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Chapter 4

TAXONOMY, BIOSTRATIGRAPHY, AND PHYLOGENY OF OLIGOCENE *CATAPSYDRAX*, *GLOBOROTALOIDES*, AND *PROTENTELLOIDES*

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ABSTRACT

The taxonomy, biostratigraphy, and phylogeny of Oligocene *Catapsydrax, Globorotaloides*, and *Protentelloides* is reviewed. *Catapsydrax* and *Globorotaloides* are long-ranging genera with robust and dissolution-resistant tests. Both genera appeared in the early Eocene. *Catapsydrax* disappeared in the late Miocene while *Globorotaloides* has living representatives. *Catapsydrax* is ubiquitous in its distribution and highly variable in test size. Oligocene species of *Globorotaloides* are typically small (<250 µm) and usually rare in the tropics but may be common in high latitude and upwelling regions. After little evolutionary change in the Eocene and early Oligocene, *Globorotaloides* and *Catapsydrax* diversified at low latitudes in the mid- to late Oligocene resulting in the appearance of several new species and the quasi-clavate genus *Protentelloides* in the late Oligocene. So far *Protentelloides* spp. have only been found in the equatorial Atlantic Ocean. The following species are recognized as valid: *Catapsydrax dissimilis* (Cushman and Bermúdez), *Catapsydrax indianus* Spezzaferri and Pearson, *Catapsydrax unicavus* Bolli, Loeblich, and Tappan, *Globorotaloides atlanticus* Spezzaferri and Coxall n. sp., *Globorotaloides eovariabilis* Huber and Pearson, *Globorotaloides hexagonus* (Natland), *Globorotaloides quadrocameratus* Olsson, Pearson and Huber, *Globorotaloides stainforthi* (Bolli, Loeblich, and Tappan), *Globorotaloides suteri* Bolli, *Globorotaloides testarugosus* (Jenkins), *Globorotaloides variabilis* Bolli, *Protentelloides dalhousiei* Zhang and Scott, and *Protentelloides primitivus* Zhang and Scott.

INTRODUCTION

Catapsydrax and *Globorotaloides* are long-ranging cosmopolitan taxa that are persistent elements of Eocene to Neogene planktonic foraminiferal assemblages (Kennett and Srinivasan, 1983; Olsson and others, 2006a). They are united here, together with the short-ranging late Oligocene genus *Protentelloides,* by their macroperforate, strongly cancellate wall, tendency to possess a terminal bulla, or bulla-like final chamber, and a deep-dwelling, sub-thermocline planktonic ecology. The ancestry of *Catapsydrax* and *Globorotaloides* is uncertain. Olsson and others (2006a) suggested that *Globorotaloides* evolved from *Parasubbotina varianta* in the early Eocene and *Catapsydrax unicavus* shortly after from *Globorotaloides quadrocameratus* (Olsson and others, 2006a, fig. 5.1). Descent from a subbotinid ancestor was also considered (Olsson and others, 2006b:76). Subsequent morphological parallels between *Catapsydrax* and *Globorotaloides* are probably the result of homeomorphy.

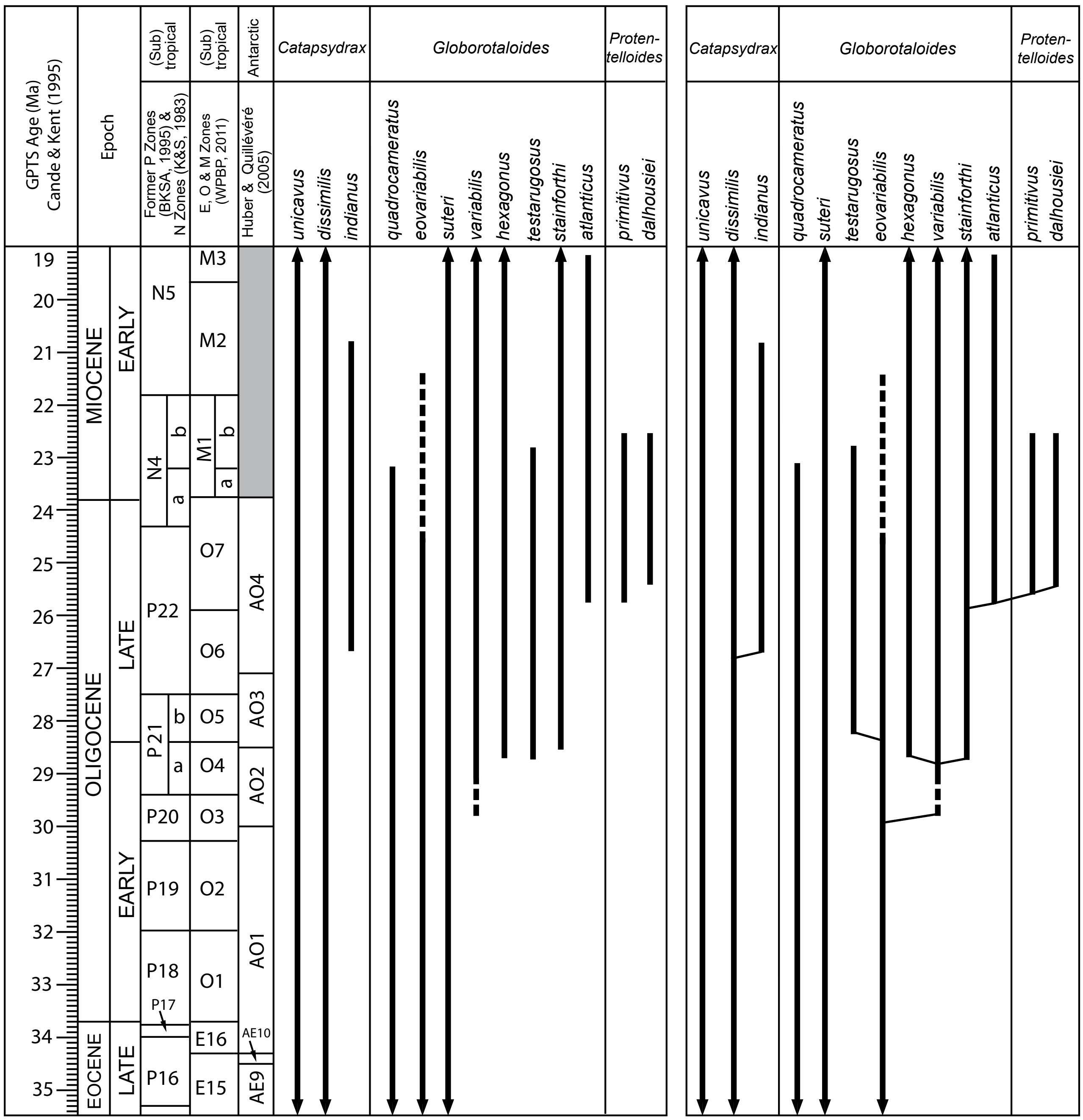

FIGURE 4.1. Stratigraphic ranges and inferred phylogenetic relationships of Oligocene species of *Catapsydrax, Globorotaloides,* and *Protentelloides* discussed in this chapter. BKSA, 1995 = Berggren and others, 1995; K&S, 1983 = Kennett and Srinivasan, 1983; WPBP, 2011 = Wade and others, 2011.

Confusion over the morphologic limits of *Catapsydrax* and *Globorotaloides* has resulted in much interchange of species between genera in published taxonomies. This is especially so in the Oligocene where the frequency of *Catapsydrax*-like bullae increases in *Globorotaloides*.

Here we present a refined morphological framework that should aid the diagnosis of *Catapsydrax* and *Globorotaloides*. Under our classification, species with involute coiling, an umbilical aperture and an obligate bulla are referred to *Catapsydrax*. Forms with 4 or more chambers in the final whorl, low trochospiral coiling, lateral flattening (especially of the pre-adult spiral), and an umbilical-extraumbilical aperture (occurring with or without a bulla) are referred to *Globorotaloides*. These definitions mostly work although we recognize that there is drift towards a *Catapsydrax*-type umbilical aperture in some Oligocene *Globorotaloides* and that *Catapsydrax* can occur without a bulla, possibly in pre-gametogenic individuals. Specimens of *Globorotaloides* are often small (<250 μm) and rare, but may become larger and can occur in greater numbers in low latitude upwelling regions and the high latitudes (Berggren, 1972; Huber, 1991; Spezzaferri, 1995).

Following the *Atlas of Eocene Planktonic Foraminifera* (Pearson and others, 2006), *Catapsydrax* and *Globorotaloides* are united in the family Globigerinidae with other cancellate spinose species, although whether these genera actually possessed spines throughout their ranges is uncertain. The following species are recognized from the Oligocene: *Catapsydrax unicavus, Catapsydrax dissimilis, Catapsydrax indianus, Globorotaloides eovariabilis, Globorotaloides hexagonus, Globorotaloides quadrocameratus, Globorotaloides suteri, Globorotaloides stainforthi, Globorotaloides testarugosus,* and *Globorotaloides variabilis*. The clade experienced a phase of radiation in the Oligocene resulting in increased diversity in both genera at low latitudes and the evolution of the quasi-clavate genus *Protentelloides*, represented by *Protentelloides primitivus* and *Protentelloides dalhousiei* in the late Oligocene. We describe a new species of *Globorotaloides, Globorotaloides atlanticus* Spezzaferri and Coxall n. sp., which is transitional in morphology between *Globorotaloides* and *Protentelloides*.

