) "Globigerinoides" as originally understood possesses three types of wall texture: a sacculifer-type, typical of the modern species "Globigerinoides" sacculifer. This wall texture is characterized by a markedly cancellate pattern, strongly symmetrical (honeycomb), with spines having a circular or slightly triangular cross-section placed at the intersection of the ridges. The *ruber*-type wall texture is present in the modern species Globigerinoides ruber. It is characterized by a more irregular cancellate and asymmetrical wall texture, bearing thinner spines that are less regularly distributed with respect to the sacculifer-type. Finally, the ruber/sacculifer -type possesses a marked honeycomb and symmetrical texture in parts of the wall and asymmetrical in some other parts. Following the wall texture classification of Hemleben and Olsson (2006) we identify only the ruber/sacculifer- and sacculifer-type wall texture for the early members of this genus. According to Aurahs and others (2011) the G. ruber lineage and the related wall texture possibly originated and diversified only in the late Miocene.

A recent joint effort of the Paleogene Planktonic Foraminiferal Working Group (PPFWG) and the Scientific Committee on Oceanic Research/International Geosphere-Biosphere Programme (SCOR/IGBP) Working Group 138 "Planktonic foraminifera and ocean changes" has confirmed the long-standing view that modern "Globigerinoides" is polyphyletic.

Merging genetic and fossil evidence of "Globigerinoides" in a new approach to trace their "total evidence phylogeny" since the beginning of their range, Spezzaferri and others (2015) demonstrated the existence of two independent lineages appearing at the Paleogene-Neogene transition that evolved independently. One group includes "Globigerinoides" trilobus and its ancestor and descendants: "G." primordius and the extant "Globigerinoides" sacculifer, Orbulina universa and Sphaeroidinella dehiscens. The second group includes the Globigerinoides ruber clade with the extant G. conglobatus and G. elongatus, and their ancestors. These two groups both evolved supplementary apertures on the spiral side approximately concomitantly, but independently, as they descended from different species of Globoturborotalita. Therefore, they amended the generic concept of Globigerinoides (type species G. ruber) and established the new genus Trilobatus Spezzaferri, Kucera, Pearson, Wade, Rappo, Poole, Morard and Stalder (type species T. trilobus). In the new concept, the genus Trilobatus is paraphyletic and gave rise to the *Praeorbulina/Orbulina* and *Sphaeroidinellopsis/* Sphaeroidinella lineages (Spezzaferri and others, 2015). The two genera can be traced down to their last common ancestor G. paracancellata Olsson and Hemleben n. sp. in the lower Oligocene, which in turn originated the T. trilobus group on one side and the G. ruber group on the other side within the range of Paragloborotalia kugleri (Chapter 8, this volume).

Here we present a refined morphological framework that will aid the diagnosis of the genera *Globigerinoides* and *Trilobatus* near the beginning of their range. The main characters which differentiate the two genera are 1) the wall texture, which is *sacculifer*-type in *Trilobatus* and *ruber/sacculifer*-type in *Globigerinoides*; 2) the aperture, which is generally low arched and asymmetrical in *Trilobatus* and high arched and symmetrical in *Globigerinoides*.

Valid Oligocene to early Miocene *Globigerinoides* species are *G. altiaperturus* Bolli, *G. bollii* Blow,

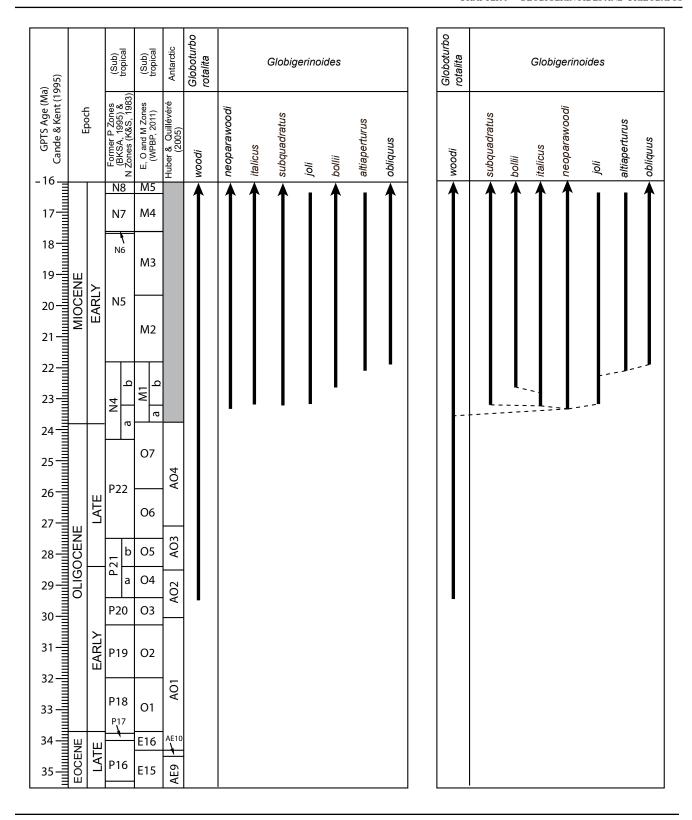


FIGURE 9.1. Stratigraphic ranges and inferred phylogenetic relationships of the lower Miocene *Globigerinoides*. BKSA, 1995 = Berggren and others, 1995; K&S, 1983 = Kennett and Srinivasan, 1983; WPBP, 2011 = Wade and others, 2011.

G. italicus Mosna and Vercesi, G. joli Spezzaferri n. sp., G. neoparawoodi Spezzaferri n. sp., G. obliquus Bolli, and G. subquadratus Brönnimann, all of which possess a ruber/sacculifer-type wall texture. Valid Oligocene to early Miocene *Trilobatus* species are *T.* altospiralis Spezzaferri n. sp., T. immaturus (LeRoy), T. praeimmaturus (Brönnimann and Resig), T. primordius (Blow and Banner), T. quadrilobatus (d'Orbigny), T. subsacculifer (Cita, Premoli Silva, and Rossi) and T. trilobus (Reuss), which possess a sacculifer-type wall texture. The pore density (pores/50 µm² test surface area) shows only little variation in the different Globigerinoides and Trilobatus species, hence this criterion is not used to distinguish species (Chapter 3, this volume). The species range-chart and phylogeny is presented in Figures 9.1 and 9.2.

#### SYSTEMATIC TAXONOMY

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

Genus *Globigerinoides* Cushman 1927, emended by Spezzaferri and others, 2015

Globigerinanus Ouda, 1978:366

TYPE SPECIES.— Globigerina rubra d'Orbigny, 1839.

#### DESCRIPTION.

Type of wall: Cancellate, irregular honeycomb, with spines irregularly distributed. Gametogenetic calcification may obscure spines holes. It may be *ruber*-or *ruber/sacculifer*-type sensu Hemleben and Olsson (2006). Only the *ruber/sacculifer*-type wall is present in Oligocene and lower Miocene *Globigerinoides*.

Test morphology: Low to moderately high trochospiral consisting of 2½-3 whorls. The peripheral margin is rounded, the test outline varies from subcircular to slightly ovate or subtriangular to subrectangular and lobate with globular to ovate chambers, may become radially compressed and asymmetrical, three to four in the last whorl, increasing gradually in size as added. The primary aperture is umbilical and is generally set in a wide and open umbilical area. Supplementary apertures are present on the spiral side; they may be one or more

and are placed at the intersection of the spiral sutures. Thin lips may be present on the primary and supplementary apertures. The last chamber may be smaller (kummerform) than the previous ones.

DISTINGUISHING FEATURES.— Distinguishing features of *Globigerinoides* are the supplementary apertures on the spiral side, which are not present in *Globigerina*, *Globoturborotalita*, *Subbotina*, and some other globular forms. *Globigerinoides* is characterized by *ruber*- and *ruber/sacculifer*-types wall texture, whereas *Trilobatus* possesses a *sacculifer*-type wall texture. The primary aperture in *Globigerinoides* is umbilical, highly arched and centered and symmetrical whereas in *Trilobatus* it is asymmetrical, generally low arched and tending toward the peripheral margin.

DISCUSSION.— Cushman (1927) erected this genus and described it as similar to Globigerina but possessing numerous and large supplementary apertures on the spiral side of the last whorl only. Bolli (1957) informally included in the genus those species with supplementary apertures on the spiral side also in chambers from the inner whorls. Blow (1979) officially emended the description of Cushman (1927) and excluded from the genus all Paleocene species such as Globoconusa daubjergensis Brönnimann, all Eocene species with the exception of "Globigerinoides" higginsi Bolli [(now Guembelitrioides nuttalli (Hamilton)], and all Oligocene species. He considered as "Globigerinoides" only Neogene species with several spiral supplementary apertures in chambers prior to the last with the exception of the phylogenetically primitive "Globigerinoides" quadrilobatus primordius Blow and Banner, which possesses only one. Blow and Banner (1962) suggested that the first representative of the genus ("Globigerinoides" primordius) originated from Globigerina praebulloides occlusa by developing supplementary apertures on the spiral side. "Globigerinoides" primordius is now attributed to the genus Trilobatus (Spezzaferri and others, 2015) and the suggested phylogenetic link is no longer supported.

"Globigerinoides" has been for a long time considered as polyphyletic. However, the re-investigation of the fossil record coupled with genetic studies has now solved the problem of the polyphyletism of the genus, which can now be considered as monophyletic (Spezzaferri and others, 2015). The bullate forms described as Globigerinanus Ouda (1978) and interpreted as evolving from the genus Globigerinoides in the Burdi-

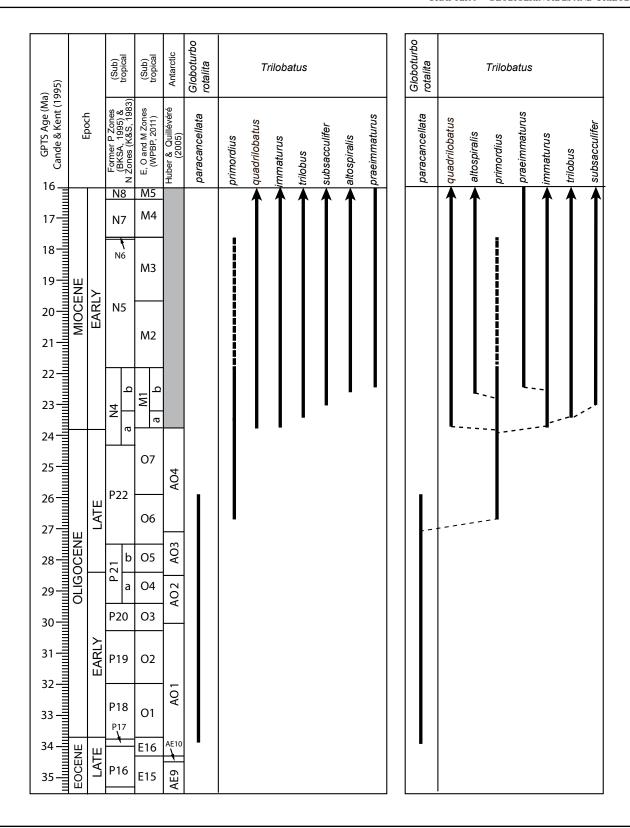


FIGURE 9.2. Stratigraphic ranges and inferred phylogenetic relationships of the upper Oligocene and lower Miocene *Trilobatus*. BKSA, 1995 = Berggren and others, 1995; K&S, 1983 = Kennett and Srinivasan, 1983; WPBP, 2011 = Wade and others, 2011.

galian resemble well known species of *Globigerinoides* (e.g., *Globigerinoides ruber*) displaying a bulla-like gametogenetic last chamber, smaller or larger than the previous one and therefore, the genus *Globigerinanus* is not retained here.

PHYLOGENETIC RELATIONSHIPS.— Globige-rinoides evolved from Globoturborotalita woodi and diversified in lower Miocene Subzone M1a (e.g., Spezzaferri, 1994).

STRATIGRAPHIC RANGE.— From Subzone M1a to the Recent (e.g., Hemleben and others, 1989).

GEOGRAPHIC DISTRIBUTION.— *Globigerinoides* is typical and abundant at low and middle latitudes (e.g., Hemleben and others, 1989).

#### Globigerinoides altiaperturus Bolli, 1957

PLATE 9.1, FIGURES 1-22 (Pl. 9.1, Figs. 1-3: new SEMs of holotype of *Globigerinoides triloba altiapertura* Bolli)

Globigerinoides triloba altiapertura Bolli, 1957:113, pl. 25, figs. 7a-c, 8 [lower Miocene *Catapsydrax dissimilis* zone, Cipero Fm., Trinidad].

Globigerinoides altiaperturus Bolli.—Jenkins, 1971:174, pl. 20, figs. 604-606 [lower Miocene, Hokianga South Heads Section, New Zealand].—Bolli and Saunders, 1985:192, fig. 20(10) [holotype re-illustrated].—Kennett and Srinivasan, 1983:54, pl. 10, fig. 1; pl. 11, figs. 4-6 [lowermost Miocene, Subzone N4b, DSDP Site 208, North Lord Howe Rise, South Pacific Ocean].—Borsetti and others, 1984, pl. IX, figs. 4a-c [lower Miocene, Monte Arligo Section, Italian Apennines].—Chaisson and Leckie, 1993:57, pl. 2, figs. 9, 10 [lower Miocene Zone M2-M3, ODP Site 806, Ontong Java Plateau, western equatorial Pacific Ocean].—Stewart and others, 2012, pl. 2, fig. 2a-c [lower Miocene, base of Subzone M1b, ODP Hole 925A, equatorial Atlantic Ocean].

"Globigerinoides" altiaperturus Bolli.—Spezzaferri, 1994:35, pl. 11, figs. 3a-c [lower Miocene Subzone M1b, DSDP Site 151, Gulf of Mexico], 4a-c, 5a-c [lower Miocene Zone M2, DSDP Site 151, Gulf of Mexico].

#### DESCRIPTION.

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

Test morphology: Low trochospiral, subrectangular and lobulate in outline, chambers globular arranged in 2½ whorls, in the last whorl three to 3½ chambers increasing rapidly in size, the last chamber is equal to half of the test; sutures depressed, straight and radial in the inner whorls and slightly arched on both sides; umbilicus open and deep, enclosed by surrounding chambers. Primary aperture umbilical, a distinct and generally very rounded high arch. One very high arched supplementary sutural aperture on the spiral side opposite to the primary aperture.