The stratigraphic highest occurrence of *Catapsydrax dissimilis* has been used as a zonal marker in the lower Miocene (Bolli, 1957; Blow, 1979; Berggren and Pearson, 2005; Wade and others, 2011) and *Globorotaloides stainforthi* has given its name to a partial range zone of the lower Miocene (Bolli, 1957). Otherwise these taxa are of limited biostratigraphic use. Stable isotopic evidence of fossil species and plankton-observations for extant *Globorotaloides hexagonus* suggests all members of the group live or lived deep in the water column within or below the thermocline (Poore and Matthews, 1984; Boersma and others, 1987; Arthur and others, 1989; Barrera and Huber, 1991; van Eijden and Ganssen, 1995; Ortiz and others, 1996; Wade and others, 2007; Pearson and Wade, 2009).

As described by Olsson and others (2006a) there is evidence, in the form of sparsely distributed "spine holes" on some specimens, that *Catapsydrax* and *Globorotaloides* possessed spines in life (see below). Living *Globorotaloides hexagonus,* however, appears to be nonspinose (Hemleben and others, 1989; M. Kučera, personal communication). This suggests either that *G. hexagonus* is unrelated to the Paleogene forms, or, more likely, that spines were lost over time. The species-level range-chart and phylogeny is presented in Figure 4.1. Characteristic wall textures are discussed and illustrated in Chapter 3 (this volume).

SYSTEMATIC TAXONOMY

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

Globoquadrinidae Blow, 1979

DISCUSSION.— The family Globoquadrinidae was erected by Blow (1979) to include *Globoquadrina* and *Dentoglobigerina* plus other genera (*Globorotaloides* and *Globigerinita*, which is now regarded as a microperforate genus) that are no longer believed to be closely related. The critical feature that linked these groups, according to Blow, was a shift in aperture from a more extraumbilical to intraumbilical position during ontogeny, and significant differences in wall textures were not taken into account. Olsson and others (2006a) retained the family but in a very different sense, uniting two genera (*Globoquadrina* and *Dentoglobigerina*) that were believed, at that time to be nonspinose, and hence were excluded from the spinose Globigerinidae. These genera are now regarded as spinose or descended from a closely related spinose form (see Pearson and Wade, 2015, and Chapter 11, this volume) hence they are now included in family Globigerinidae.

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

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

DESCRIPTION.

Type of wall: Coarsely cancellate, *sacculifer*-type or *ruber/sacculifer*-type, probably spinose in life, with tendency to develop a thick (gametogenic) crust in some species.

Test morphology: Globular, lobulate or compact, 3-4 chambers in the final whorl; chambers moderately inflated, appressed; primary aperture is umbilical and nearly always covered by bulla with one or more infralaminal apertures in the adult stage; 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, umbilical primary aperture (compared to the umbilical-extraumbilical aperture in *Globorotaloides*), fewer, more appressed chambers in the final whorl (3-4 compared to 4-6 in *Globorotaloides*). The thick *Catapsydrax* wall may be strongly cancellate and *sacculifer*-type or more weakly cancellate and thus *ruber/sacculifer*-type (see Chapter 3, this volume). In contrast, the wall texture of *Globorotaloides* is always *sacculifer*-type. *Catapsydrax usually* possesses a terminal bulla with a uniform continuous rim bordering single or multiple infralaminal aperture(s). *Globorotaloides* can also develop a bulla but this is obligate only in one species (*Globorotaloides stainforthi*). *Catapsydrax* is distinguished from bullate forms of *Dentoglobigerina*, *Subbotina, Globigerinita*, and *Globoturborotalita* by the more compact form, typically (but not exclusively) flattened bulla, rimmed infralaminal aperture(s) and thickened coarsely cancellate wall texture.

DISCUSSION.— *Catapsydrax* was erected by Bolli, Loeblich, and Tappan (1957:36) to encompass several species that are characterized in the adult stage by an umbilical bulla with at least one accessory infralaminal aperture. *Globigerina dissimilis* Cushman and Bermúdez, 1937 was selected as the type species. Bolli, Loeblich, and Tappan's holotype and paratype of *dissimilis*, now *Catapsydrax dissimilis* (Cushman and Bermúdez) (Plate 4.1, Figs. 1-3), have two infralaminal apertures, although our emended diagnosis permits 2-4 in *dissimilis*. Most species of *Catapsydrax* (except for *C. indianus*) are long-ranging and of limited biostratigraphic use, although the extinction of *C. dissimilis* in the lower Miocene is an important biozone boundary. Isotopic studies reveal a consistent, deep, sub-thermocline ecology that can provide a stable climatic index for subsurface water masses.

The highest occurrence (HO) of *Catapsydrax* is uncertain due to the uncertain taxonomic affinity of *Catapsydrax parvulus*, described by Bolli, Loeblich, and Tappan (1957) from the upper Miocene *G. mayeri* Zone of the Lengua Fm., Trinidad. Kennett and Srinivasan (1983:26, text fig. 7) record this species as ranging above the extinction of *C. unicavus* (Zone N6= uppermost M3, close to the HO of *C. dissimilis*) into the late Miocene (Zone N15 = Zone M12). New images of the holotype of *Catapsydrax parvulus* have been examined (not shown but available at the USNM collection archive) and bring new information, although they do not answer all the questions. The problem is that the holotype specimen is small and poorly preserved. Indications of a coarse wall hint at *Catapsydrax*, yet there does not appear to be a bulla. The somewhat lateral compression and flattened spiral side are reminiscent of *Globorotalia* but it could equally be some kind of benthic species. In contrast, the SEM images of *C. parvulus* of Kennett and Srinivasan (1983, pl. 7, figs. 3-9) have a prominent bulla and are very close to *Catapsydrax unicavus,* although they are perhaps smaller and more compact than typical. We conclude that the holotype of *Catapsydrax parvulus* Bolli, Loeblich, and Tappan is not a *Catapsydrax*, while *C. parvulus* of Kennett and Srinivasan is, and include the latter in our concept of *C. unicavus,* including middle Miocene forms (Pl. 4.3, Fig. 13). The total range, therefore, of *C. unicavus* (and thus *Catapsydrax*) is lower Eocene to late Miocene Zone M12 based on the observation of Kennett and Srinivasan (1983).

Diagnosis of *Catapsydrax* can be problematic because bullae occur in several other genera, particularly in the Oligocene. Where preservation permits, distinctions should be possible based on wall texture. Moreover, the bullae in *Subbotina, Dentoglobigerina* and *Globoturborotalita* are usually more inflated than in *Catapsydrax*. Removal or natural breakage of catapsydracid bullae reveals a small primary umbilical aperture, sometimes with a thin lip (Pl. 4.3, Figs. 8, 14). Based on wall texture views of new holotype SEM images, we exclude bulla-bearing *Catapsydrax martini scandretti* (Blow and Banner, 1962) from *Catapsydrax* and refer it instead to *Globoturborotalita* (see Chapter 8, this volume), where it is regarded as a junior synonym of *Globoturborotalita martini*. Borsetti's (1959) taxon *Catapsydrax venzoi*, described from the lower Oligocene of northern Italy, has a bulla similar to *C. dissimilis*, however it has a much higher spire than is typical. Comparison with the holotype of *Subbotina gortanii*, originally described as *Catapsydrax gortanii* Borsetti (1959), which was described from the same locality in Italy and recorded as having the same stratigraphic rage as *C. venzoi*, suggests these forms are conspecific and we place *C. venzoi* in synonymy with *S. gortanii* (Chapter 10, Pl. 10.4, this volume). The similar '*Catapsydrax*-like' appearance of the wall in these two Italian species we suggest is a function of extensive recrystallization, which is typical of the foraminifera described in Borsetti's study.

PHYLOGENETIC RELATIONSHIPS.— Uncertain. Olsson and others (2006b:76) suggested that *Catapsydrax* evolved form a subbotinid ancestor in the early Eocene. However, it seems more probable that *Catapsydrax* evolved from *Globorotaloides quadrocameratus* (Olsson and others, 2006a), which would preserve *Catapsydrax* as a sister clade of *Globorotaloides*.

STRATIGRAPHIC RANGE.— *Catapsydrax* appeared in the early Eocene (Olsson and others, 2006b) and disappeared in the late Miocene (top of Zone M12; see discussion above).

GEOGRAPHIC DISTRIBUTION.— Global. Especially common at high latitudes and in upwelling regions. Dissolution resistant.

Catapsydrax dissimilis (Cushman and Bermúdez, 1937)

Plate 4.1, Figures 1-16
(Pl. 4.1, Figs. 6-8 new SEMs of the holotype of *Globigerinita dissimilis ciperoensis* Blow and Banner)
(Pl. 4.1, Fig. 14 new SEM of the holotype of *Globigerinita riveroae* Bermúdez)

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 (re-illustration of holotype drawing), figs. 7a-8c [Oligocene-Miocene, Cipero Fm., Trinidad].—Blaicher, 1970:189, pl. 2, figs. 1a-c [lower Oligocene, Sub-Menilite Marls, Polish Carpathians].—Kennett and Srinivasan, 1983:22, pl. 2, figs. 1, 3-8 [lower Miocene '*Globoquadrina dehiscens* Zone', DSDP Site 206, Tasman Sea, South Pacific Ocean].—Bolli and Saunders, 1985:186, figs. 17-1a-c (re-illustration of holotype), figs. 17-2a-b ['Oligo-Miocene', Cipero Fm., Trinidad].—Huber, 1991:439, pl. 5, fig. 19 [Oligocene Zone N1-N3, ODP Hole 744A, Kerguelen Plateau, southern Indian Ocean].—Leckie and others, 1993, pl. 3, figs. 16, 17 [upper Oligocene Subzone P21b, ODP Hole 803D, Ontong Java Plateau, western equatorial Pacific Ocean].—Galeotti and others, 2002:378, pl. 3, fig. 13 [Oligocene Zone 'P18-P22', ODP Hole 1090B, Agulhas Ridge, sub-Antarctic Atlantic Ocean].—Olsson and others, 2006a:71, pl. 5.3, figs. 18-20 [SEM of holotype].—Wade and others, 2007:177, pl. 2, fig. q [upper Oligocene Zone O5, ODP Hole 1218B, equatorial Pacific Ocean].—Pearson and Wade, 2009:200, pl. 2, figs. 1, 3a-6b [upper Oligocene Zone O6 (=O7 of this work), Cipero Fm., Trinidad].

Globigerinita dissimilis dissimilis (Cushman and Bermúdez).—Blow and Banner, 1962:106, pl. 14, fig. D [upper Eocene *Globigerapsis semi-involuta* Zone, Lindi, Tanzania].

Globigerinita dissimilis (Cushman and Bermúdez).—Brönnimann and Resig, 1971:1303, pl. 25, figs. 7, 8 [upper Oligocene/lower Miocene Zone N4, DSDP Hole 64, Ontong Java Plateau, western equatorial Pacific Ocean].—Raju, 1971:29, pl. VI, figs. 2, 3 [upper Oligocene/lower Miocene *Globorotalia kugleri* / *Globigerinoides primordius* Zone (=O7/M1), KKL-2 borehole, Cauvery Basin, south east India].—Berggren, 1972: pl. 3, figs. 16, 17 [lower Oligocene, DSDP Site 116, Rockall Basin, North Atlantic Ocean].—Jenkins and Orr, 1972, pl. 16, figs. 10-12 [lower Miocene *Globigerinita dissimilis* Zone, DSDP Hole 77B, eastern equatorial Pacific Ocean].

Catapsydrax dissimilis dissimilis (Cushman and Bermúdez).—Fleisher, 1974:1016, pl. 4, fig. 5 [Oligocene Zones O3-O5, DSDP Site 223, Arabian Sea].—Quilty, 1976:641, pl. 7, figs. 12, 13 [upper Oligocene/lower Miocene Zone N4, DSDP Hole 320, southeastern Pacific Ocean].—Krasheninnikov and Pflaumann, 1977:592, pl. 7, figs. 2, 3a-d [upper Oligocene Zone P21, DSDP Hole 369A, African margin, eastern equatorial Atlantic Ocean].—Huber, 1991:439, pl. 5, fig. 19 [lower Miocene, ODP Hole 744A, Kerguelen Plateau, southern Indian Ocean].—Spezzaferri and Premoli Silva, 1991:236, pl. 1, fig. 1a-d [upper Oligocene Zone P22, DSDP Hole

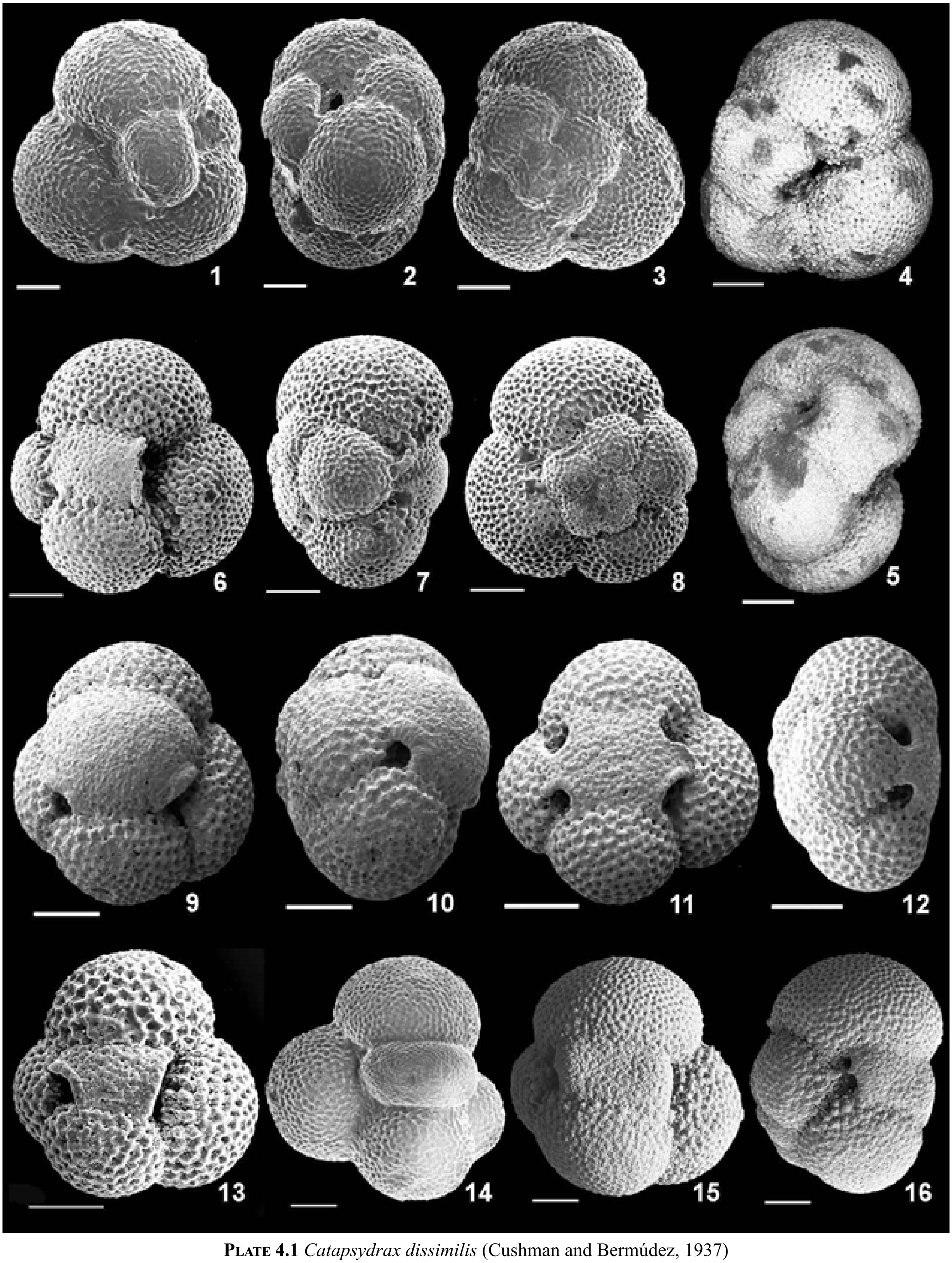

Plate 4.1 *Catapsydrax dissimilis* (Cushman and Bermúdez, 1937)

538A, Gulf of Mexico].—Spezzaferri, 1994:48, pl. 33, fig. 1a-c [upper Oligocene Zone P22, DSDP Hole 538A, Gulf of Mexico].

Catapsydrax cf. *stainforthi* Bolli, Loeblich, and Tappan.—Jenkins, 1960:356, pl. 3, figs. 6a-c [probably lower Miocene *Globigerina woodi* Zone ('Zone 3'), Lakes Entrance oil shaft, Victoria, south-eastern Australia]. [Not Bolli, Loeblich, and Tappan, 1957.]

Globigerinita riveroae Bermúdez, 1961:1266, pl. 7, fig. 7a-c [lower Oligocene, Oceanic Fm., Condrington College Marl beds, Barbados].

Globigerinita dissimilis ciperoensis Blow and Banner, 1962:107, pl. XIV, figs. a-c [lower Oligocene *Globigerina ampliapertura* Zone, Cipero Fm., Trinidad].

Catapsydrax dissimilis ciperoensis (Blow and Banner).—Quilty, 1976:641, pl. 7, fig. 11 [upper Oligocene/lower Miocene Zone N4, DSDP Site 320, southeastern Pacific Ocean].—Spezzaferri and Premoli Silva, 1991:237, pl. 1, fig. 4a-b [upper Oligocene Zone P22, DSDP Hole 538A, Gulf of Mexico].

Globorotaloides suteri Bolli.—Spezzaferri, 1994:45, pl. 34, fig. 5a-c [lower Oligocene Subzone P21a, ODP Hole 709B, equatorial Indian Ocean]. [Not Bolli, 1957.]

DESCRIPTION.

Type of wall: Coarsely cancellate, *sacculifer*-type, probably spinose; in adult stage wall becomes thickened.

Test morphology: Test moderately large, compact, low-moderate trochospiral of 2½-3 whorls, involute, lobate with 4 chambers in the final whorl, enlarging slowly. Later chambers are inflated, subglobular but slightly appressed and embracing. The early ontogenetic whorl, comprising 4½-5 chambers, is flattened or raised slightly above the adult whorl as seen in spiral view. Sutures are straight and depressed on the umbilical side and moderately depressed and slightly curved on spiral side. The primary aperture is a low umbilical arch covered by a single slightly inflated or flattened bulla less coarsely cancellate than the rest of test, with 2 or more (up to 4) rimmed infralaminal openings.

Size: Maximum diameter of holotype ~0.5 mm, thickness ~0.3 mm.