Size: Maximum diameter of holotype 0.55 mm.

DISTINGUISHING FEATURES.— The primary and supplementary apertures are distinctive high arches. Globigerinoides altiaperturus differs from G. joli by the higher arched primary and supplementary aperture and the more subrectangular outline. It differs from T. quadrilobatus by its ruber/sacculifer-type wall and by the less lobate profile, the larger last chamber and the higher arched apertures on both sides. It differs from T. trilobus by its ruber/sacculifer-type wall texture, the high arched primary and supplementary apertures and by its more lobate profile. Globigerinoides altiaperturus differs from its descendant G. obliquus by its more symmetrical primary aperture and by its last chamber which is not laterally compressed.

DISCUSSION.— The first occurrence of this species is documented just after the radiation level of *Globigerinoides* (Spezzaferri, 1994, 1996; Iaccarino and others, 1996) and it may represent an end member stage in the trend for the enlarging of the supplementary apertures on the spiral side. Bolli (1957) and Bolli and Saunders (1985) considered *G. altiaperturus* as a subspecies of *T. trilobus*, however it is here ranked as a species and considered separate from *T. trilobus* on account of the different wall texture.

PHYLOGENETIC RELATIONSHIPS.— Globigerinoides altiaperturus probably evolved from Globigeri-

Plate 9.1 Globigerinoides altiaperturus Bolli ,1957

1-3 (holotype, USNM P5632), lower Miocene *Catapsydrax dissimilis* Zone, Cipero Fm., Trinidad; 4-5 (paratype, USNM P5633), locality and level as holotype; 6-8 (same specimen), 9-11 (same specimen), 12-14 (same specimen), and 15-18 (same specimen), Zone M3, Sample K3-F10-76 PJ 259, Cipero Fm., Trinidad; 19-22, upper part of Subzone M1b Sample DSDP 94/10/2, 22-24 cm, Gulf of Mexico. Scale bars: 1-3 = 200 μm; 4-17, 19-21 = 100 μm; 18 = 20 μm; 22 = 10 μm.

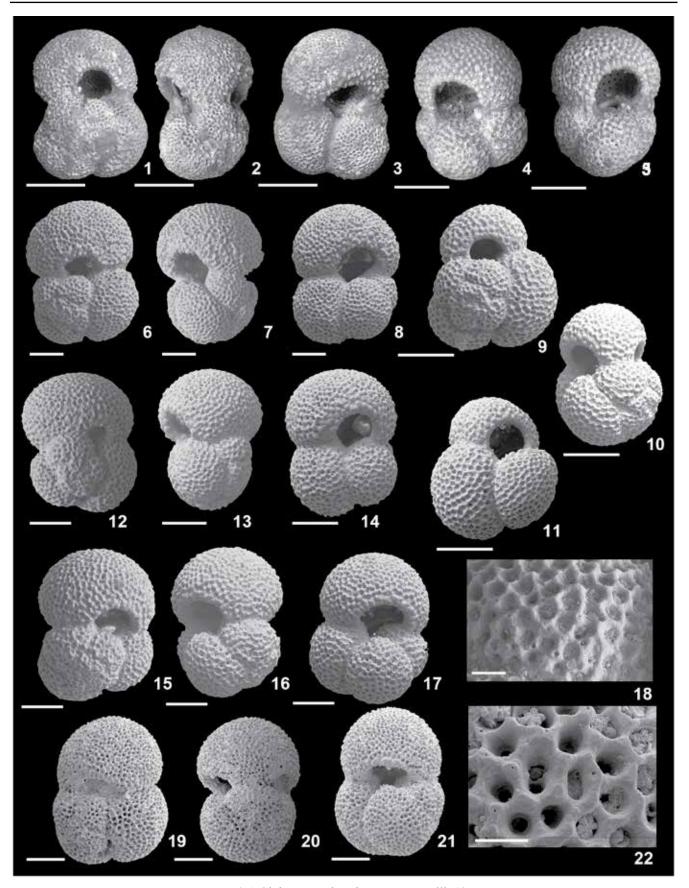


PLATE 9.1 Globigerinoides altiaperturus Bolli, 1957

*noides joli* n. sp. in the upper part of Subzone M1b. It gave rise to *G. obliquus* at the very end of Subzone M1b.

TYPE LEVEL.— Basal Miocene part of the Cipero Formation, Trinidad.

STRATIGRAPHIC RANGE.— From Subzone M1b, just below the boundary between Zone M1/M2 (Spezzaferri, 1996; Iaccarino and others, 1996) to Zone M4 (Kennett and Srinivasan, 1983; Spezzaferri, 1994). It is a useful marker species for the lower Miocene (e.g., Kennett and Srinivasan, 1983; Bolli and Saunders, 1985). In Hole 516F in the Atlantic Ocean this species first occurs at the base of Zone M2 (= N5) (Spezzaferri, 1994; Spezzaferri and Pearson, 2009) at 21.8 Ma (Wade and others, 2011). At the Aquitanian GSSP at Lemme (Italy) the FO of *G. altiaperturus* is documented at 13 m, in Subchron C6AAr2r, in the upper part of Subzone M1b, just below the Subzone M1/M2 boundary (Spezzaferri, 1996; Iaccarino and others, 1996).

GEOGRAPHIC DISTRIBUTION.— Common at mid to low latitudes, outside upwelling zones (Kennett and Srinivasan, 1983; Spezzaferri, 1994).

STABLE ISOTOPE PALEOBIOLOGY.— Globige-rinoides altiaperturus is a surface water dweller with lowest  $\delta^{18}$ O and highest  $\delta^{13}$ C in the assemblage where it is found (Stewart and others, 2012).

REPOSITORY.— Holotype (P5632) deposited at the Smithsonian Museum of Natural History, Washington, D.C.

#### Globigerinoides bollii Blow, 1959

PLATE 9.2, FIGURES 1-16 (Pl. 9.2, Figs. 1-3: new SEMs of holotype of *Globigerinoides bollii* Blow)

Globigerinoides bollii Blow, 1959:189, pl. 10, figs. 65a-c [Miocene Globorotalia menardii menardii/Globigerina nepenthes Zone, Pozón Fm., Eastern Falcon, Venezue-la].—Kennett and Srinivasan, 1983:70, pl. 15, figs. 4-6 [upper Miocene Neogloboquadrina continuosa Zone,

DSDP Site 208, North Lord Howe Rise, South Pacific Ocean].—Bolli and Saunders, 1985:192, fig. 20(8) [holotype re-illustrated].—Spezzaferri, 1994:36, pl. 15, figs. 1a-c [lower Miocene Zone M2-M3 interval, DSDP Site 151, Gulf of Mexico].

#### DESCRIPTION.

*Type of wall*: Normal perforate, spinose, *ruber/sacculifer*-type wall, strongly pustulose.

Test morphology: Compact, low trochospiral consisting of 2½-3 whorls. Outline subtriangular in 4 chambered specimens to subrectangular in 3½ chambered ones, the inner whorls are not visible because of the compact coiling; chambers embracing and subglobular; gradually increasing in size. Sutures slightly depressed, straight to slightly curved on both sides, umbilicus narrow and fairly deep. Primary aperture umbilical, a medium to rarely low semicircular arch. One (sometimes two) supplementary apertures occur on the spiral side ranging from a small and subcircular arch to a very small slightly arched slit placed on the suture between the last and the penultimate chambers.

Size: Maximum diameter of holotype 0.34 mm.

DISTINGUISHING FEATURES.—It is distinguished from *G. altiaperturus* by the strongly embracing chambers in the last whorl, the more compact test and the primary aperture, which is a small rounded arch. It differs from *G. italicus* by the completely umbilical and smaller aperture and from *G. neoparawoodi* n. sp. by the more compact test and smaller primary aperture. It differs from *G. subquadratus* by the smaller primary aperture and by its  $3\frac{1}{2}$ -4 chambers in the last whorl instead of three.

DISCUSSION.—This species was originally described as ranging from the Miocene *Globorotalia mayeri* Zone (Vindobonian) to the *Globigerina bulloides* Zone. However, its range was extended into the lower Miocene Subzone M1b by Spezzaferri (1994). It first occurs after the radiation level of *Globigerinoides* (Spezzaferri, 1994) but it is very rare until the middle Miocene. Specimens at the beginning of the range possess only one very small supplementary aperture on the spiral side (Spezzaferri, 1994), whereas younger specimens

Plate 9.2 Globigerinoides bollii Blow, 1959

1-3 (holotype, USNM 625717), Miocene *Globorotalia menardii menardii/Globigerina nepenthes* Zone, Pozón Fm., Eastern Falcon, Venezuela; 4–6 (paratype, USNM 625718); 7-9, Zone M2, DSDP Sample 151/4/2, 135-137 cm, Gulf of Mexico; 10-12 (reproduced from Spezzaferri, 1994, pl. 15, figs. 1a-c), Zone M2, DSDP Sample 151/4/1, 127-128 cm, Gulf of Mexico; 13-16, Subzone M1b, DSDP Sample 94/10/2, 22-24 cm, Gulf of Mexico. Scale bars: 1-15 = 100 μm; 16 = 20 μm.

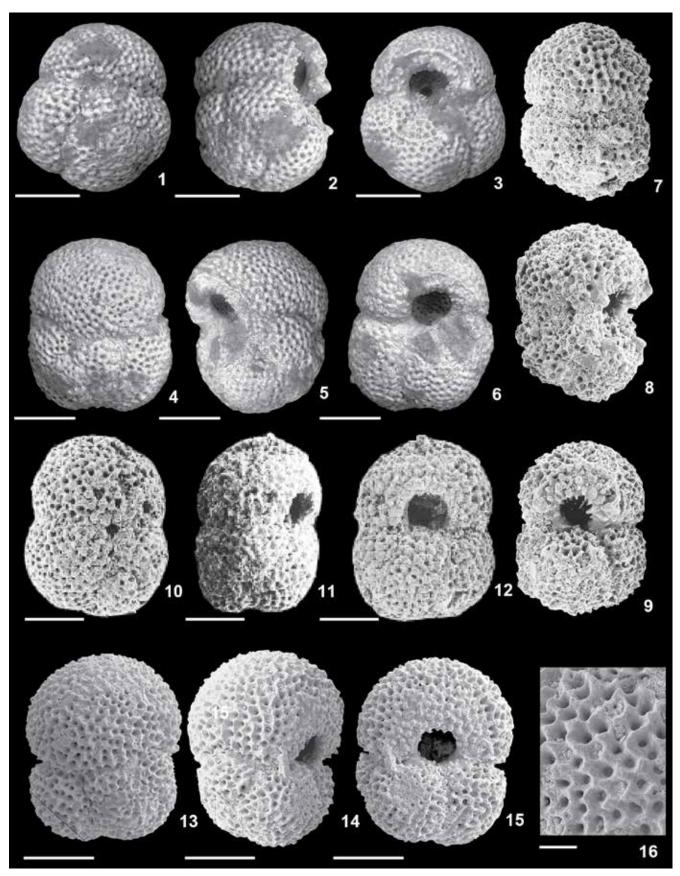


PLATE 9.2 Globigerinoides bollii Blow, 1959

may have 2 supplementary apertures (Blow, 1959; Kennett and Srinivasan, 1983). Keller (1981) suggested *Globoturborotalita woodi* as a possible direct ancestor for this species but that phylogenetic relationship is not retained here.

PHYLOGENETIC RELATIONSHIPS.— It probably evolved from *Globigerinoides italicus* in the middle part of Subzone M1b.

TYPE LEVEL.— Miocene (Vindobonian), Husito marly-clay member, Pozón Formation, Venezuela.

STRATIGRAPHIC RANGE.— Rarely found from the middle part of Subzone M1b (Chaisson and Leckie, 1993; Spezzaferri, 1994) to the upper Pliocene Zone PL 4-5 interval (Kennett and Srinivasan, 1983).

GEOGRAPHIC DISTRIBUTION.— Typical of low latitudes, most abundant in the equatorial Atlantic Ocean (Spezzaferri, 1994).

STABLE ISOTOPE PALEOBIOLOGY.— No data available.

REPOSITORY.— Holotype (USNM 625717) deposited at the Smithsonian Museum of Natural History, Washington, D.C.

#### Globigerinoides italicus Mosna and Vercesi, 1975

PLATE 9.3, FIGURES 1-16
(Pl. 9.3, Figs. 1-4: new SEMs of holotype of *Globigerinoides italicus* Mosna and Vercesi)
(Pl. 9.3, Figs. 5-7 and 9-11: new SEMs of paratype of *Globigerinoides italicus* Mosna and Vercesi)
(Pl. 9.3, Figs. 8, 12, 16: new SEMs of holotype of *Globigerinoides parawoodi* Keller)
(Pl. 9.3, Figs. 13-15: new SEMs of paratype of *Globigerinoides parawoodi* Keller)

Globigerinoides italicus Mosna and Vercesi, 1975:14-15, pl. 3, figs. 1-6 [lower Pliocene, Andora, western Liguria, Italy]. Globigerinoides parawoodi Keller, 1981:304 (partim), pl. 4, figs. 4, 6-8 [lower Miocene Subzone M1b, DSDP Site 292, northwestern Pacific Ocean].—Spezzaferri, 1994:36, pl. 14, figs. 3a-c [lower Miocene Subzone M1a, DSDP Site 94, Caribbean Sea].

#### DESCRIPTION.

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

Test morphology: Low trochospiral, consisting of about 2½-3 whorls, subtriangular, rather compact and massive, slightly lobate in outline, chambers globular; 3½-4 subspherical chambers in the last whorl, increasing slowly in size. Sutures slightly depressed, straight to slightly curved on both sides, umbilicus small. Primary aperture umbilical, an elongated arch, higher than it is wide, tending to become oblique and to move laterally, in several specimens it is narrow at the base and more enlarged towards its upper part, resembling a reversed drop, bordered by a thin rim. A small supplementary aperture is placed over the sutures separating the last and the penultimate chamber, an additional very small aperture may be seen in some specimens and is placed over the sutures between the penultimate and antepenultimate chambers.

Size: Maximum diameter of holotype about 0.40 mm.