DISTINGUISHING FEATURES.— *Catapsydrax dissimilis* is distinguished from *C. unicavus* by having 2-4 infralaminal openings around the bulla compared to 1 in *C. unicavus*. The chambers of the final whorl are also usually of more similar size in *C. dissimilis* compared to *C. unicavus*, giving *C. dissimilis* a more lobed peripheral outline. It is distinguished from *Globorotaloides suteri* by the higher trochospire, the umbilically centered primary aperture (although concealed) and bulla with multiple infralaminal apertures. It further differs from *Globorotaloides stainforthi* by having one fewer chamber in the final whorl and from *Catapsydrax indianus* by the less globular form and simple non-lobed bulla.

DISCUSSION.— Whether Cushman and Bermúdez's (1937) holotype of *dissimilis,* which is described as from the "Eocene of Cuba", does in fact have two infralaminal apertures is debatable, even after additional SEM imaging, because adhering material clogs the umbilical region (Pl. 4.1, Figs. 1-3). Our new SEM images of the paratype of *dissimilis*, from the same locality as the holotype, however, clearly show two infralaminal apertures (Pl. 4.1, Figs. 4-5), thus we can give the holotype the benefit of the doubt and consider the second opening to be concealed, as is consistent with the traditional understanding of this species.

As described by Blow (1979), many authors' concept of *dissimilis* is based on Oligocene specimens that are closer to Blow and Banner's (1962) subspecies *Globigerinita dissimilis ciperoensis* (Pl. 4.1, Figs. 6-8) (compact, flattened bulla) from the lower Oligocene of Trinidad, than to the Eocene holotype of *C. dissimilis* (Pl. 4.1, Figs. 1-3). Both holotypes exhibit a bulla and two infralaminal apertures but the bulla and test are generally more inflated in *C. dissimilis* sensu stricto. Because the concept of *C. dissimilis* is well entrenched we take a conservative approach and regard *dissimilis ciperoensis* as a junior synonym of the former (see also discussion in Pearson and Wade, 2009). Morphological evolution of *Catapsydrax* through the late Oligocene involved expansion of the bulla across the ventral surface and an

Plate 4.1 *Catapsydrax dissimilis* (Cushman and Bermúdez, 1937)

1-3, holotype (Olsson and others, 2006a: pl. 5.3, figs. 18-20) Eocene, Havana Province, Cuba; **4**, **5**, paratype USNM23429B of *Globigerina dissimilis* Cushman and Bermúdez, 1937) Eocene, Havana Province, Cuba; **6-8**, holotype of *Globigerinita dissimilis ciperoensis* Blow and Banner, 1962, *G. ampliapertura* Zone, Cipero Fm. Trinidad; **9**, **10**, Zone M2, ODP Hole 904, New Jersey slope, North Atlantic Ocean; **11**, **12**, (umbilical and edge views) Zone M1, ODP Hole 904A/35/5, 101-106 cm, New Jersey slope, North Atlantic Ocean); **13**, Zone O5, ODP Hole 1218B/15H/3, 60-62 cm, equatorial Pacific Ocean (reproduced from Wade and others, 2007, pl. 2, fig. q); **14**, holotype of *Globigerinita riveroae* Bermúdez (1961), USNM 642534, lower Oligocene, Oceanic Fm., Condrington College Marl beds, Barbados; **15**, **16** (umbilical and edge views) Zone M1, ODP Hole 588C/9R/3, 137-139 cm, Tasman Sea. Scale bars: **1-16** = 100 µm.

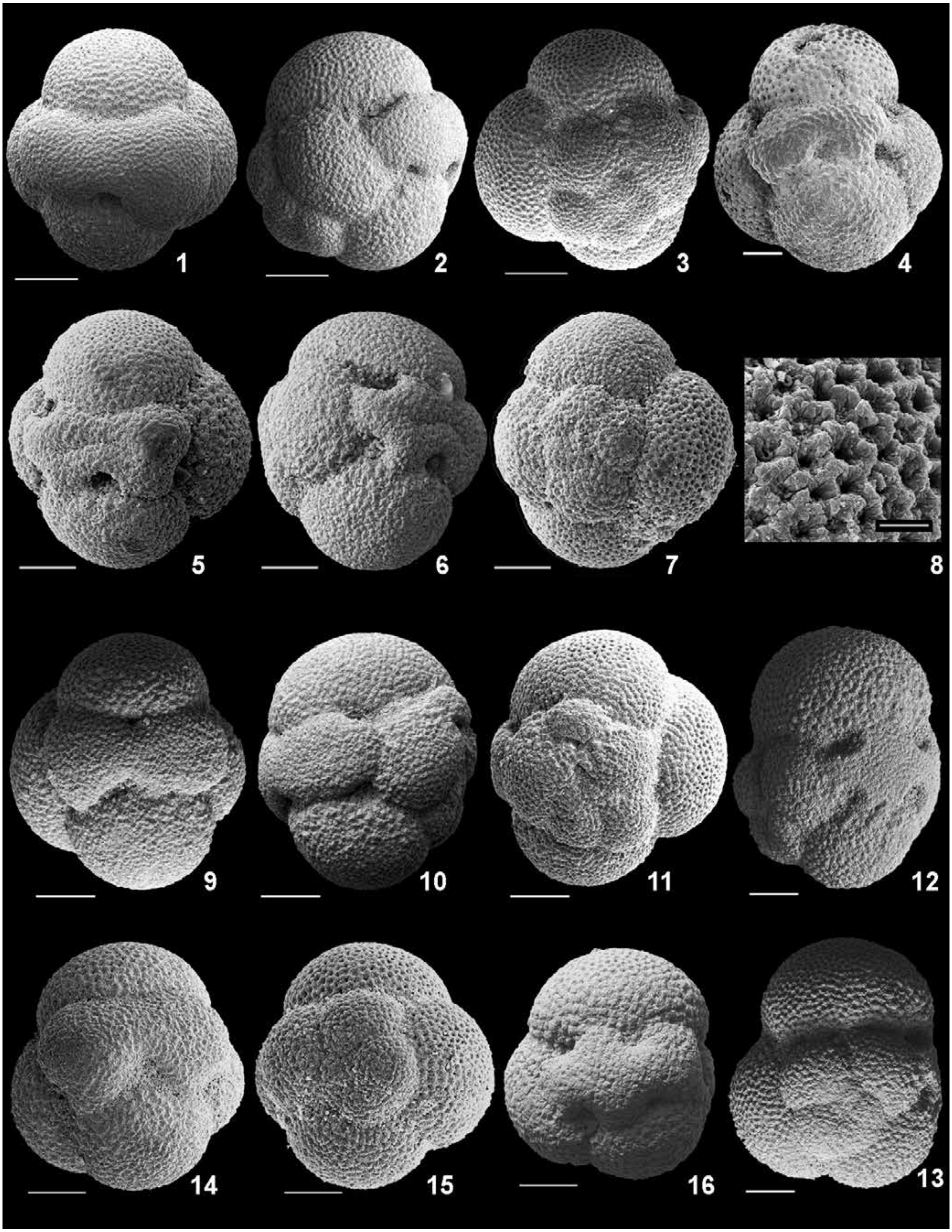

Plate 4.2 *Catapsydrax indianus* Spezzaferri and Pearson, 2009

increase in the number of infralaminal openings (up to 4) on a simple (non-lobed) bulla. Under our taxonomy *Catapsydrax dissimilis* is expanded to include these morphologies (Plate 4.1, Fig. 11).

Globigerinita riveroae Bermúdez (1961) is tentatively placed as a junior synonym of *C. dissimilis* (Plate. 4.1, Fig. 14), although it is possible that this species is closer to *Subbotina corpulenta,* owing to the large size and globular form.

PHYLOGENETIC RELATIONSHIPS.— *Catapsydrax dissimilis* evolved from *C. unicavus* in the upper middle Eocene Zone E13 (Blow and Banner, 1962). Blow (1979) suggested that the ancestor was *Globigerinita simulans* (Bermúdez) but the specimens he ascribed to that species are here included in the synonymy of *unicavus* (see below).

TYPE LEVEL.— The only information on the type level is that the holotype is "from the Eocene, 1 km. N. of Arroyo Arenas on road to Jaimanitas (water well), Havana Province, Cuba (Bermudez Sta. 31)". The level within the Eocene is uncertain, but elsewhere the species is only known from the uppermost middle Eocene and younger.

STRATIGRAPHIC RANGE.— According to Blow and Banner (1962:106-107) "*Globigerinita dissimilis dissimilis* ranges from at least the upper part of the *Truncorotaloides rohri* Zone, Navet Formation, middle Eocene, to the top of the *Globigerinita stainforthi* Zone (Aquitanian) in southern Trinidad. In Tanganyika [=Tanzania] it is known to occur also from the upper part of the *Truncorotaloides rohri* Zone, ranging up into the Aquitanian". The oldest specimen figured by Blow and Banner (1962) is from the "*Globigerapsis semi-involuta* Zone" (=E14/E15 of Wade and others, 2011). In summary, *C. dissimilis* extends from the upper middle Eocene (Zone E13) (Blow and Banner, 1962) to the lower Miocene Zone bearing the taxon's name, i.e. Zone M3, the *Globigerinatella* sp./*Catapsydrax dissimilis* Concurrent range Zone (Bolli, 1957; Spezzaferri, 1994; Wade and others, 2011), where it has been found to occur commonly (Bolli, 1957; Berggren and others, 1995). The highest occurrence of *Catapsydrax dissimilis* remains a marker in standard biostratigraphic zonal schemes (Bolli, 1957; Kennett and Srinivasan, 1983; Bolli and Saunders, 1985; Berggren and others, 1995; Wade and others, 2011) and is calibrated to 17.62 Ma on the time scale of Cande and Kent (1995) (Wade and others, 2011).