DISTINGUISHING FEATURES.— Globigerinoides italicus is distinguished from all other species of Globigerinoides by the size, shape and position of the primary aperture, an inverse drop-like and elongated arch, higher than it is wider. It differs from G. bollii by the shape and position of the primary aperture and the slightly more lobate outline. It differs from G. subquadratus by having  $3\frac{1}{2}$  to 4 chambers in the last whorl instead of 3 and its narrower primary aperture.

DISCUSSION.— The species Globigerinoides parawoodi was established by Keller (1981) to include

#### Plate 9.3 Globigerinoides italicus Mosna and Vercesi, 1975

1-4 (holotype, Laboratory of Micropaleontology, Department of Earth and Environmental Sciences, University of Pavia, Italy), lower Pliocene, Andora, western Liguria, Italy; 5-7 (paratype), locality and level as holotype; 8, 12, 16 (holotype of *Globigerinoides parawoodi* Keller, 1981, USNM 307083); 9-11 (paratype of *Globigerinoides italicus*, Department of Earth and Environmental Sciences, University of Pavia, Italy, locality and level as holotype); 13-15 (paratype of *Globigerinoides parawoodi* Keller, 1981, USNM 307088). Scale bars: 1-3, 5-16 = 100 μm; 4 = 20 μm.

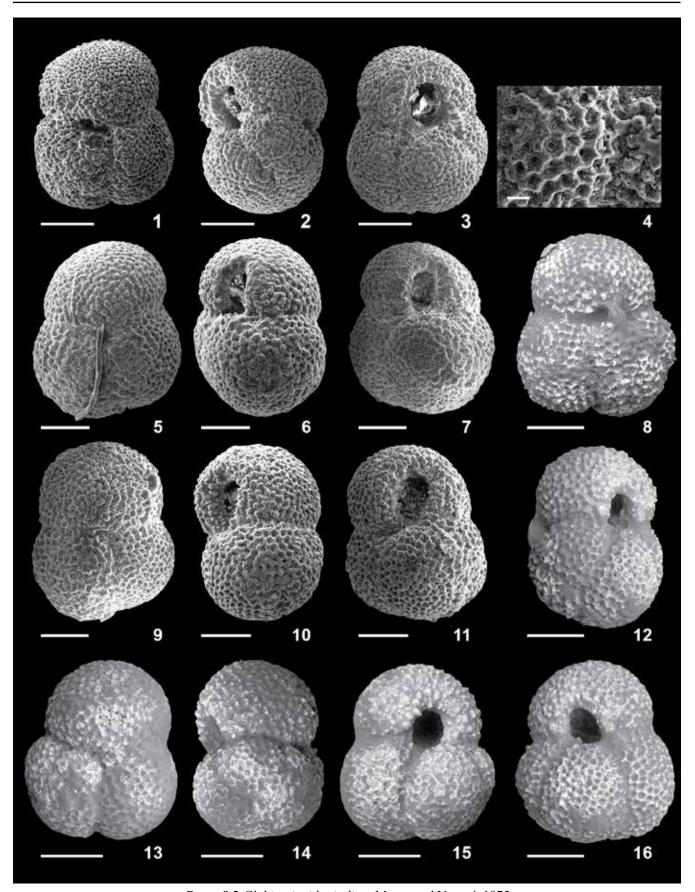


PLATE 9.3 Globigerinoides italicus Mosna and Vercesi, 1975

specimens of Globigerinoides that she thought derived from Globoturborotalita woodi. However, the holotype of G. parawoodi does not show direct lineage affinity with G. woodi (Plate 9.3, Figs. 8, 12, 16, this chapter). On the contrary, the holotype of *G. parawoodi* strongly resembles in outline and wall texture Globigerinoides italicus Mosna and Vercesi 1975 (even if the wall of G. italicus is more heavily calcified and recrystallized). Globigerinoides parawoodi Keller is here placed in synonymy with G. italicus by comparing the holotypes of the two species (Plate 9.3). Although Globigerinoides parawoodi Keller has been the more commonly used name, G. italicus has been also cited by Brambilla and others (1983); and in the geological map of Italy N. 369 (Centamore and others, 2006). Therefore, we have synonymized the two species and retained the name G. italicus as the senior synonym.

Confusingly the so-called "holotype" of *G. parawoodi* documented by Keller (1981, pl. 4, figs. 6-8) is composed of two specimens, the image of the spiral side (pl. 4, fig. 6) shows a sinistrally coiled specimen, whereas the image of the umbilical side shows a dextrally coiled specimen (pl. 4, fig. 8). In addition neither of the two documented images corresponds to the holotype deposited at the Smithsonian Museum of Natural History, Washington, D.C. with the reference number 307083 (Plate 9.3, Figs. 8, 12, 16).

PHYLOGENETIC RELATIONSHIPS.— *Globigerinoides italicus* probably evolved from *G. neoparawoodi* n. sp. at the top of Subzone M1a.

TYPE LEVEL.—Lower Pliocene *Globorotalia margaritae* Zone, Andora, Savona Province, western Liguria, Italy.

STRATIGRAPHIC RANGE.— This species is described from the lower Pliocene of western Liguria, Italy; however, due to the synonymy of *G. parawoodi* Keller with *G. italicus*, its range should be extended to the top of Subzone M1a in the lower Miocene within the range distribution of *P. kugleri*.

GEOGRAPHIC DISTRIBUTION.— Low to middle latitudes, including the Pacific Ocean and Mediterranean Sea.

STABLE ISOTOPE PALEOBIOLOGY.— No data available.

REPOSITORY.— Holotype deposited in the collection of the Laboratory of Micropaleontology, Department of Earth and Environmental Sciences, University of Pavia, Italy. No reference number is given.

#### Globigerinoides joli Spezzaferri, new species

PLATE 9.4, FIGURES 1-18

Globigerinoides parawoodi Keller.—Spezzaferri, 1994:pl. 13, figs. 6a-c [lower Miocene Subzone M1b, DSDP Hole 516F, South Atlantic Ocean].

ETYMOLOGY.—Named *joli*, which means beautiful in French.

#### DESCRIPTION.

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

Test morphology: Low trochospiral, subovate and lobulate in outline, chambers globular arranged in 3 whorls, chambers in the last whorl increase regularly and rapidly in size, sutures depressed, straight and radial on both sides; umbilicus open, wide, enclosed by surrounding chambers. Primary aperture an umbilical and distinct circular high arch bordered by a distinct rim. One low to moderately high arched supplementary sutural aperture on the spiral side opposite the primary aperture.

Size: Maximum length of holotype 0.4 mm, maximum width 0.29 mm.

DISTINGUISHING FEATURES.— Globigerinoides joli strongly differs from the holotype of G. parawoodi (Keller, 1981) here placed in synonymy with G. italicus Mosna and Vercesi by having a more lobate profile, a

#### Plate 9.4 Globigerinoides joli Spezzaferri, new species

1-4 (holotype 32505, Natural History Museum Fribourg), lower Miocene Subzone M1b, Sample Bolli 407, Cipero Fm., Trinidad; 5-8 (paratype 32506, Natural History Museum Fribourg), lower Miocene Subzone M1b, Sample Bolli 407, Cipero Fm., Trinidad; 9-12 (paratype 32507, Natural History Museum Fribourg), lower Miocene Subzone M1b, Sample Bolli 407, Cipero Fm., Trinidad; 13-15, lower Miocene unzoned, ODP Sample 1137A/13R/2, 45-47 cm, Kerguelen Plateau; 16-18 (paratype 32508, Natural History Museum Fribourg), lower Miocene Subzone M1b, Sample Bolli 407, Cipero Fm., Trinidad. Scale bars: 1-3 = 200 μm; 5-7, 9-11, 13-18 = 100 μm; 4 = 50 μm; 8, 12 = 10 μm.

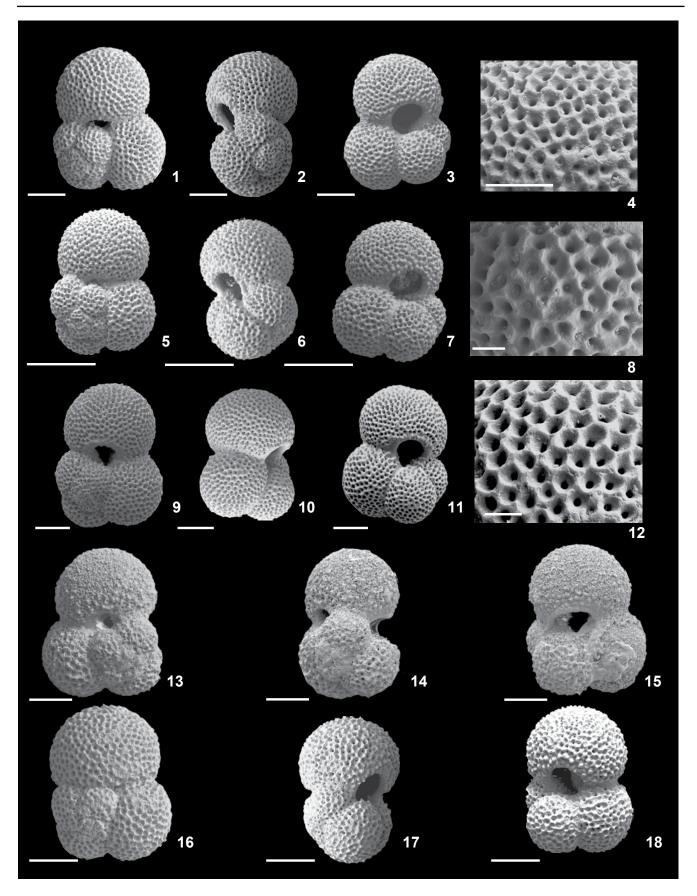


PLATE 9.4 Globigerinoides joli Spezzaferri, new species

more elongated outline, and a higher arched and circular umbilical aperture bordered by a rim, rather than the oblique and drop-like (higher than wide arch) aperture of *G. italicus*. It differs from *G. altiaperturus* by the somewhat lower arched primary and supplementary apertures and by the more lobate profile. It differs from *G. neoparawoodi* n. sp. by the more lobate outline and the thick rim bordering the aperture. It differs from *T. quadrilobatus* and *T. primordius* by the *ruber/sacculifer*-type wall, by having a higher arched primary aperture bordered by a thick rim, which is lacking in *T. quadrilobatus* and slightly tends to the peripheral margin in *T. primordius*.

DISCUSSION.—Specimens of *G. joli* were first documented by Spezzaferri (1994) and named *G. parawoodi*.

PHYLOGENETIC RELATIONSHIPS.— *Globigerinoides joli* probably evolved from *G. neoparawoodi* n. sp. in Subzone M1b.

TYPE LEVEL.—Lower Miocene Subzone M1b (upper part of the *Paragloborotalia kugleri* Zone), Sample Bolli 407, Cipero Formation, Trinidad.

STRATIGRAPHIC RANGE.— Globigerinoides joli ranges from Subzone M1b to Zone M4? Spezzaferri (1994). Additional studies are needed to confirm the presence of this species in younger Miocene sediments.

GEOGRAPHIC DISTRIBUTION.— Observed at high latitudes, in the Caribbean Sea, Gulf of Mexico, and at temperate latitudes in the South Atlantic Ocean. Rarely present in the Kerguelen Plateau region.

STABLE ISOTOPE PALEOBIOLOGY.— No data available.

REPOSITORY.— Holotype (32505) and paratypes (32506, 32507 and 32508) deposited at the Museum of Natural History of Fribourg, Switzerland.

## Globigerinoides neoparawoodi Spezzaferri, new species

PLATE 9.5, FIGURES 1-17 (Pl. 9.5, Figs. 1-3: new SEMs of paratype of *Globigerinoides parawoodi* Keller)

Globigerinoides parawoodi Keller 1981 (partim, not holotype):pl. 4, figs. 1-3, 9-11 [lower Miocene Zone N4, DSDP Site 292, northwestern Pacific Ocean].—Spezzaferri, 1994:pl. 13, figs. 6a-c [lower Miocene Subzone M1b, DSDP Hole 516F, South Atlantic Ocean].

ETYMOLOGY.— Named "neo" because it is a new description of a species with a typical *G. woodi*-derived morphology but with a supplementary aperture on the spiral side fitting the concept sometimes applied to *G. parawoodi* Keller. Since the holotype of *G. parawoodi* is placed in synonymy with *G. italicus*, a new name is required.

#### DESCRIPTION.

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

Test morphology: Low to moderately high trochospiral, subovate to subtriangular and moderately lobulate in outline, globular chambers arranged in 3 whorls, increasing slowly in size,  $3\frac{1}{2}$ -4 in the last whorl, sutures depressed, straight and radial on both sides; umbilicus open, wide, enclosed by surrounding chambers. Primary aperture an umbilical and distinct circular high arch sometimes bordered by a thin rim. One low and small arched supplementary sutural aperture on the spiral side is opposite to the primary aperture.

Size: Maximum length of holotype 0.30 mm, maximum width 0.26 mm.

DISTINGUISHING FEATURES.— Globigerinoides neoparawoodi strongly differs from the holotype of G. parawoodi Keller (here considered a junior synonym of G. italicus) by having a more lobate profile and a higher arched and circular centered umbilical aperture, rather

Plate 9.5 Globigerinoides neoparawoodi Spezzaferri, new species

1-3 (paratype of *Globigerinoides parawoodi* Keller, USNM 307090 = holotype of *Globigerinoides neoparawoodi* n. sp.), Subzone M1b, DSDP Site 292/15/1, 90-94 cm, Pacific Ocean; 4-6 (paratype of *Globigerinoides neoparawoodi* n. sp., Natural History Museum Fribourg 32513), Subzone M1b, Bolli Sample 407, Cipero Fm., Trinidad; 7-9, Zone M2, DSDP Site 151/4/2, 135-137 cm, Gulf of Mexico; 10-13, Subzone M1b, Bolli Sample 407, Cipero Fm., Trinidad; 14-17, Subzone M1b, Bolli Sample 407, Cipero Fm., Trinidad. Scale bars: 1-12, 14-16 = 100 μm; 13 = 20 μm; 17 = 10 μm.

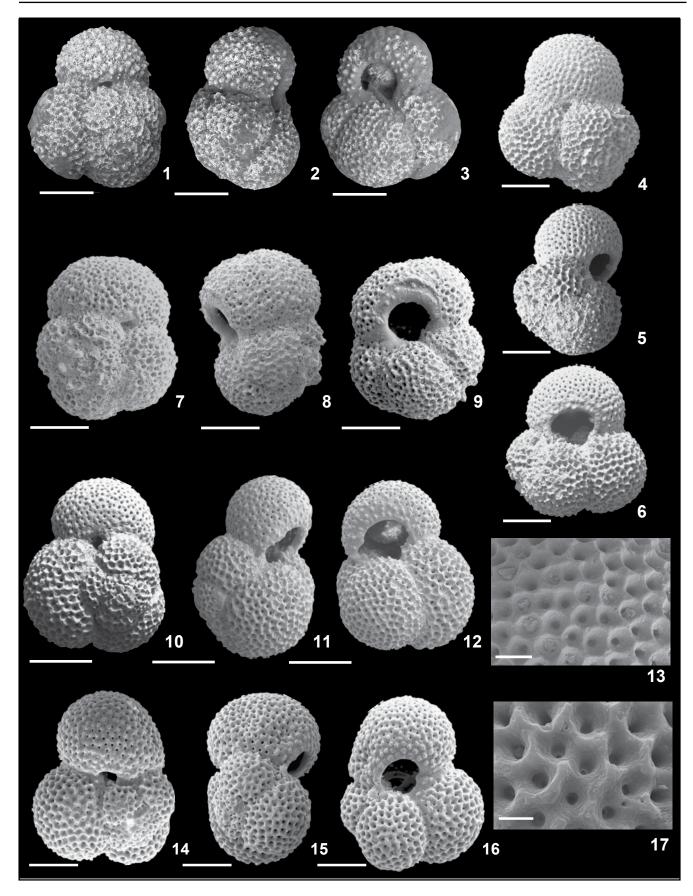


PLATE 9.5 Globigerinoides neoparawoodi Spezzaferri, new species

than an oblique and drop-like arch (higher than wide). It differs from *G. altiaperturus* by the lower arched primary and supplementary apertures and by the more lobate profile. It differs from *G. bollii* by its more lobate profile and wider primary aperture. It differs from *G. joli* n. sp. by its more compact outline and by lacking the thick rim bordering the primary aperture. It differs from *T. quadrilobatus* and *T. primordius* by its *ruber/sacculifer*-type wall texture and by having a higher arched primary aperture bordered by a rim, which is lacking in *T. quadrilobatus* and tends to the peripheral margin in *T. primordius*.

DISCUSSION.—The holotype of *G. parawoodi* Keller is here placed in synonymy with *G. italicus*. However, we consider the paratype of *G. parawoodi* (USNM 307090) as a distinct species, and is here erected as *G. neoparawoodi* (Article 23 and 72.6 of the International Code of Zoological Nomenclature). Chaisson and Leckie (1993) considered forms very similar to *G. neoparawoodi*, deriving from *G. woodi* (and named *G. parawoodi*) as possible ecophenotypes of *G. woodi* rather than a separate species. However, since these morphologies are clearly distinguished within the variability of the genus at the beginning of its range we retain them as a separate species.

PHYLOGENETIC RELATIONSHIPS.— *Globigerinoides neoparawoodi* n. sp. evolved from *G. woodi* in the upper part of Subzone M1a.

TYPE LEVEL.—DSDP Site 292/15/1, 90-94 cm, northwestern Pacific Ocean.

STRATIGRAPHIC RANGE.— *Globigerinoides neoparawoodi* n. sp. ranges from the upper part of Subzone M1a to Zone M6 (Norris, 1998).

GEOGRAPHIC DISTRIBUTION.—Cosmopolitan but more abundant at low latitudes (Keller, 1981; Spezzaferri, 1994).

STABLE ISOTOPE PALEOBIOLOGY.— No data available.

REPOSITORY.—Holotype (USNM 307090) deposited at the Smithsonian Museum of Natural History, Washington, D.C. Paratype (32513) deposited at the Natural History Museum Fribourg, Switzerland.

#### Globigerinoides obliquus Bolli, 1957

PLATE 9.6, FIGURES 1-18
(Pl. 9.6, Figs. 1-3: new SEMs of holotype of *Globigerinoides obliquus* Bolli)

Globigerinoides obliquus Bolli, 1957:113, pl. 25, figs. 10a-c [middle Miocene Globorotalia mayeri Zone, Lengua Fm., near Lengua Settlement, southern Trinidad].— Jenkins, 1971:177, pl. 21, figs. 613-615 [Pliocene-Pleistocene, Palliser Bay Section, Sample N165/554, New Zealand].—Kennett and Srinivasan, 1983:56, pl. 11, figs. 7-9 [middle Miocene Zone N9, DSDP Site 289, Ontong Java Plateau, western Pacific Ocean].—Spezzaferri, 1994:38, pl. 14, figs. 2a-c [lower Miocene Subzone N4b, ODP Site 709C, equatorial Indian Ocean].

Globigerinoides obliquus obliquus Bolli and Saunders, 1985, fig. 20(12) [holotype re-illustrated].

Globigerinoides fournieri Bermúdez, 1961:1228-1229, pl. 12, fig. 5a, 5b, [lower Miocene *Globigerinita dissimilis* Zone, Bissex Hill, Barbados].

#### DESCRIPTION.

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

Test morphology: Low trochospiral consisting of about 3 whorls, quadrangular in outline and slightly lobate. Subspherical to ovate chambers; 4 in the last whorl gradually increasing in size. The last chamber is laterally compressed and oblique. Sutures depressed, straight to slightly curved on both sides. Umbilicus fairly open and deep. Primary aperture umbilical, medium-sized high and wide arch. One small to moderately high supplementary aperture is opposite to the primary aperture.

Plate 9.6 Globigerinoides obliquus Bolli, 1957

1-3 (holotype, USNM P6534), middle Miocene, *Globorotalia mayeri* Zone, Lengua Fm., Trinidad; 4-6 (reproduced from Spezzaferri, 1994, pl. 14, figs. 2a-c), upper part of Subzone M1b, ODP Hole 709C/20/2, 120-122 cm, Indian Ocean; 7-10, Zone M4, Sample K3-F40-78, Cipero Fm., Trinidad; 11-14, Zone M2, DSDP Site 151/4/2, 135-137 cm, Gulf of Mexico; 15-18, Zone M2 ODP Hole 709C/19/CC, Indian Ocean. Scale bars: 1-9, 11-13, 15-17 = 100 μm; 10, 14, 18 = 20 μm.

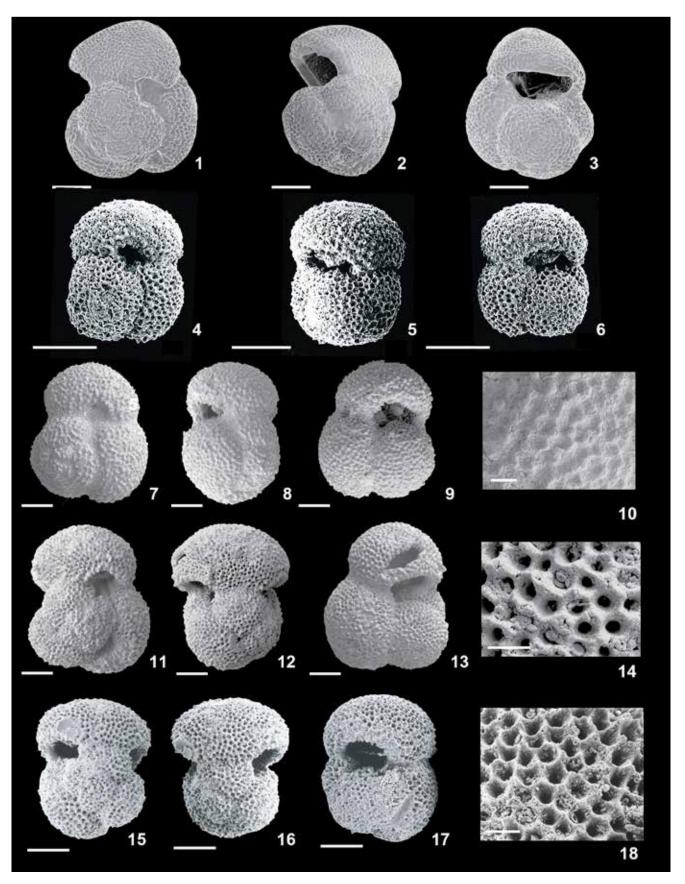


PLATE 9.6 Globigerinoides obliquus Bolli, 1957

Size: Maximum diameter of holotype 0.5 mm.

DISTINGUISHING FEATURES.— Globigerinoides obliquus differs from other Globigerinoides with a similar outline (e.g., G. neoparawoodi) by having a more quadrangular profile due to the compressed oblique last chamber and generally ovate-reniform chambers in the last whorl instead of globular, and from G. bollii by its larger aperture as well as the oblique last chamber.

DISCUSSION.—At the beginning of its range the last chamber of this species is only slightly oblique and compressed. It acquires the morphology typical of the holotype only during the Miocene starting from Zone M3 (Plate 9.6, Figs. 1-3). Kennett and Srinivasan (1983) and Chaisson and Leckie (1993) proposed *G. altiaperturus* as the ancestor of *G. obliquus* by lateral elongation of the aperture preceding the lateral compression of the chambers. This relationship is retained here.

Globigerinoides fournieri Bermúdez described from the Globigerinita dissimilis Zone is placed in synonymy with G. obliquus because its holotype (not shown) resembles the holotype of G. obliquus with the exception of the aberrant last chamber.

PHYLOGENETIC RELATIONSHIPS.— Globigerinoides obliquus probably evolved from G. altiaperturus at the very end of Subzone M1b by developing lateral elongation of the aperture and compression of chambers.

TYPE LEVEL.—Lowermost part of the Lengua Formation, Trinidad, Zone M11 (*Globorotalia mayeri* Zone).

STRATIGRAPHIC RANGE.— From the top of Subzone M1b (Spezzaferri, 1994) to the Pleistocene (Kennett and Srinivasan, 1983).

GEOGRAPHIC DISTRIBUTION.— Cosmopolitan, it is more common at middle and high latitudes.

STABLE ISOTOPE PALEOBIOLOGY.— Chaisson and Ravelo (1997) described this species as mixed-layer dweller. Nikolaev and others (1998) identified a sub-

surface habitat niche from 25 to 75 m depth for the late Miocene and from 25 to 100 m depth for the Pliocene.

REPOSITORY.— Holotype (USMN P5634) deposited at the Smithsonian Museum of Natural History, Washington, D.C.

#### Globigerinoides subquadratus Brönnimann, 1954

PLATE 9.7, FIGURES 1-20 (Pl. 9.7, Figs. 1-3: new SEMs of holotype of *Globigerinoides subquadrata* Brönnimann)

Globigerinoides subquadrata Brönnimann, 1954, in Brönnimann and Todd, 1954:680, pl. 1, figs. 8a-c [lower Miocene Zone M3-M4, Saipan, Mariana Islands].

Globigerinoides subquadratus Brönnimann.—Kennett and Srinivasan, 1983:74, pl. 16, figs. 1-3 [lower Miocene Catapsydrax dissimilis Zone, DSDP Site 208, North Lord Howe Rise, South Pacific Ocean].—Bolli and Saunders, 1985, fig. 20(6) [holotype re-illustrated].—Spezzaferri, 1994:37, pl. 12, figs. 5a-c [lower Miocene Zone M5, DSDP Site 151, Gulf of Mexico].—Fox and Wade, 2013:400, fig. 11.3 [lower Miocene Subzone M5a, IODP Hole U1338B, equatorial Pacific Ocean].

#### DESCRIPTION.

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

Test morphology: Low trochospiral, consisting of about 3½ whorls, subquadrate outline, with three, subglobular slightly compressed tending to subreniform chambers in the last whorl increasing rapidly in size. The last chamber is about half of the entire test, and placed perpendicularly to the last two chambers. Sutures depressed and straight on the umbilical side, straight to slightly arched on the spiral side. Primary aperture symmetrically positioned over the sutures before the penultimate and antepenultimate chambers is a high umbilical arch very often bordered by a pustulose rim. One to two very small and rounded supplementary apertures are present on the spiral side.

Size: Maximum length of holotype 0.58 mm.

Plate 9.7 Globigerinoides subquadratus Brönnimann, 1954

1-3 (holotype USNM 548881), Zone M3-M4, Saipan, Mariana Islands; 4-6 (hypotype, USNM 548882), Zone M3-M4, Saipan, Mariana Islands; 7-9, Zone M5-M6, DSDP Site 151/4/1, 71-72 cm, Gulf of Mexico; 10-13, Zone M4, Sample K3-F40-78, Cipero Fm., Trinidad; 14-17, Subzone M1b, DSDP Site 94/10/2, 22-24 cm, Gulf of Mexico; 18-20, Subzone M1b, DSDP Hole 588C/9/3, 137-139 cm, Tasman Sea. Scale bars: 1-12, 14-16, 18-20 =100 μm; 13, 17 = 10 μm.

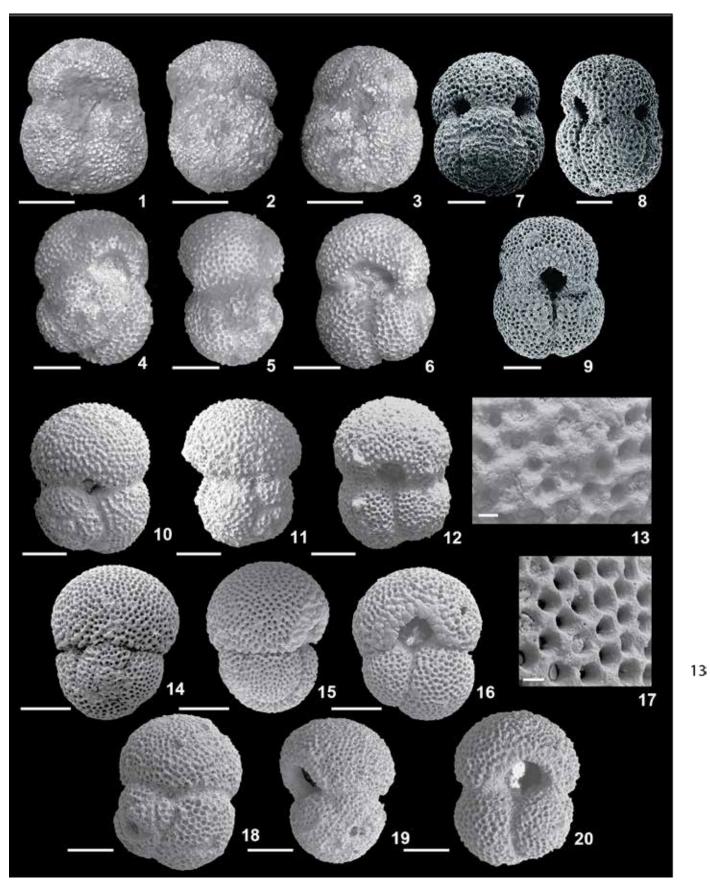


PLATE 9.7 Globigerinoides subquadratus Brönnimann, 1954

DISTINGUISHING FEATURES.— Globigerinoides subquadratus differs from its descendant G. ruber by its less lobate and more quadrangular profile and by the less developed supplementary apertures. It differs from all other Globigerinoides by its subquadrangular and compact test and by having only 3½ chambers in the last whorl.