GEOGRAPHIC DISTRIBUTION.— Global, low to high latitudes, including New Zealand, the subantarctic and high North Atlantic Ocean (Berggren, 1972; Huber, 1991; Galeotti and others, 2002). It is more common in upwelling regions (Spezzaferri, 1995).

STABLE ISOTOPE PALEOBIOLOGY.— *Catapsydrax dissimilis*, like other species of *Catapsydrax*, registers among the most positive $\delta^{18}O$ values within an assemblage, and lowest $\delta^{13}C$ indicating it was a sub-thermocline calcifier and among the deepest dwelling of the Oligocene planktonic foraminifera (Poore and Matthews, 1984; van Eijden and Ganssen, 1995; Wade and others, 2007; Pearson and Wade, 2009; Spezzaferri and Pearson, 2009; Moore and others, 2014).

REPOSITORY.— Holotype (USNM 23430) deposited at the Smithsonian Museum of Natural History, Washington, D.C.

Catapsydrax indianus Spezzaferri and Pearson, 2009

Plate 4.2, Figures 1-16

Catapsydrax dissimilis ciperoensis (Blow and Banner) 1962.—Fleisher, 1974:1015, pl. 4, fig. 4, [upper Oligocene Zone P22, DSDP Site 223, Arabian Sea, northern Indian Ocean]. [Not Banner and Blow, 1962.]

Catapsydrax dissimilis (Cushman and Bermúdez) subsp. 1, Molina, 1979:289, pl. 25, figs. 3a–d. [upper Oligocene/lower Miocene *Globigerinoides primordius* Zone (*Globorotalia* (*Turborotalia*) *semivera* subzone), central Betic Cordilleras Béticas, Spain]. [Not Cushman and Bermúdez, 1937.]

Globorotaloides sp. 2, Premoli Silva and Spezzaferri, 1990: pl. 34, figs. 4a-b, [lower Miocene Zone N4, ODP Hole 709B, equatorial Indian Ocean].

Plate 4.2 *Catapsydrax indianus* Spezzaferri and Pearson, 2009

1-3, holotype (Spezzaferri and Pearson, 2009, pl. 1, fig. 1a-c); **5-15**, Zone M1, ODP Sample 709B/21X/6, 78-80 cm, Mascarene Plateau, Indian Ocean; **9-11** (reproduced from Spezzaferri and Pearson, 2009, pl. 1, fig. 2a-c), **4** (reproduced from Stewart and others, 2012, pl. 2, fig. 6a), Zone M1, ODP Sample 925A/22R/4, 30-32 cm, Ceara Rise, equatorial Atlantic Ocean; **16**, Zone M1, DSDP Sample 588C/9R/3, 130-132 cm, Tasman Sea. Scale bars: **1-7**, **9-16** = 100 µm, **8** = 20 µm.

Catapsydrax indianus Spezzaferri and Pearson, 2009:114, pl. 1, figs. 1a–3c [lower Miocene Zone M1, ODP Hole 709B, Mascarene Plateau, Indian Ocean].—Stewart and others, 2012:85, pl. 2, fig. 6a [lower Miocene Zone M1, ODP Hole 925A, Ceara Rise, equatorial Atlantic Ocean].

DESCRIPTION.

Type of wall: Strongly cancellate, with hexagonal pores located in deep pore pits, *sacculifer*-type to *ruber/sacculifer*-type; evidence for a gametogenic calcite crust. Although evidence for spines has not been observed in the studied specimens, Olsson and others (2006a) regarded the genus *Catapsydrax* as probably spinose. Generally, the bulla is less coarsely cancellate than the rest of the test.

Test morphology: Globular, globigeriniform coiling mode with a moderately high trochospire consisting of about 2½-3 whorls. Profile subcircular with a rounded to slightly lobed peripheral margin. Early ontogenetic whorl, comprising 4½-5 chambers, is typically raised slightly above the adult whorl; final adult whorl consists of 3½-4 subspherical chambers, gradually increasing in size. Sutures straight, depressed on the umbilical side; moderately depressed and slightly curved on the spiral side.

The umbilicus is moderately deep and covered by a bulla in adult specimens. The primary aperture is a small and semicircular low umbilical arch, visible only when the bulla is broken or missing. The bulla has multiple lobes and may consist of two parts (Plate 4.2, Fig. 6). Around the bulla are 4-5 often arched infralaminal apertures bordered by weak rims; four of these apertures open over the sutures with one usually opening over the central part of the antepenultimate chamber; size of accessory apertural openings over the antepenultimate is variable (see Plate 4.2).

Size: Maximum diameter of holotype ~0.38 mm, thickness ~0.38 mm. Tests may be medium to large but are commonly large.

DISTINGUISHING FEATURES.—This species differs from *Catapsydrax dissimilis* and *Catapsydrax unicavus* in the more globular form, the lobed and/or two part morphology of the bulla and the possession of 4-5 infralaminal accessory apertures. It differs from *Globorotaloides stainforthi*, which also has multiple infralaminal apertures, in the globular subspherical shape of the test.

DISCUSSION.— *Catapsydrax indianus* represents an extreme end member in the trend for bulla extension and increased numbers of accessory (infralaminal) openings seen in Oligocene to Miocene catapsydracids. This distinctive taxon is a useful guide fossil in the Indian Ocean for the Oligocene/Miocene boundary interval (Spezzaferri and Pearson, 2009). Note that the figured specimens from ODP Site 709 are recrystallized, as shown by replacement of the original cancellate wall structure with euhedral crystals (Pl. 4.2, Fig. 8).

PHYLOGENETIC RELATIONSHIPS.— *Catapsydrax indianus* evolved from *Catapsydrax dissimilis* (Spezzaferri and Pearson, 2009).

TYPE LEVEL.— Lower Miocene Zone M1 (=N4), ODP Sample 115/709B/21/6, 78-80 cm, Mascarene Plateau, western tropical Indian Ocean.

STRATIGRAPHIC RANGE.— It ranges from the lower third of upper Oligocene Zone P22 (= O6) to lower Miocene Zone N5 of Blow (1979) (Spezzaferri and Pearson, 2009), which is equivalent to Zone M2/M3 of Wade and others (2011).

GEOGRAPHIC DISTRIBUTION.— Global, low to mid-latitudes (Spezzaferri and Pearson, 2009).

STABLE ISOTOPE PALEOBIOLOGY.— *Catapsydrax indianus* registers among the most positive $\delta^{18}O$ values of assemblages and lowest $\delta^{13}C$ indicating it was a sub-thermocline calcifier (Spezzaferri and Pearson, 2009).

REPOSITORY.— Holotype deposited at the Natural History Museum of Basel, Switzerland (Ref. C9820).

Catapsydrax unicavus Bolli, Loeblich, and Tappan, 1957

Plate 4.3, Figures 1-16

Catapsydrax unicavus Bolli, Loeblich, and Tappan 1957:37, pl. 7: fig. 9a-c [upper Oligocene *Globigerina ciperoensis ciperoensis* Zone, Cipero Fm., Trinidad], pl. 37, fig. 7a, b [middle Eocene *Truncorotaloides rohri* Zone, Navet Fm., Trinidad].—Leckie and others, 1993:123, pl. 3, fig. 15 [lower Oligocene Zone P19, ODP Hole 803D, Ontong Java Plateau, western equatorial Pacific Ocean].—Cicha and others, 1998:89, pl. 40, figs. 1, 2 [lower Kiscellian = lower Oligocene, Central Paratethys, Austrian Molasse

Basin].—Olsson and others, 2006a:75, (partim) pl. 5.3, figs. 1-3 [SEM of holotype of *C. unicavus*], figs. 4, 14 and 16 [middle Eocene Zone E11, Guayabal Fm, Tampico, Mexico].—Pearson and Wade, 2009:200-202, pl. 2, fig. 2a-g [upper Oligocene 'Biozone O6' (now O7), Cipero Fm., Trinidad].—Pearson and Wade, 2015:8, figs. 4.1a-d [SEM of holotype of *Globigerinita unicava primitiva* Blow and Banner], figs. 4.2a-c [lower Oligocene Zone O1, TDP Site 17, Tanzania], figs. 4.3a-4 [lower Oligocene Zone O1, TDP Site 12, Tanzania], fig. 4.5a-c [upper Eocene Zone E15/16, TDP Site 12, Tanzania].

Globorotaloides suteri Bolli.—Bolli, 1957:116 (partim, not holotype), pl. 27, figs. 9-13b [mid- Oligocene *Globigerina ampliapertura* Zone, Cipero Fm., Trinidad].—Blow and Banner, 1962:112-113, pl. XIII, figs. N-P [lower Oligocene *Globigerina oligocaenica* Zone, Lindi area, Tanzania].—Blow, 1979:1358, pl. 247, figs. 9, 10 [lower Oligocene Zone P18, Lindi, Tanzania].—Spezzaferri, 1994:45, pl. 34, fig. 5a-c [lower Oligocene Subzone P21a, ODP Hole 709B, equatorial Indian Ocean]. [Not Bolli, 1957.]

Globigerinita unicava (Bolli, Loeblich, and Tappan).—Brönnimann and Resig, 1971:1307, pl. 25, fig. 5 [upper Oligocene Zone N2, DSDP Hole 64, Ontong Java Plateau, western equatorial Pacific Ocean].—Krasheninnikov and Pflaumann, 1977:592, pl. 7, figs. 4a,b, 5, 6a-c [upper Oligocene Zone P18/P19, DSDP Hole 369A, African margin, eastern equatorial Atlantic Ocean].