DISCUSSION.— Brönnimann and Todd (1954) documented this species in sediments attributed to the Chattian, however, he reported "Globigerinoides" bisphericus, and Globigerinatella insueta as accompanying species, therefore the assemblage he investigated contains species of different Miocene ages and can be attributed to the lower Miocene Zone M3-M4. This species is often considered as a homeomorph of G. ruber (Chaisson and Leckie, 1993; Pearson and others, 1997), however, it is distinguished from G. ruber, in having a more quadrangular outline and a ruber/sacculifer-type wall texture. At the beginning of its range it has one very small supplementary aperture on the suture between the last and the penultimate chambers, younger specimens may have a second and small supplementary aperture over the suture between the penultimate and the antepenultimate chamber, which is visible also in edge views (Plate 9.7, Figs. 7-9). By combining data from the fossil record with molecular phylogeny and the molecular clock, Aurahs and others (2011) demonstrated that the G. ruber lineage originated and diversified in the late Miocene, and therefore, all earlier documentation of G. ruber refer to the distinct G. subquadratus lineage.

PHYLOGENETIC RELATIONSHIPS.— *Globigerinoides subquadratus* probably originated from *G. italicus* at the top of Subzone M1a.

TYPE LEVEL.—Marine andesitic tuff interbedded with andesitic lava, southwest of Saipan, Mariana Islands, dated as old as upper Oligocene (Brönnimann and Todd, 1954) but probably lower Miocene due to the presence of *Globigerinatella insueta* and "*Globigerinoides*" bisphericus.

STRATIGRAPHIC RANGE.— Upper part of Subzone M1a (Spezzaferri, 1994) up to the *Globorotalia fohsi* Zone (M9) at 11.46 Ma (Wade and others, 2011).

GEOGRAPHIC DISTRIBUTION.— *Globigerinoides subquadratus* is characteristic of low to middle latitudes,

abundant in the Caribbean region (Brönnimann and Todd, 1954).

STABLE ISOTOPE PALEOBIOLOGY.—Isotopic data indicate a similar depth habitat for *G. subquadratus* and *G. ruber* (Pearson and others, 1997), which is one of the shallowest dwelling species of all planktonic foraminifera (Emiliani, 1971; Fairbanks and others, 1982; Ravelo and Fairbanks, 1992).

REPOSITORY.— Holotype (USNM 548881) deposited at the Smithsonian Museum of Natural History, Washington, D.C.

Genus *Trilobatus* Spezzaferri, Kucera, Pearson, Wade, Rappo, Poole, Morard, and Stalder, 2015

TYPE SPECIES.— Globigerina triloba Reuss, 1850.

#### DESCRIPTION.

*Type of wall*: Cancellate, honeycomb, *sacculif-er*-type, with spines regularly distributed. Gametogenetic calcification may obscure spines holes.

Test morphology: Low to high trochospiral consisting of 3 whorls. The peripheral margin is rounded, the test outline is compact to lobate, slightly ovate or subtriangular to subrectangular. Chambers can be globular to ovate, symmetrical to enlarged and embracing or irregular and laterally compressed. They are generally 3 to rarely 4 in the last whorl increasing from fast to gradually in size as added. The primary aperture is an umbilical-extraumbilical elongated slit, sometimes moderately high arched and characterizes a generally narrow and concealed umbilical area. Supplementary apertures are present on the spiral side, slit-like or low to high arched, placed at the intersection of the spiral sutures, one per chamber. Thin lips may be present on the primary and supplementary apertures. The last chamber may be sac-like.

DISTINGUISHING FEATURES.— *Trilobatus* has supplementary apertures on the spiral side, which are not present in *Globoturborotalita*, *Subbotina*, and in other globular forms. Typical of *Trilobatus* is the *sacculifer*-type wall texture and the primary aperture which is asymmetrical, generally slit-like and extending toward the peripheral margin.

DISCUSSION.—This genus was erected by Spezzaferri

and others (2015) to avoid the polyphyly of the genus "Globigerinoides" as it was previously defined. They employed fossil and genetic evidence to distinguish two main groups of taxa derived from Globoturborotalita in the late Oligocene and early Miocene that independently evolved supplementary apertures on the spiral side of the test. In the new concept the genus *Trilobatus* is paraphyletic.

PHYLOGENETIC RELATIONSHIPS.— *Trilobatus* evolved from *Globoturborotalita paracancellata* in upper Oligocene Zone O6.

STRATIGRAPHIC RANGE.— The genus *Trilobatus* appeared in Zone O6 with *T. primordius* and it is presently one of the most abundant planktonic foraminifers worldwide.

GEOGRAPHIC DISTRIBUTION.— This genus is cosmopolitan throughout the Cenozoic although it is most abundant at low and temperate latitudes.

#### Trilobatus altospiralis Spezzaferri, new species

PLATE 9.8, FIGURES 1-22

Globigerinoides sp.1.—Spezzaferri, 1994:127, pl. 15, figs. 3a-c [lower Miocene Subzone N4a, DSDP Site 588C, South Pacific Ocean], figs. 4a-c [lower Miocene Subzone N4a, DSDP Site 516F, South Pacific Ocean].

ETYMOLOGY.— Named *altospiralis* for its characteristic high spiral side.

#### DESCRIPTION.

*Type of wall*: Normal perforate, spinose, *sacculifer*-type wall.

Test morphology: High to very high trochospiral consisting of about 2½ whorls. Subcircular to triangular or subtriangular profile, markedly lobate outline with globular chambers; 3½-4 chambers in the last whorl gradually increasing in size. Sutures strongly depressed, straight on both sides, umbilicus very narrow, almost absent and fairly deep. Primary aperture an umbilical very low arch tending to become an elongated slit. Sutural, slit-like to low arched supplementary apertures are placed over the sutures separating the last and the penultimate chambers and between the penultimate chamber and the inner spire.

Size: Maximum length of holotype 0.37 mm, maximum width 0.32 mm.

DISTINGUISHING FEATURES.— This species differs from *T. primordius* by having a high trochospire, up to 4 chambers in the last whorl, and slit-like primary and supplementary apertures. It differs from *T. immaturus*, *T. praeimmaturus* and *T. trilobus* by its very lobate outline, by having 3½-4 chambers in the last whorl and the very high spiral side.

DISCUSSION.— Spezzaferri (1994) identified this species as *Globigerinoides* sp. 1.

PHYLOGENETIC RELATIONSHIPS.— *Trilobatus altospiralis* evolved from *Trilobatus primordius* in the middle part of Subzone M1b.

TYPE LEVEL.—Lower Miocene, Subzone M1b, DSDP Sample 526A-27-1, 30-32 cm, South Atlantic Ocean, 30°08.36' S, 03°08.28'E, water depth 1054 mbsf, foraminifer-nannofossil ooze.

STRATIGRAPHIC RANGE.— *Trilobatus altospiralis* ranges from middle Subzone M1b to the middle Miocene Zones M13-M14 interval (Spezzaferri, 1994).

GEOGRAPHIC DISTRIBUTION.— This species is more abundant at middle to high latitudes in the southern hemisphere (Spezzaferri, 1994).

STABLE ISOTOPE PALEOBIOLOGY.— No data available.

REPOSITORY.— Holotype (32498) and paratypes (32499 and 32500) are deposited at the Natural History Museum of Fribourg, Switzerland.

#### Trilobatus immaturus (LeRoy, 1939)

PLATE 9.9, FIGURES 1-21
(Pl. 9.9, Figs. 1-4: new SEMs of holotype of Globigerinoides sacculiferus (Brady) var. immaturus LeRoy)

Globigerinoides sacculiferus (Brady) var. immaturus LeRoy, 1939:236, pl. 3, figs. 19-21 [Miocene, Rokan-Tapanoeli area, Central Sumatra, Indonesia].

Globigerinoides trilobus immaturus LeRoy.—Keller, 1981,

pl. 1 [lower Miocene Zone N4, DSDP Site 292, northwest Pacific Ocean].—Bolli and Saunders, 1985, fig. 20(14) [holotype re-illustrated].

Globigerinoides immaturus LeRoy.—Kennett and Srinivasan, 1983:64, pl. 10, fig.3; pl. 13, figs. 7-9 [upper Miocene Zone N16, DSDP Site 289, Ontong Java Plateau, western equatorial Pacific Ocean].—Spezzaferri, 1994:37, pl. 13, figs. 3a-c [lower Miocene, Subzone N4a, DSDP Hole 516F, southeastern Atlantic Ocean].

#### DESCRIPTION.

*Type of wall*: Normal perforate, spinose, *sacculifer*-type wall.

Test morphology: Low trochospiral, consisting of about 2½-3 whorls, subrectangular to ovate, moderately lobulate in outline, chambers globular; 3½ subspherical chambers in the last whorl, increasing moderately to rapidly in size. Sutures depressed, straight to slightly curved on both sides, umbilicus narrow and tending to close. Primary aperture umbilical, a low arch tending to become extraumbilical and encompassing the antepenultimate chamber, sometimes bordered by a thin rim. A single small to medium sized slightly arched supplementary aperture is placed over the sutures separating the last and the penultimate chamber. Rarely two supplementary apertures are present.

Size: Height of holotype 0.43 mm.

DISTINGUISHING FEATURES.— Although very similar to *T. trilobus* (Bolli and Saunders, 1985) this species is slightly more lobate and the primary aperture is a low umbilical arch across the antepenultimate chamber, whereas in *T. trilobus* it is an elongated slit encompassing the penultimate and antepenultimate chambers. Although Bolli (1957) distinguished *T. trilobus* from *T. immaturus* by the larger last chamber in *T. trilobus*, this criterion is not retained here because of large size variability of the last chamber in both species. It differs from *T. altospiralis* n. sp. by having 3-3½ chambers in the last whorl instead of 4, by its less lobulate profile, and a more elongated subrectangular outline. It differs from *T. subsacculifer* because it lacks the last sac-like chamber and for its more elongated profile.

DISCUSSION.— LeRoy (1939) described this form from Sumatra, Java and Borneo, and considered it either an immature form of *T. sacculifer*, or a *T. sacculifer* lacking the typical sac-like chamber due to ecological influence. Kennett and Srinivasan (1983), described a lineage consisting of *trilobus-immaturus-quadrilobatus-sacculifer*. However, successive observations in Spezzaferri (1994) show that the base of *T. immaturus* preceded the base of *T. trilobus*. Therefore the lineage of Kennett and Srinivasan (1983) is not retained.

PHYLOGENETIC RELATIONSHIPS.— It evolved from *T. primordius* just above the base of Subzone M1a and probably gave origin to *T. trilobus*.

TYPE LEVEL.— Neogene, Miocene, transitional sand and clay series, Tapung-Kiri area, Rokan-Tapanoeli region, Central Sumatra.

STRATIGRAPHIC RANGE.— From the lower Miocene lower part of Subzone M1a (Spezzaferri, 1994) to the Recent (e.g., Bolli and Saunders, 1985). The FO of *T. trilobus* s. l. given in Wade and others (2011) at 23.73 Ma. However, this datum is based on the taxonomic concept of Pearson and Chaisson (1997) that lumps *T. trilobus* and *T. immaturus*, and was astronomically calibrated by Shackleton and others (2000). Since the FO of *T. immaturus* is observed before the FO of *T. trilobus*, the datum of 23.73 Ma is here retained for the FO of *T. immaturus*.

GEOGRAPHIC DISTRIBUTION.—Cosmopolitan but more abundant at middle and low latitudes.

STABLE ISOTOPE PALEOBIOLOGY.— This species records the lowest  $\delta^{18}O$  values and high  $\delta^{13}C$  values within the assemblages where it is found (Gasperi and Kennett, 1993). Nikolaev and others (1998) indicate a surface habitat range of this species between 25 and 100 m.

REPOSITORY.—Holotype (PS1077a) deposited at the

Plate 9.8 Trilobatus altospiralis Spezzaferri, new species

1-4 (holotype 32498, Natural History Museum Fribourg), Subzone M1b, DSDP Sample 526A/27/1, 30-32 cm, South Atlantic Ocean; 5-8 (paratype 32499, Natural History Museum Fribourg), locality and level as holotype; 9-12 (paratype 32500, Natural History Museum Fribourg), Subzone M1b, DSDP Hole 526A/28/2, 120-123 cm, South Atlantic Ocean; 13-16, Subzone M1b, DSDP Hole 526A/28/2, 120-123 cm, South Atlantic Ocean; 17-19, Subzone M1b, DSDP Hole 516F/9/1, 140-141 cm, South Atlantic Ocean; 20-22, Zone M1, Sample RDL Sample 463, Mosquito Creek, Trinidad. Scale bars: 1-3, 5-7, 9-11, 13-15, 17-21 =  $100 \mu m$ ; 8,  $16 = 50 \mu m$ ; 4,  $12 = 20 \mu m$ ; 22 =  $50 \mu m$ <sup>2</sup> surface area.

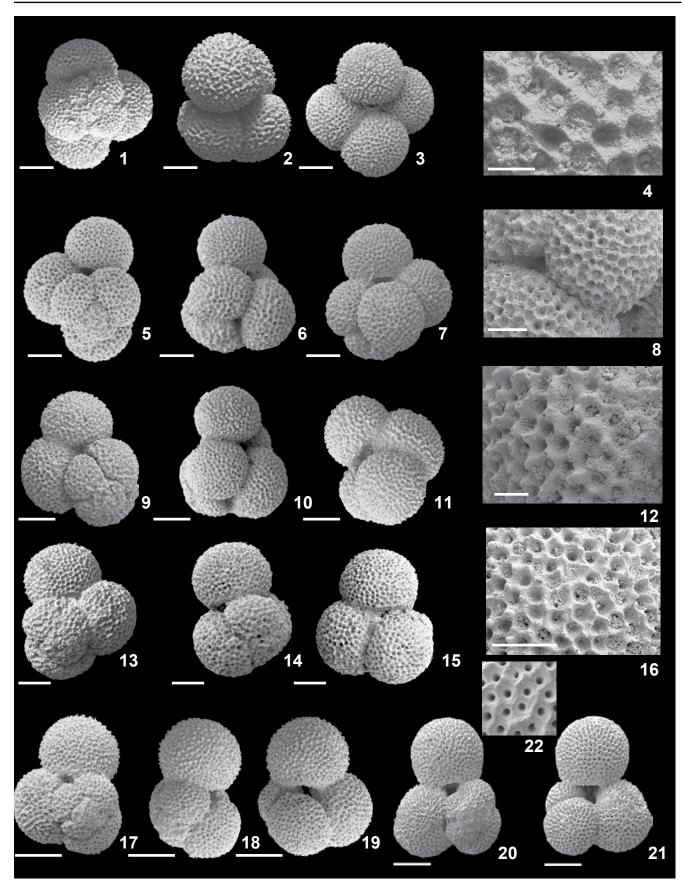


PLATE 9.8 Trilobatus altospiralis Spezzaferri, new species

Government Geological Museum of Bandung, West Java, Indonesia.

### Trilobatus praeimmaturus (Brönnimann and Resig, 1971)

PLATE 9.10, FIGURES 1-21 (Pl. 9.10, Figs. 1-3: new SEMs of holotype of Globigerinoides praeimmaturus Brönnimann and Resig)

Globigerinoides praeimmaturus Brönnimann and Resig, 1971:1272-1273, pl. 10, figs. 5, 6, 8 [lower Miocene Zone M4, DSDP Site 64, Ontong Java Plateau, western equatorial Pacific Ocean].

Globigerinoides sp. 2.—Spezzaferri, 1994:pl. 16, figs. 3a-c [lower Miocene Subzone M1a, ODP Hole 667A, equatorial Atlantic Ocean].

#### DESCRIPTION.

*Type of wall*: Normal perforate, spinose, *sacculifer*-type wall.

Test morphology: Low trochospiral, subglobular to ovate, compact in outline consisting of about 2½-3 whorls, 3½-4 subglobular chambers in the last whorl, increasing rapidly in size. Sutures depressed, straight to slightly curved on both sides, umbilicus narrow and tending to close. Primary aperture umbilical to extraumbilical, a low arch encompassing the penultimate chamber, and lacking any lip or rim but sometimes showing short blunt or composite pustules fused together. A single triangular slit-like to low arched supplementary aperture is placed over the sutures separating the last and the penultimate chamber.

*Size*: Maximum diameter of holotype 0.22 mm, its axial height is about 0.19 mm.

DISTINGUISHING FEATURES.— *Trilobatus prae-immaturus* is distinguished form *T. immaturus* and *T. trilobus* by its more subcircular and compact outline, by the slit-like aperture encompassing the penultimate chamber, and by having mainly 4 chambers in the last whorl.

DISCUSSION.— Brönnimann and Resig (1971) considered this form as a subspecies of *T. quadrilobatus* and related it to *T. quadrilobatus immaturus*. The holotype they describe is covered by a relatively thick cortex ("secondary shell substance") concealing the sutures of the last whorl. *Trilobatus praeimmaturus* has been overlooked and possibly attributed to other *Globigerinoides* species, although it is relatively abundant.

PHYLOGENETIC RELATIONSHIPS.— *Trilobatus* praeimmaturus evolved from *T. immaturus* in the middle part of Subzones M1b.

TYPE LEVEL.— Lower Miocene Zone N7/N8, DSDP Site 64-2-6, 15-17 cm. Water depth 2052 m, northern slope of Ontong Java Plateau, western equatorial Pacific Ocean.

STRATIGRAPHIC RANGE.— From the middle part of Subzone M1b to Zone M5 (Brönnimann and Resig, 1971). Additional investigations are needed to prove its presence in younger Miocene sediment.

GEOGRAPHIC DISTRIBUTION.— Cosmopolitan, abundant in the South Atlantic and southwestern Pacific Oceans.

STABLE ISOTOPE PALEOBIOLOGY.— No data available.

REPOSITORY.— Holotype (USNM 219454) deposited at the Smithsonian Museum of Natural History, Washington, D.C.

#### Trilobatus primordius (Blow and Banner, 1962)

PLATE 9.11 FIGURES 1-20 (Pl. 9.11, Figs. 1-4: new SEMs of holotype of *Globigerinoides primordius* Blow and Banner)

Globigerinoides primordius Blow and Banner, 1962:15, pl. ix, figs. Dd-Ff [lower Miocene Globorotalia kugleri Zone, Cipero Fm., Trinidad].—Kennett and Srinivasan, 1983:54, pl. 11, figs. 1-3 [uppermost Oligocene Sub-

Plate 9.9 Trilobatus immaturus (LeRoy, 1939)

1-4 (holotype P. S. 1077a, Government Geological Museum, Bandung, West Java, Indonesia), Miocene, Rokan-Tapanoeli area, Central Sumatra, Indonesia; 5-8, Subzone M1b, Bolli Sample 407, Cipero Fm., Trinidad; 9-12, Zone M2, DSDP Site 151/4/2, 135-136 cm, Gulf of Mexico; 13-15, Subzone M1b, Sample Bolli 407, Cipero Fm., Trinidad; 16-18, Subzone M1b, Bolli Sample 407, Cipero Fm., Trinidad; 19-21, Subzone M1b, Bolli Sample 407, Cipero Fm., Trinidad. Scale bars: 1-3, 5-7, 9-11, 13-21 = 100 μm; 4 = 50 μm; 12 = 20 μm; 8 = 10 μm.

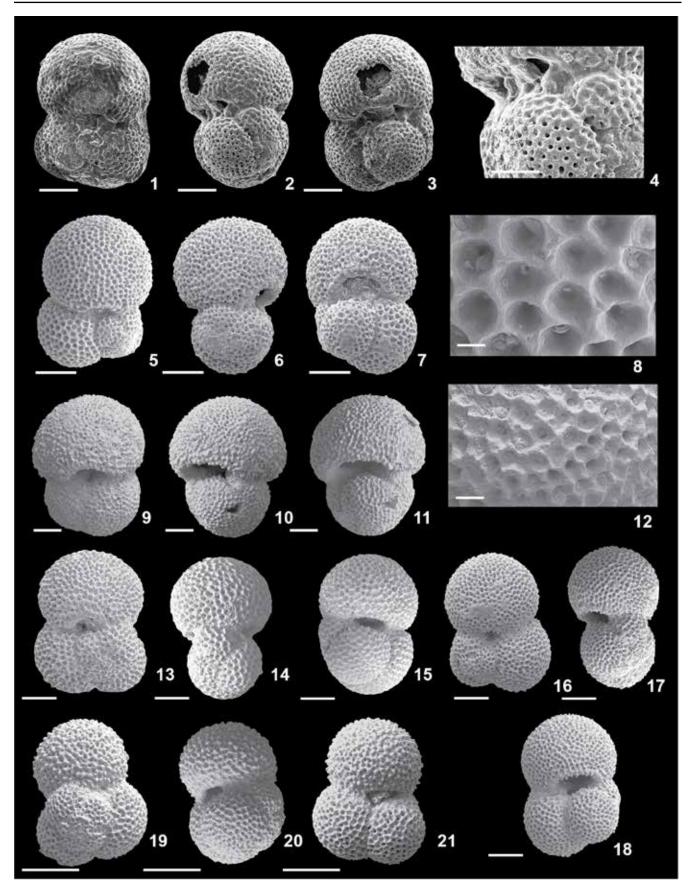


PLATE 9.9 Trilobatus immaturus (LeRoy, 1939)

zone N4a, DSDP Site 289, western equatorial Pacific Ocean].—Bolli and Saunders, 1985, fig. 20(16) [holotype re-illustrated].—Spezzaferri and Premoli Silva, 1991, pl. VIII, figs. 3a, 4a-d [upper Oligocene base of Zone O6, DSDP Hole 538A, Gulf of Mexico].—Spezzaferri, 1994:35, pl. 11, figs. 1a-d; pl. 12, figs. 2a-b [upper Oligocene base of Zone P22, DSDP Site 116, North Atlantic Ocean].—Stewart and others, 2012, pl. 2, figs. 1a-c [lower Miocene Zone M1, ODP Hole 925A, equatorial Atlantic Ocean].

#### DESCRIPTION.

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

Test morphology: Low trochospiral, subovate and lobulate in outline, chambers globular arranged in 2½-3 whorls, in spiral view 3½ globular, slightly embracing chambers in the last whorl, increasing rapidly in size. The last chamber is half of the entire test. The sutures are depressed, straight to slightly curved on both sides; umbilicus small, but open and deep, enclosed by surrounding chambers. Primary aperture umbilical, a low to moderately high arch, slightly extending from the umbilicus towards the periphery, bordered by a thin rim; one supplementary sutural small and low arched aperture on the spiral side.

Size: Maximum diameter of holotype 0.28 mm.

DISTINGUISHING FEATURES.— *Trilobatus primordius* differs from *T. quadrilobatus* by the primary aperture slightly tending toward the peripheral margin and by its more markedly subovate outline and the larger last chamber, and from *G. altiaperturus* by its *sacculifer*-type wall texture and the lower arched primary and supplementary apertures.

DISCUSSION.—The wall texture of *T. primordius* may appear *bulloides*-type in places of the same specimen, but in some case could be an artifact due to differential preservation. Blow and Banner (1962) identified *Globigerina praebulloides occlusa*, which is presently placed in *Globoturborotalita* (Chapter 8, this volume) as the ancestor of "*G.*" *primordius*. They identified this form as the precursor of the whole "*G.*" *quadrilobatus* 

stock and therefore considered "G." primordius as a "G." quadrilobatus subspecies possessing only one supplementary aperture on the spiral side compared to the two often displayed by "G." quadrilobatus. Trilobatus primordius is here ranked as a species.

PHYLOGENETIC RELATIONSHIPS.— We suggest *Globoturborotalita paracancellata* Olsson and Hemleben n. sp. (Chapter 8, this volume) as the ancestral form of *T. primordius*.

TYPE LEVEL.—Aquitanian, Cipero Formation, Trinidad.

STRATIGRAPHIC RANGE.— Upper Oligocene Zone O6 to Zone M3, where it is rare. Shafik and Chaproniere (1978) reported the co-occurrence of "Globigerinoides" and Paragloborotalia opima, but that observation is not presently proven. Lamb and Stainforth (1976), Stainforth and others (1975), Berggren and others (1985), Iaccarino (1985), Premoli Silva and Spezzaferri (1990), Spezzaferri and Premoli Silva (1991), and Spezzaferri (1994), all reported the first occurrence of the first member of the genus "Globigerinoides" ("G." primordius) in upper Oligocene Zone O7. Leckie and others (1993) provided constraints on its first occurrence at 25.6 Ma within Zone O7, on the Ontong Java Plateau (Hole 803D), and Bahamas Bank (Hole 628A). Berggren and others (1995) and Wade and others (2011) place the base of this species in Zone O6 at 26.7 Ma and its Lowest Common Occurrence at 24.3 Ma. We find this species present, although rare until Zone M3 (Spezzaferri, 1994; Spezzaferri and others, 2015).

GEOGRAPHIC DISTRIBUTION.— Cosmopolitan, sometimes dominant at low-middle latitudes (Spezzaferri, 1994).

STABLE ISOTOPE PALEOBIOLOGY.— The isotopic ratio of this species indicates a mixed-layer habitat and a symbiotic life habit (Poore and Matthews, 1984; Pearson and others, 1997; Pearson and Wade, 2009). These oxygen isotope values indicative of a mixed-layer

Plate 9.10 Trilobatus praeimmaturus (Brönnimann and Resig, 1971)

1-3 (holotype, USNM 219454), lower Miocene, DSDP Site 64, Ontong Java Plateau, western equatorial Pacific Ocean; 4-6, Subzone M1b, Bolli Sample 407, Cipero Fm., Trinidad; 7-9, Subzone M1b, Sample Bolli 407, Cipero Fm., Trinidad; 10-13, Subzone M1b, DSDP Site 94/10/2, 22-24 cm, Gulf of Mexico; 14-17, Subzone M1b, DSDP Hole 526A/28/2, 120-122 cm, southeast Atlantic Ocean; 18-21, Subzone M1b, Bolli Sample 407, Cipero Fm., Trinidad. Scale bars: 1-12, 14-16, 18-20 = 100 μm; 13, 17, 21 = 10 μm.

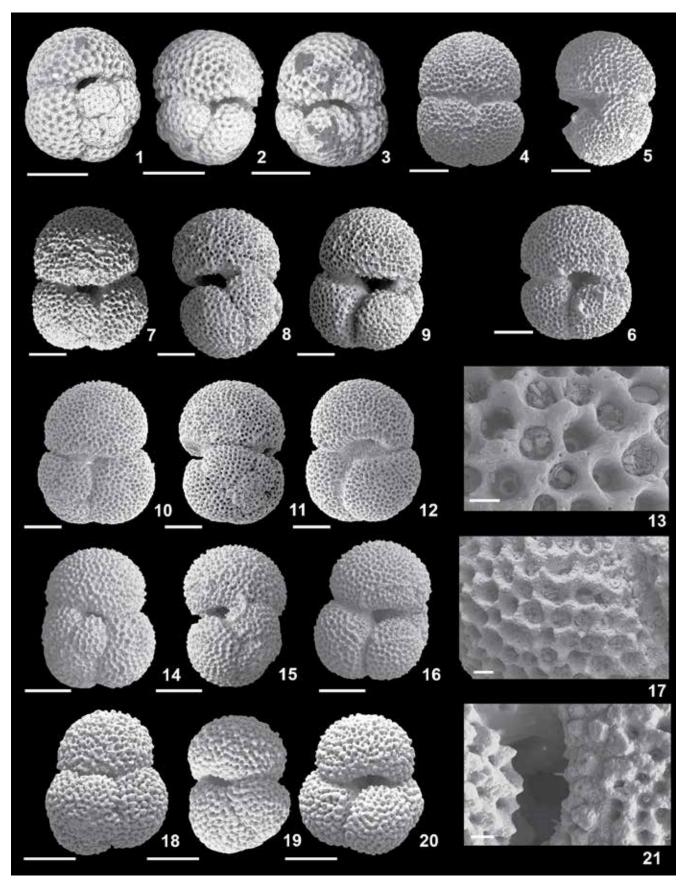


PLATE 9.10 Trilobatus praeimmaturus (Brönnimann and Resig, 1971)

habitat are very close to those measured in specimens identified as *Globigerina* cf. *bulloides* (here named *Globoturborotalita pseudopraebulloides* n. sp. (Chapter 8, this volume) from the Cipero Formation of Trinidad (Pearson and Wade, 2009).