Catapsydrax unicava unicava Bolli, Loeblich, and Tappan.—Quilty, 1976, pl. 8, figs. 2, 3, [lower Oligocene Zone P19, DSDP Hole 321, Nazca Plate, southeastern Pacific Ocean].

Globigerinita unicava unicava (Bolli, Loeblich, and Tappan).—Hooyberghs and others, 1992:9, pl. 6, figs. 10-13 [lower Oligocene Zone P19, Boom Clay, Belgium].

Globigerina simulans Bermúdez, 1961:1198, pl. 6, fig. 1a; pl. 15, fig. 3a-b; pl. 6, fig. 16 [upper Eocene, Jacabo Fm., Cuba].

Globigerinita simulans (Bermúdez).—Blow, 1979:1343-1345, pl. 186, figs. 6, 7 [middle Eocene Zone P12, DSDP Site 19, central South Atlantic Ocean].

Globigerinita unicava primitiva Blow and Banner, 1962:114-115, pl. XIV, figs. J-L [upper Eocene *Globigerapsis semi-involuta* Zone, Lindi area, Tanzania].— Brönnimann and Resig, 1971:1307, pl. 25, figs. 7, 8 [upper Oligocene Zone N4, DSDP Hole 64, Ontong Java Plateau, western equatorial Pacific Ocean].—Krasheninnikov and Basov, 1983:839, pl. 6, figs. 9, 10 [lower Oligocene, DSDP Hole 513A, Falkland Plateau, South Atlantic Ocean].—Hooyberghs and others, 1992:9, pl. 6, figs. 6-9 [lower Oligocene Zone P19=O2, Boom Clay, Belgium].

Catapsydrax unicava primitiva (Blow and Banner).—Quilty, 1976:641, pl. 8, fig. 1 ["specimen since lost" exact sample not given but listed range: upper Eocene to lower Miocene Zone N4, DSDP Hole 320B/321, Nazca Plate, southeastern Pacific Ocean].

Globigerinita pera (Todd).—Brönnimann and Resig, 1971:1306, pl. 25, figs. 1-3, [upper Oligocene Zone N3, DSDP Hole 64, Ontong Java Plateau, western equatorial Pacific Ocean].—Krasheninnikov and Basov, 1983:839, pl. 6, figs. 3, 4 [upper Eocene, DSDP Hole 511, Falkland Plateau, South Atlantic Ocean].—Hooyberghs and others, 1992:9, pl. 6, figs. 3-5 [lower Oligocene Zone P20, Boom Clay, Belgium]. [Not Todd, 1957.]

Catapsydrax pera (Todd).—Quilty, 1976:641, pl. 7, figs. 20, 21 [lower Oligocene Zone P18, DSDP Hole 321, Nazca Plate, southeastern Pacific Ocean].—Cicha and others, 1998:88, pl. 40, figs. 3-5 [sporadic range up to Kiscellian, lower Kiscellian = lower Oligocene, Pouzdrany unit, Moravia, Czech Republic, Central Paratethys]. [Not Todd, 1957.]

Catapsydrax perus (Todd).—Fleisher, 1974:1016, pl. 4, fig. 7 [Oligocene Zone P18-P19, DSDP Hole 219, Arabian Sea, northern Indian Ocean]. [Not Todd, 1957.]

Globigerinita martini scandretti Blow and Banner.—Hooyberghs and De Meuter, 1972:32, pl. 11 figs. 2a-c [upper Oligocene, Edegem Sands, Antwerpen-Zuidstation section, Belgium].—Hooyberghs and others, 1992:9, pl. 5, figs. 19, 20, pl. 6, figs. 1, 2, [lower Oligocene Zone P20, Boom Clay, Belgium]. [Not Blow and Banner, 1962.]

Catapsydrax boweni (Brönnimann and Resig).—Quilty, 1976:641, pl. 7, figs. 9, 10 [upper Oligocene/lower Miocene Zone N8, DSDP Site 319, Nazca Plate, southeastern Pacific Ocean]. [Not Brönnimann and Resig.]

Catapsydrax martini martini (Blow and Banner).—Quilty, 1976:641, pl. 7, figs. 16, 17 [lower Oligocene Zone P18, DSDP Site 321, Nazca Plate, southeastern Pacific Ocean]. [Not Blow and Banner, 1962.]

Globigerinita martini martini (Blow and Banner).—Hooyberghs and others, 1992:9, pl. 5, figs. 15-18 [lower Oligocene Zone P20, Boom Clay, Belgium]. [Not Blow and Banner, 1962.]

Globigerinita martini Blow and Banner.—Krasheninnikov and Basov, 1983:839, pl. 6, figs. 5-8 [lower Oligocene, DSDP Hole 513A, Falkland Plateau, South Atlantic Ocean]. [Not Blow and Banner, 1962.]

Catapsydrax parvulus Bolli, Loeblich, and Tappan.—Quilty, 1976:679, pl. 7, figs. 18, 19 [lower Miocene Zone N8 = M5, DSDP Hole 319, Nazca Plate, southeastern Pacific Ocean.—Kennett and Srinivasan, 1983:26, pl. 2, fig. 2, pl. 3, figs. 7-9 [lower Miocene *Praeorbulina glomerosa* Zone, DSDP Hole 208, Lord Howe Rise, northern Tasman Sea]. [Not Bolli, Loeblich, and Tappan, 1957.]

Globorotaloides turgidus (Finlay).—Krasheninnikov and Basov, 1983:840, pl. 7, figs. 7-9 [middle Eocene, DSDP Site 512, Falkland Plateau, South Atlantic Ocean]. [Not Finlay, 1939.]

Catapsydrax cf. *riveroae* (Bermúdez).—Cicha and others,

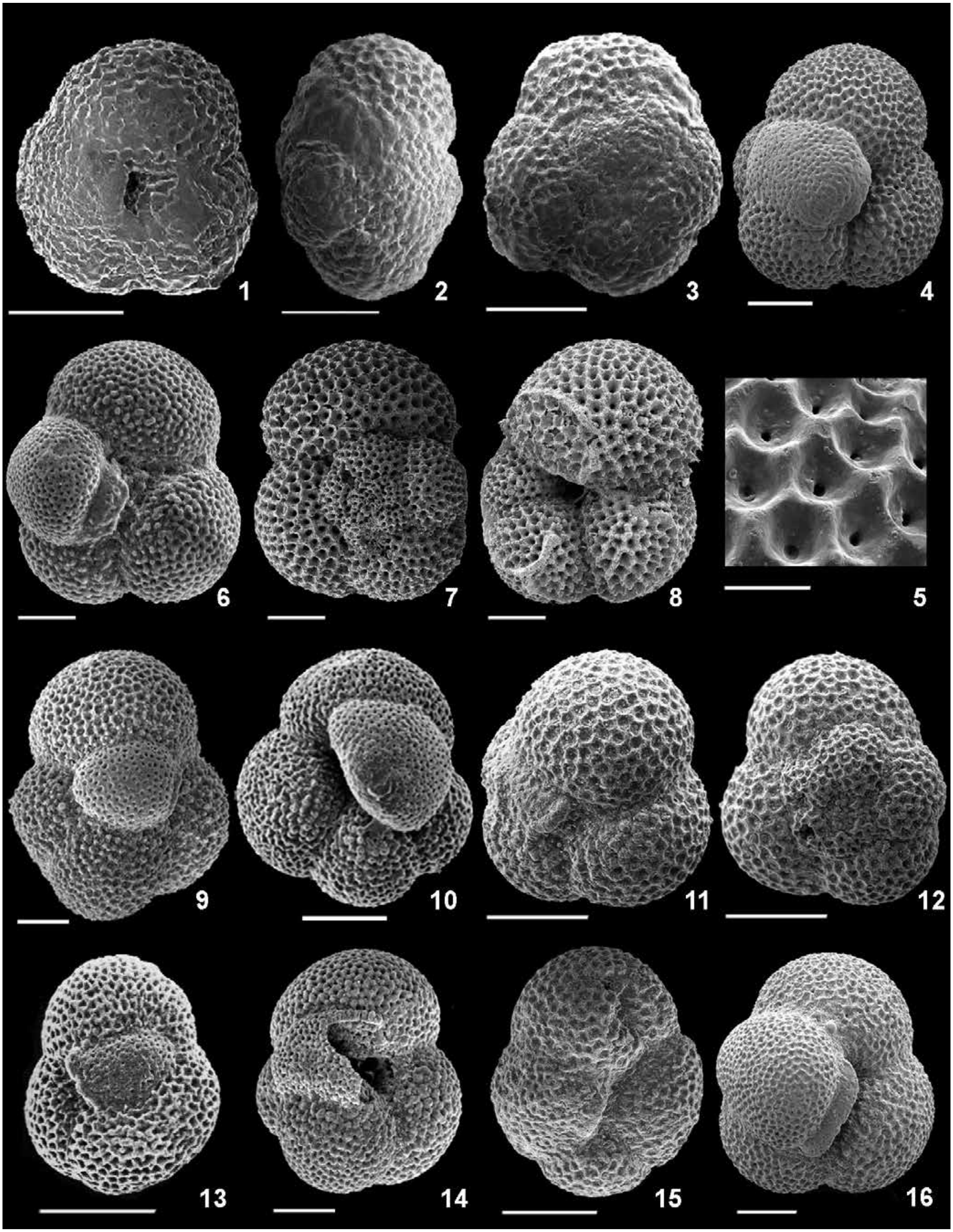

Plate 4.3 *Catapsydrax unicavus* Bolli, Loeblich, and Tappan, 1957

1998:88, pl. 40, figs. 6, 7 [lower Oligocene, Pouzdrany unit, Moravia, Czech Republic, Central Paratethys]. [Not Bermúdez, 1961.]