REPOSITORY.— Holotype (P44515) deposited at the British Museum of Natural History, London.

#### Trilobatus quadrilobatus (d'Orbigny, 1846)

PLATE 9.12, FIGURES 1-20 (Pl. 9.12, Figs. 1-5: new SEMs of lectotype of *Globigerina quadrilobata* d'Orbigny)

Globigerina quadrilobata d'Orbigny, 1846:164, pl. 9, figs. 7-10 [middle Miocene Upper Lagenid Zone (fide Papp and Schmid, 1985), vicinity of Nussdorf, north of Vienna, Vienna Basin, Austria].

Globigerinoides muratai Asano, 1962:62, pl. 23, fig. 7a-c [lower Miocene, Norimatsu Shale, Shimuta, Wakamatsu City, Kyushu, Japan].

Globigerinoides bannerblowi Popescu, in Popescu and Cioflica, 1973:195, 197, pl. 4, fig. 3a, b [middle Miocene Globorotalia (Turborotalia) bykovae Zone, upper Langhian, Notelecului Valley, Romania].

Globigerinoides quadrilobatus (d'Orbigny).—Papp and Schmid, 1985:63, pl. 54, fig. 7 [holotype of d'Orbigny (1846) re-illustrated], fig. 8 [lectotype], figs. 9-12 [middle Miocene Upper Lagenid Zone].

Globigerinoides primordius (Blow and Banner).—Chaisson and Leckie 1993:158, pl. 2, fig. 13 [lower Miocene Zone M1, DSDP Site 806B, Ontong Java Plateau, western equatorial Pacific Ocean].

Not Globigerinoides quadrilobatus (d'Orbigny).—Kennett and Srinivasan, 1983:66, pl. 14, figs. 1-3 [lower Pliocene Zone N19, DSDP Site 289, Ontong Java Plateau, western equatorial Pacific Ocean].—Spezzaferri, 1994:38, pl. 11, figs. 2a-c [lower Miocene Subzone M1a, DSDP Site 94, Gulf of Mexico].—Bolli and Saunders, 1985, fig. 20(17-18) [lectotype of Banner and Blow (1960) re-illustrated].

#### DESCRIPTION.

*Type of wall*: Normal perforate, spinose, *sacculifer*-type wall.

Test morphology: Low to medium high trochospi-

ral consisting of 3 whorls. Slightly subovate to subcircular and subtriangular in outline, 4 globular chambers in the last whorl increase slowly in size. Sutures depressed and straight to slightly curved on both sides. Umbilicus open and deep, primary aperture a moderately high umbilical arch sometimes bordered by a very thin rim. One to two small and low arched supplementary apertures may be present and are placed over the sutures.

Size: Maximum diameter of holotype 0.5 mm.

DISTINGUISHING FEATURES.— *Trilobatus quadrilobatus* is distinguished from *T. primordius* by the umbilical and more centered primary aperture, by its more subcircular to subtriangular outline and by chambers increasing slowly in size in the last whorl. It differs from *Globigerinoides* species by the *sacculifer*-type wall texture. It differs from *T. altospiralis* by its larger primary aperture and the lower trochospire. It differs from *G. neoparawoodi* n. sp. and *G. italicus* by its larger last chamber and more subovate outline and from *G. italicus* by its more lobulate profile. It differs from *G. joli* by its larger supplementary aperture, the lower arched primary aperture not bordered by a rim and the more subcircular profile.

DISCUSSION.— Originally attributed to the genus *Globigerina* (d'Orbigny, 1846) this species was assigned to *Globigerinoides* by Banner and Blow (1960) because it possesses supplementary apertures. They also considered *T. trilobus* and *T. primordius* as subspecies of *T. quadrilobatus*.

The taxonomy of this species has been so far misinterpreted and its history is rather complicated. D'Orbigny did not designate a holotype, and the lectotype of Banner and Blow (1960) no longer exists and only drawings are available. Papp and Schmid (1985) selected a replacement lectotype from d'Orbigny's original material from the Vienna Basin. However, their choice was not ideal as most authors (e.g., Kennett and Srinivasan, 1983) agree that the lectotype of Banner and Blow (1960) and the replacement lectotype of Papp and Schmid (1985) are not conspecific. During the revision of this species it became clear that the selection of the

Plate 9.11 Trilobatus primordius (Blow and Banner, 1962)

1-4 (holotype P44515, BMNH London), *Paragloborotalia kugleri* Zone, Cipero Fm., Trinidad; 5-8, Subzone M1b, Bolli Sample 407, Cipero Fm., Trinidad; 9-12, Subzone M1b, Bolli Sample 407, Cipero Fm., Trinidad; 13-15, Zone O7, Atlantic Slope Project 5B/16B/29-35", western North Atlantic slope; 16-20, Zone O7, Atlantic Slope Project 5B/16B/29-35", western North Atlantic slope. Scale bars: 1-3, 5-7, 9-11, 13-15, 17-20 = 100 μm; 4, 8, 12, 16 = 10 μm.

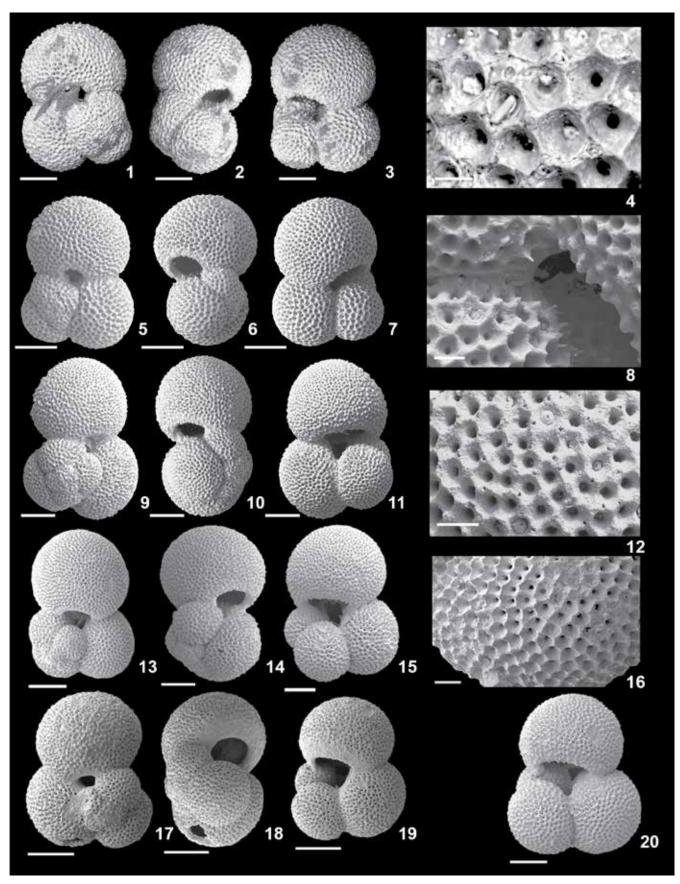


PLATE 9.11 Trilobatus primordius (Blow and Banner, 1962)

replacement lectotype made by Papp and Schmid (1985) is better in agreement with the original description of d'Orbigny, which implies 4 approximately equidimensional chambers in the last whorl. The replacement lectotype is presently the only existing type of this species and all other morphotypes (e.g., the lectotype of Banner and Blow 1960) should be disregarded for comparative taxonomy.

Banner and Blow (1960), Blow and Banner (1962) and Papp and Schmid (1985) related this species to the *T. trilobus* group. André and others (2013) demonstrated that forms similar to the lectotype selected by Banner and Blow (1960) resemble *T. sacculifer* without the sac-like final chamber, and that they have identical DNA and all correspond to a single biological species. The re-illustration of the neotype by Papp and Schmid (1985) and its new SEM images shows that it has a high arched aperture centered in the umbilicus and that it does not resemble a *T. sacculifer* without the last sac-like chamber.

The specimen described by Kennett and Srinivasan (1983) has a morphology similar to the Banner and Blow (1960) lectotype and therefore, it is a *T. sacculifer* without the sac-like final chamber. Therefore, their mention of the intergradation among *T. immaturus*, *T. quadrilobatus*, and *T. sacculifer* should be regarded as intergradation among *T. immaturus*, *T. sacculifer* without the sac-like chamber, and *T. sacculifer*. The specimen illustrated in Spezzaferri (1994), pl. 11, figs. 2a-c resemble a *T. subsacculifer* with a large primary aperture rather than *T. quadrilobatus*.

The wall texture of the replacement lectotype is very poorly preserved and does not clearly show the symmetrical patterns of pore and reticulation (Pl. 9.12, Figs. 1-3), therefore, Spezzaferri and others (2015) placed this species in *Globigerinoides*. The details of the wall textures recently made available show better the *sacculifer*-type wall (Pl. 9.12, Figs. 4-5), and this species is now re-attributed to *Trilobatus*.

Both *Globigerinoides bannerblowi* Popescu and *G. muratai* Asano are here placed in synonymy with *T. quadrilobatus* because their holotypes closely resemble the replacement lectotype of Papp and Schmid (1985).

PHYLOGENETIC RELATIONSHIPS.— *Trilobatus quadrilobatus* probably evolved from *T. primordius* in Subzone M1a.

TYPE LEVEL.—Middle Miocene Upper Lagenid Zone (Badenian), near the village of Nussdorf, Vienna Basin, Upper Austria.

STRATIGRAPHIC RANGE.— *Trilobatus quadrilobatus* ranges from Subzone M1a to at least the Pliocene (Popescu and Cioflica, 1973; Nikolaev and others, 1998). Additional investigations are needed to clarify if this species is present until the Recent.

GEOGRAPHIC DISTRIBUTION.—Cosmopolitan.

STABLE ISOTOPE PALEOBIOLOGY.— Nikolaev and others (1998) identify for this species a subsurface habitat niche from 25-100 m depth for the late Miocene and from 25-75 m depth for the Pliocene. Chaisson and Ravelo (1997) described this species as a mixed-layer dweller.

REPOSITORY.—Lectotype (1981/03/263) deposited in the Hauer-d'Orbigny collection stored at the Geological Survey of Austria, Vienna.

## Trilobatus subsacculifer (Cita, Premoli Silva, and Rossi, 1965)

PLATE 9.13, FIGURES 1-20 (Pl. 9.13, Figs. 1-3: new SEMs of holotype of *Globigerinoides sacculifer subsacculifer* Cita, Premoli Silva, and Rossi)

Globigerinoides sacculifer subsacculifer Cita, Premoli Silva and Rossi, 1965:268, pl. 31, fig. 3a-c [Tortonian, Tortona, Piedmont, northern Italy].—Bizon and Bizon, 1972:242, figs. 1-4 [lower Miocene *G. trilobus* Zone, Epirus, northwestern Greece].

Globigerinoides sacculifer (Brady).—Chaisson and Leckie 1993:158, pl. 2, fig. 16 [lower Miocene Subzone M1b, DSDP Site 806B, Ontong Java Plateau, western equatorial Pacific Ocean]. [Not Brady, 1877.]

Globigerinoides subsacculifer Cita, Premoli Silva and

Plate 9.12 Trilobatus quadrilobatus (d'Orbigny, 1846)

1-5 (lectotype, Geological Survey of Austria, Vienna), middle Miocene, Upper Lagenid Zone, Vienna Basin, Austria; 6-8, 9-12, 17-20, Subzone M1b, Bolli Sample 407, Cipero Fm., Trinidad, 13-16, Subzone M1b, DSDP Hole 526A/28/2, 120-122 cm, southeastern Atlantic Ocean. Scale bars: 1-3, 5-11, 13-15, 17-19 =  $100 \mu m$ ; 4 =  $20 \mu m$ ; 12, 16, 20 =  $10 \mu m$ .

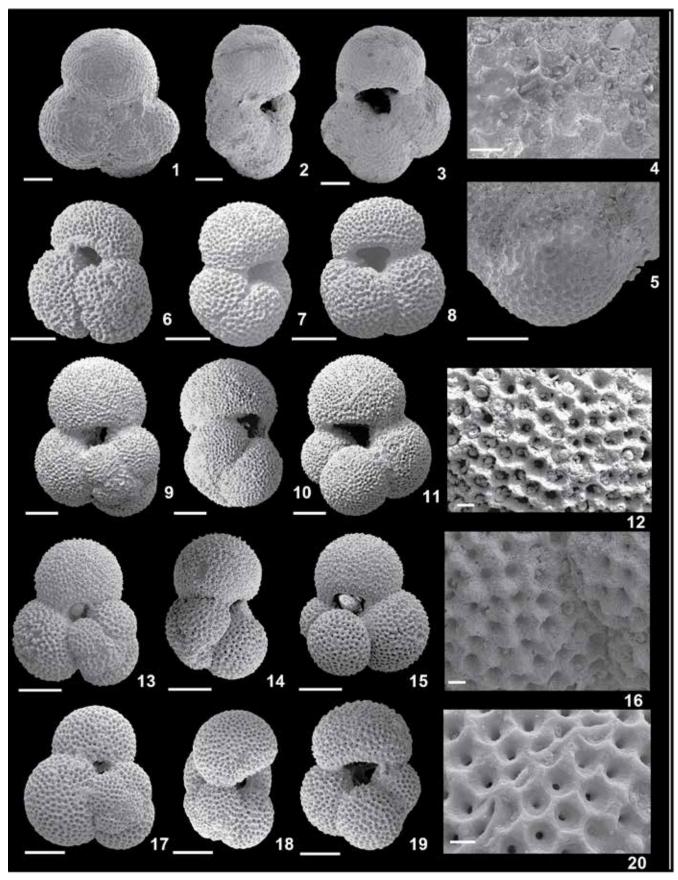


PLATE 9.12 Trilobatus quadrilobatus (d'Orbigny, 1846)

Rossi.—Spezzaferri, 1994:38, pl. 13, figs. 4a-c [lower Miocene Zones N5-N6, DSDP Hole 548A, North Atlantic Ocean]; figs. 5a-c [lower Miocene Zone N5, DSDP Site 151, Gulf of Mexico].