Not *Catapsydrax unicavus* Bolli, Loeblich, and Tappan.— Olsson and others, 2006a:75 (partim), pl. 5.3, figs. 9-11 [SEMs of holotype of *Globorotaloides suteri*].

DESCRIPTION.

Type of wall: Cancellate, *sacculifer*-type wall texture, generally with heavy gametogenetic calcification in adult specimens.

Test morphology: Moderately low trochospiral, compact to slightly lobulate test consisting of about 2½-3 whorls. Chambers globular, embracing, increasing rapidly in size with a terminal bulla extending over the umbilicus. The bulla may be flattened or inflated, and has a continuous, thickened imperforate rim and a single infralaminal aperture in a posterior position. The early ontogenetic whorl, comprising ~5 chambers, is somewhat flattened and typically raised slightly above the adult whorl. The adult whorl has 3-4 globular chambers increasing rapidly in size. Sutures, straight on the umbilical side, slightly curved on the spiral side and moderately depressed. The primary aperture small, semi-circular low umbilical arch, visible only when the bulla is broken or missing. The edge profile is an ovoid revealing the embracing bulla.

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

DISTINGUISHING FEATURES.— *Catapsydrax unicavus* is distinguished from *Catapsydrax dissimilis* by having a relatively compact test and a single infralaminal aperture which is always at the posterior (umbilical) end of the bulla. The chambers of the final whorl also typically increase more gradually in size. It differs from *Globorotaloides suteri* also by the more compact coiling and higher trochospire, the inner whorl of *G. suteri* being distinctly flattened. It differs from bullate forms of *Subbotina* such as *S. corpulenta,* by the typically flatter bulla, coarse catapsydracid wall, usually with a thick calcite crust, and more continuous peripheral outline. It differs from bullate *Globigerinita* by the coarsely cancellate macroperforate wall texture.

DISCUSSION.— *Catapsydrax unicavus* is the most common and long-ranging species in the genus, extending from the early Eocene to early Miocene. An important aspect of our taxonomy is the resurrection of *Globorotaloides suteri* Bolli. In the *Atlas of Eocene Planktonic Foraminifera*, *Globorotaloides suteri* was considered a junior synonym of *Catapsydrax unicavus* because of similarities between the holotypes (Olsson and others, 2006a). These early images of the holotype of *Globorotaloides suteri*, however, were of limited quality. Based on evidence from new SEM images of the *G. suteri* type, which better represent the morphology of the spiral side, we now separate the two (see discussion under the *Globorotaloides suteri* entry). It is now clear that *G. suteri* has a distinctly flattened spiral side (Pl. 4.10, Figs. 5-7 and 11-13), as originally described by Bolli and others (1957). Moreover, *C. unicavus* has an obligate bulla whereas bullate and non-bullate forms of *G. suteri* occur. The type specimen of Blow and Banner's (1962) subspecies *Globigerinita unicava primitiva* from the upper Eocene of Tanzania was illustrated and discussed by Pearson and Wade (2015) where it was included in synonymy with *Catapsydrax unicavus* Bolli, Loeblich, and Tappan, although we recognize there may be grounds for separation of the taxa based on the greater inflation of both chambers and bulla in *primitiva* (see Pearson and Wade, 2015, for additional discussion). *Catapsydrax unicavus* is common in the type region of the Oligocene Chattian and Rupelian stages in Boreal northwest Europe (Hooyberghs and De Meuter, 1972; Hooyberghs and others, 1992). The various forms from the North Sea 'Boom Clay' and 'Edgdem Sands', referred by Hooyberghs and De Meuter (1972) and Hooyberghs and others (1992) to a variety of species and subspecies of *Globigerinita* (including *pera, scandretti,*

Plate 4.3 *Catapsydrax unicavus* Bolli, Loeblich, and Tappan, 1957

1-3 (holotype, USNM 4216 SEMs; Olsson and others, 2006a, pl. 5.3, figs. 1-3), *Globigerina ciperoensis ciperoensis* Zone, Cipero Fm., Trinidad; **4-5**, Zone O1, ODP Sample 647A/30R/3, 67-69, southern Labrador Sea; **6**, (paratype of *Globigerina simulans* Bermúdez, 1961) middle Eocene, Guayabal Fm., Veracruz, Mexico; **7**, **8**, Zone O1, IODP Sample U1334B/26X/4, 128-130 cm, equatorial Pacific Ocean; **9**, lower Oligocene Zone O2, Istra More-3 well, Sample 1189.5-1195.5, Adriatic Sea; **10** (holotype of *Globigerinita unicava primitiva* Blow and Banner) BMNH P44557, '*Globigerapsis semi-involuta'* Zone, Lindi area, Tanzania (Pearson and Wade, 2015, fig. 4.1a); **11-12**, upper Oligocene Zone O5, Cipero Fm., Trinidad; **13** ('*Catapsydrax parvulus*', reproduced from Kennett and Srinivasan, 1983, pl. 3, fig. 7), *Praeorbulina glomerosa* Zone, DSDP Sample/208/21/5, 41 cm, Tasman Sea; **14**, lower Oligocene Zone O2, Istra More-3 well, Sample 1189.5-1195.5, Adriatic Sea; **15**, Zone O1, NKK1 borehole Sample 33b, 45-105, Nanggulan Fm., Java; **16**, Zone O4, NKK1 borehole Sample 12, 30-40, Nanggulan Fm., Java. Scale bars: **1-4**, **6-16** = 100 µm, **5** = 20 µm.

primitiva and *unicavus*), we now regard as *C. unicavus*.

In the *Atlas of Eocene Planktonic Foraminifera* Olsson and others (2006a) regarded *Globigerina simulans* Bermúdez (1961), which has a flat bulla covering the umbilical region, as a junior synonym of *C. dissimilis.* New SEM images of the holotype of *simulans* (not shown but available at the USNM collection archive), show that it has a single posterior infralaminal aperture, which is a definitive characteristic of *C. unicavus*.

As discussed, by including *Catapsydrax parvulus* Bolli, Loeblich, and Tappan of Kennett and Srinivasan (1983) in our concept of *C. unicavus*, the range of this species (and thus the genus *Catapsydrax),* extends into the upper Miocene (Zone M12).

PHYLOGENETIC RELATIONSHIPS.— The origin of *Catapsydrax unicavus* is uncertain. It probably evolved from *Globorotaloides quadrocameratus* in the early Eocene, which would preserve *Catapsydrax* as a sister clade of *Globorotaloides* (Olsson and others, 2006a). Another possibility is that it was derived from a subbotinid such as *Subbotina cancellata* (Olsson and Others, 2006b).

TYPE LEVEL— Upper Oligocene *Globigerina ciperoensis* Zone (=Zone O6), Cipero Fm., Trinidad.

STRATIGRAPHIC RANGE.— Lower Eocene Zone E2 (Olsson and others, 2006a) to the upper Miocene Zone M12 (= N15) (Kennett and Srinivasan, 1983). See discussions above.

GEOGRAPHIC DISTRIBUTION.— Global, including high latitudes.

STABLE ISOTOPE PALEOBIOLOGY.— *Catapsydrax unicavus*, like other species of *Catapsydrax*, registers among the highest $\delta^{18}O$ values of assemblages and lowest $\delta^{13}C$ indicating it was a thermocline to sub-thermocline calcifier (Poore and Matthews, 1984; Arthur and others, 1989; van Eijden and Ganssen, 1995; Sexton and others, 2006; Wade and others, 2007; Pearson and Wade, 2009; Spezzaferri and Pearson 2009; Moore and others, 2014).

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

Genus *Globorotaloides* Bolli, 1957

TYPE SPECIES.— *Globorotaloides variabilis* Bolli, 1957.

DESCRIPTION.

Type of wall: Normal perforate, cancellate, *sacculifer*-type wall texture. Possibly spinose in Eocene and Oligocene morphospecies, becoming nonspinose in the two extant species.

Test morphology: Low trochospiral, globular, lobulate, with 4-6 chambers in the final whorl; in spiral view the inner whorl of chambers 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; in edge view chambers globular, near spherical. The aperture is extraumbilical, bordered by thin continuous lip. A flattened bulla occurs in some species and within some populations of typically non-bullate forms; where present bullae may be umbilical, becoming extraumbilical to marginal in some upper Oligocene forms; there maybe one or more infralaminal aperture(s) that are bordered by a continuous narrow thickened lip or rim. There is a tendency to develop an imperforate peripheral band in some Eocene and early Oligocene forms.

DISTINGUISHING FEATURES.— Genus *Globorotaloides* is distinguished from *Parasubbotina* and *Catapsydrax* by the *Globorotalia*-like flattened inner coil, the outer coil of globigeriniform chambers and the strongly cancellate wall texture with distinctly funnel shaped pores. The genus exhibits more evolute coiling, a flattened spiral side and typically has more chambers in the final whorl than *Catapsydrax.* Forms occur with and without bulla.