#### DESCRIPTION.

*Type of wall*: Normal perforate, spinose, *sacculifer*-type wall.

Test morphology: Low trochospiral, consisting of 3 whorls, subtriangular to triangular and lobate in outline, 4 subspherical to reniform chambers in the last whorl, increasing slowly in size. The last chamber is slightly sac-like and may be smaller than the previous ones. Sutures are depressed, slightly curved on the spiral side and straight on the umbilical side. Umbilicus narrow and slightly depressed. Primary aperture a low umbilical arch, sometimes bordered by a thin rim. One to two supplementary small low arched apertures are present along the sutures.

Size: Maximum diameter of holotype 0.25 mm.

DISTINGUISHING FEATURES.— The last slightly pronounced sac-like chamber is similar to, although less-developed than that of *T. sacculifer*. *Trilobatus subsacculifer* is generally smaller that *T. sacculifer* (maximum length of holotype 1 mm). The primary aperture is a lower and smaller arch than in *T. sacculifer*. It differs from *T. immaturus* and *T. trilobus* by a slightly sac-like last chamber.

DISCUSSION.— Cita and others (1965) suggest that *T. subsacculifer* evolved into *T. sacculifer* in the middle Miocene, acquiring specialized characters such as the well-developed sac-like last chamber. However, additional material is needed to prove this phylogenetic relationship.

PHYLOGENETIC RELATIONSHIPS.— *Trilobatus subsacculifer* evolved from *T. trilobus* just above the Subzone M1a/M1b boundary.

TYPE LEVEL.— Miocene from the Tortonian stage type section, Rio Mazzapiedi Section, Tortona-Alessandria region, northern Italy.

STRATIGRAPHIC RANGE.— *Trilobatus subsacculifer* ranges from just above the Miocene Subzone M1a/M1b boundary (Spezzaferri, 1994) to the Tortonian, upper Miocene Zone M13 (Cita and others, 1965). Additional and comparative material is needed to prove its presence in sediments younger than Zone M13.

GEOGRAPHIC DISTRIBUTION.— This species is most abundant at middle and low latitudes (Spezzaferri, 1994).

STABLE ISOTOPE PALEOBIOLOGY.— A well constrained stable isotope paleobiology is presently not available. However, the few data reported in Bicchi and others (2003) suggest that it was a mixed-layer dweller.

REPOSITORY.— Holotype (1526) deposited in the collection of the Laboratory of Micropaleontology, Department of Earth Sciences "A. Desio", University of Milano, Italy.

#### Trilobatus trilobus (Reuss, 1850)

PLATE 9.14, FIGURES 1-21 (Pl. 9.14, Figs. 1-3: SEMs of neotype of *Globigerina triloba* Reuss)

Globigerina triloba Reuss, 1850:374, pl. 47, figs. 11a-e [middle Miocene, Bega Basin, Transylvania, Romania].
Globigerinoides triloba Kennett and Srinivasan, 1983:62, pl. 10, fig. 4; pl. 13, figs. 1-3 [lower Miocene Zone N8, DSDP Site 289, Ontong Java Plateau, western equatorial Pacific Ocean].

Globigerinoides trilobus Spezzaferri, 1994:37, pl. 13, figs. 1a-c; [lower Miocene Subzone N4b, DSDP Hole 516F, eastern South Atlantic Ocean], pl. 15, figs. 6a-c [lower Miocene, Subzone N4b, DSDP Site 98, North Atlantic Ocean].—Rögl, 2012:181-183, pl. 1, figs. 1, 2 (neotype) [middle Miocene, Badenian, Wieliczka near Krakov, Poland], pl. 1, fig. 3 [middle Miocene, lower Badenian Felso Lapugy, Siebenbürgen, Lapugiu de Sus, Bega Basin, Transylvania, Romania], pl. 1, figs. 4-8 [middle Miocene, Upper Lagenidae Zone, Badenian old brickyard, Austria], pl. 2, figs. 1, 2 [middle Miocene Badenian, Wieliczka near Krakov, Poland], pl. 2, figs. 5, 6 [middle Miocene

Plate 9.13 Trilobatus subsacculifer (Cita, Premoli Silva, and Rossi, 1965)

1-3 (holotype 1526, Laboratory of Micropaleontology, Department of Earth Sciences "A. Desio", University of Milan, Italy), Tortonian, Tortona, Piedmont, northern Italy; 4-6 (same specimen), Subzone M1b, Lemme Section at 18 m, northern Italy; 7-9 (same specimen), 10-12 (same specimen), 13-16 (same specimen), 17-20 (same specimen), Zone M2, DSDP Site 151/4/2, 135-136 cm, Gulf of Mexico. Scale bars: 1-15, 17-19 = 100 μm; 16, 20 = 20 μm.

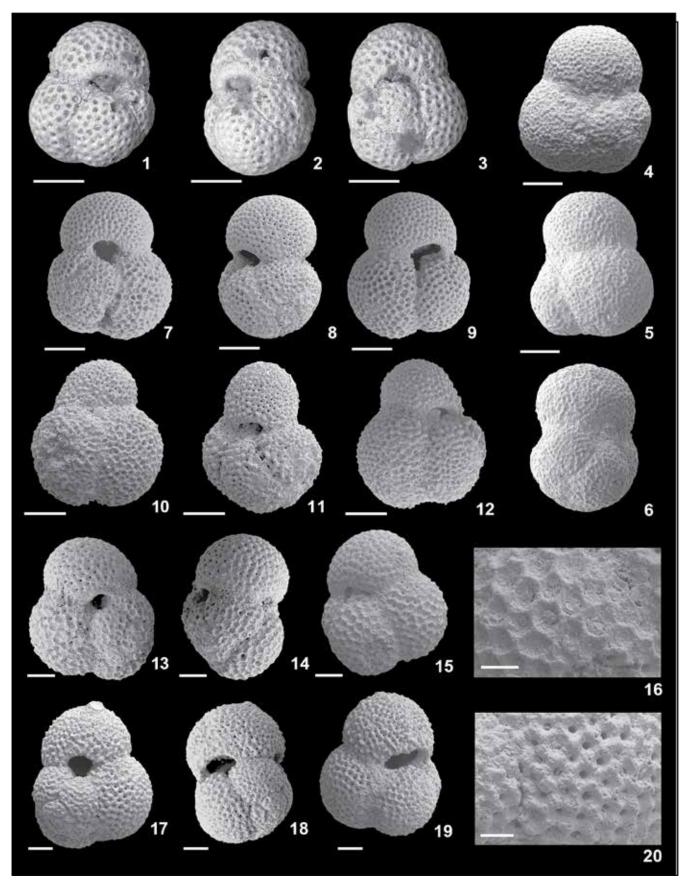


PLATE 9.13 Trilobatus subsacculifer (Cita, Premoli Silva, and Rossi, 1965)

Zone, of agglutinated foraminifera, Nussdorf, Grünes Kreuz, Austria], pl. 2, figs. 7-9 [middle Miocene lower Badenian Felso Lapugy, Siebenbürgen, Lapugiu de Sus, Bega Basin, Transylvania, Romania].

#### DESCRIPTION.

*Type of wall:* Normal perforate, spinose, *sacculifer*-type wall.

Test morphology: Low trochospiral, consisting of about 3 whorls, subrectangular, compact to slightly lobate in outline; 3 subspherical chambers in the last whorl, increasing rapidly in size. The embracing last chamber generally comprises half of the test. Sutures depressed, straight on both sides, umbilicus concealed. Primary aperture an umbilical-extraumbilical elongated slit. Supplementary aperture is an irregular slit along the spiral suture.

Size: Neotype maximum length 0.35 mm and maximum width 0.26 mm.

DISTINGUISHING FEATURES.— *Trilobatus trilobus* differs from *Globigerinoides* by its *sacculifer*-type wall and from all other species of *Trilobatus* by the umbilical-extraumbilical slit-like primary aperture, and by having only 3 chambers in the last whorl. It is distinguished from *T. immaturus* by the slit-like primary aperture, which tends to become extraumbilical and by the more compact, less lobate profile. It differs from *T. subsacculifer* because it lacks the last sac-like chamber.

DISCUSSION.— Originally described as *Globigerina* triloba, this form was attributed for the first time to the genus *Globigerinoides* by Coryell and Mossmann (1942). The evolution of *T. trilobus* to *Orbulina* was proposed by Cushman and Dorsey (1940) and successively Blow (1956), Jenkins (1968) and Pearson and Chaisson (1997) described the evolutionary steps in detail. See *T. immaturus* for the discussion of previously proposed phylogenetic relationships (e.g. Kennett and Srinivasan, 1983).

All specimens of *T. trilobus* identified by Reuss and stored at the Natural History Museum of Vienna

do have a number but the catalogue to the numbers is missing. Since it was not possible to identify the holotype from the Reuss' drawings, Rögl (2012) designated a neotype.

At the beginning of its range in Zone M1 this species displays a more ovate profile than younger Miocene specimens, when it becomes more compact, and rectangular. Based on data from the fossil record, and the molecular clock, Aurahs and others (2011) suggested a phylogenetic relationship between *T. primordius* and *T. trilobus*.

PHYLOGENETIC RELATIONSHIPS.— *Trilobatus trilobus* evolved from *T. immaturus* in Subzone M1a.

TYPE LEVEL.— Middle Miocene from the salt mine of Wieliczka near Krakov, Poland.

STRATIGRAPHIC RANGE.— Lower Miocene upper part of Subzone M1a (Spezzaferri, 1994) to Recent. The base occurrence of *T. trilobus* s.l. is calibrated to 23.73 Ma (Wade and others, 2011), however, it is here retained for *T. immaturus* (see stratigraphic range of *T. immaturus*, this chapter).

GEOGRAPHIC DISTRIBUTION.— Very abundant in the tropics (Bé and Tolderlund, 1971) but present also at middle latitudes.

STABLE ISOTOPE PALEOBIOLOGY.— Pearson and others (1997) indicate for this species mixed-layer habitat with symbiotic associations. Experiments summarized by Hemleben and others (1989) identified for *T. trilobus* a temperature tolerance of 14–31°C.

REPOSITORY.— The neotype (2011/0341/0001) is deposited at the Micropaleontological Collection of the Department of Geology and Paleontology, Natural History Museum Vienna, Austria. It has been selected from original material of Reuss, collection number 1867/0034/0037.

Plate 9.14 Trilobatus trilobus (Reuss, 1850)

1-3 (neotype 2011/0341/0001, Rögl, 2012, Natural History Museum, Vienna), middle Miocene, Wieliczka near Krakov, Poland; 4-6, Subzone M1b, Lemme Section at 10 m, Northern Italy; 7-9, Zone M3, Sample K3-F10-78, Cipero Fm., Trinidad; 10-13, Subzone M1b, DSDP Hole 588C/8/5, 95-100 cm, Tasman Sea; 14-17, Zone M2, DSDP Site 151/4/2, 135-136 cm, Gulf of Mexico; 18-21, Zone M2, DSDP Site 151/4/2, 135-136 cm, Gulf of Mexico. Scale bars: 1, 2, 4-12, 14-16, 18-20 =  $100 \mu m$ ; 3, 17, 21 =  $10 \mu m$ ; 13 =  $10 \mu m$ .

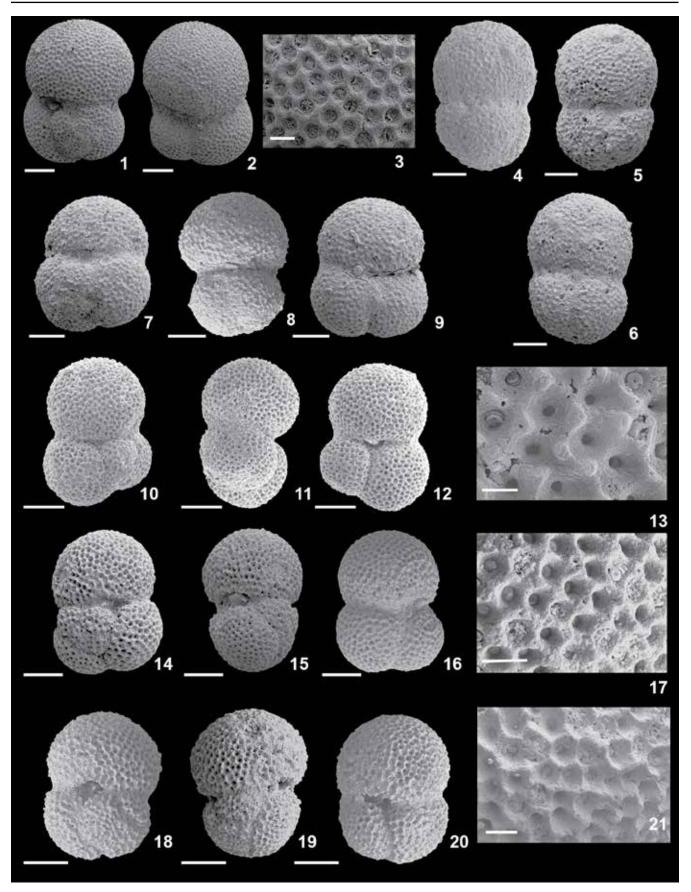


PLATE 9.14 Trilobatus trilobus (Reuss, 1850)

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#### **CITATION**

Spezzaferri, S., Olsson, R.K., and Hemleben, Ch., 2018, Taxonomy, biostratigraphy, and phylogeny of Oligocene to lower Miocene *Globigerinoides* and *Trilobatus*, *in* Wade, B.S., Olsson, R.K., Pearson, P.N., Huber, B.T. and Berggren, W.A. (eds.), Atlas of Oligocene Planktonic Foraminifera, Cushman Foundation of Foraminiferal Research, Special Publication, No. 46, p. 269-306.