DISCUSSION.— *Globorotaloides* is a long-ranging genus that extends from the early Paleogene to the Recent. First described from the upper Miocene of Trinidad (Bolli, 1957), *Globorotaloides* is distinctive but easily overlooked because individuals are usually small, thus concentrated in smaller sieve fractions (<150 μm) and often rare, especially in the low to mid-latitudes (excluding upwelling zones). According to Bolli (1957), *Globorotaloides* combines characters of several genera having an initial "*Globorotalia* stage", where the aperture is interiomarginal, umbilical-extraumbilical, a subsequent "*Globigerina* stage", where the aperture becomes umbilical and a "terminal stage" involving growth of a bulla that covers the umbilical region. According to Bolli, *Catapsydrax* lacks the globorotaliid stage. Our taxonomy builds on this concept but also considers the flattened morphology of the spiral side.

Olsson and others (2006a) suggested that *Globorotaloides quadrocameratus* evolved from *Parasubbotina* in lower Eocene Zone E2. We, however, observe *Globorotaloides*-like morphologies in the early Paleocene, including specimens that have been illustrated as *Subbotina cancellata* and '*Globigerina fringa* Subbotina' (see below), suggesting an earlier ancestry. Morphologies closely comparable to modern *Globorotaloides hexagonus* Natland, which is frequently found (at low abundance levels) in plankton nets, make their first appearance in the upper Oligocene.

The tendency for a bulla to develop in *Globorotaloides* appears to be dependent on geologic age. Early and early middle Eocene *G. quadrocameratus* and *G. eovariabilis* are typically non-bullate. Late Eocene, Oligocene and Miocene populations contain morphotypes with and without bulla. In contrast, Quaternary and living examples of *Globorotaloides hexagonus* (Natland) and *Globorotaloides trema* Lipps always lack a bulla. Reflecting on these observations, we have consolidated the set of described species, including one previously placed in *Catapsydrax* (i.e. *stainforthi*) to produce a framework through which the lineage to *G. hexagonus* can be traced. An important distinction, as originally set out by Bolli (1957), is that in *Catapsydrax* the aperture is umbilical whereas in *Globorotaloides* it is typically umbilical-extraumbilical, becoming equatorial in *Globorotaloides atlanticus* n. sp. and *Protentelloides.*

Globorotaloides maintained a low diversity through the early Oligocene but the group diversified in the mid- to late Oligocene (Figure 4.1). Development of the distinctive bullate morphospecies *G. stainforthi* was used as a zonal marker by Bolli (1957) for the early Miocene biozone bearing the name. Owing to the low abundance and patchy distribution of the nominate species the zone has not been incorporated into more recent 'N' or 'M' zonation schemes. Major modifications to the bulla in one branch of the lineage resulted in the evolution of the clavate planispiral genus *Protentelloides*. So far records of this genus are limited to the equatorial Atlantic Ocean.

An unresolved question underlying the taxonomy and phylogeny is whether *Globorotaloides* is spinose. Small circular holes occurring at the junction of cancellate ridges in some Eocene *Globorotaloides quadrocameratus* and *Parasubbotina varianta* have been interpreted as spine holes and therefore evidence that these taxa were spinose (Hemleben and Olsson, 2006, pl. 4.4, figs. 9, 12; Olsson and others, 2006a, pl. 5.5, fig. 8; pl. 5.13, figs. 15, 16). In core-top sediments (Holocene-Pleistocene) *G. hexagonus* occasionally also show similar 'apparent spine holes' supporting this idea. Living *G. hexagonus* recovered from plankton nets, however, clearly lack spines (Parker, 1962; Hemleben and others, 1989; Kucera, unpublished). Due to the close morphological similarities of wall and coiling in Paleogene and living *Globorotaloides* it seems unlikely that the genus is polyphyletic. Therefore, it is possible that spines were lost during the evolutionary transition from *G. eovariabilis* to *G. hexagonus* and/or that the holes are small pores or dissolution pits. For this reason we continue to separate *G. eovariabilis* and *G. hexagonus*, although we acknowledge the close morphologic similarity, and we note the continuous intergradation between the two in the mid- to late Oligocene.

PHYLOGENETIC RELATIONSHIPS.— The genus was probably derived from a heavily cancellate subbotinid in the early Paleocene. *Globorotaloides* likely gave rise to *Catapsydrax* in the early Eocene.

STRATIGRAPHIC RANGE.— Early Paleocene? to Recent.

GEOGRAPHIC DISTRIBUTION.— Global in middle to low latitudes during the Eocene and Oligocene. Today, *Globorotaloides* (*G. hexagonus*) is described as an "Indo-Pacific species", having reportedly become extinct in the Atlantic approximately 60,000 years ago B.P. (Pflaumann, 1986; Kucera and others, 2005).

Globorotaloides atlanticus Spezzaferri and Coxall, new species

Plate 4.4, Figures 1-15

Globorotaloides aff. *G. hexagonus* (Natland).—Spezzaferri, 1994:47 pl. 36, figs. 4a-c [upper Oligocene Zone P22, ODP Hole 667A, eastern equatorial Atlantic Ocean]. [Not Natland, 1938.]

Globorotaloides sp.—Quilty, 1976:649, pl. 17, figs. 5, 6 [Zone N2, DSDP Hole 320B, Nazca Plate, southeastern Pacific Ocean].

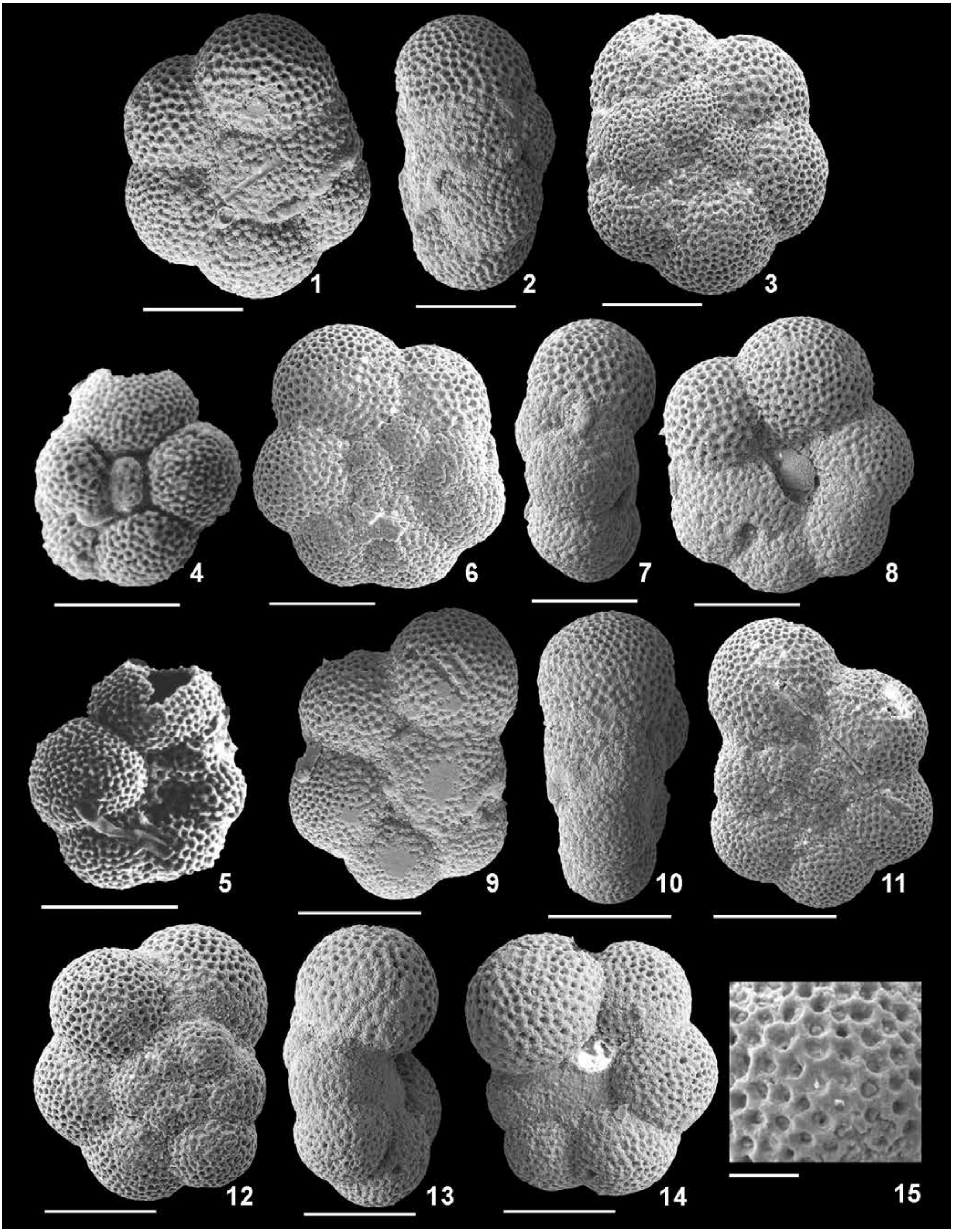

Plate 4.4 *Globorotaloides atlanticus* Spezzaferri and Coxall, new species

DESCRIPTION.

Type of wall: Spinose (?). Normal perforate, coarsely cancellate, *sacculifer*-type wall texture, with a distinctly honeycomb appearance. Pore density: ~40 pores/50 μm^2.

Test morphology: Test outline lobate, axial periphery rounded; 2-2½ whorls of inflated chambers arranged in a flattened globorotaliiform-trochospire; 11-14 chambers in adult tests, 5-7, more frequently 6 slightly compressed chambers in the final whorl, increasing moderately in size. Sutures depressed, radial on both sides, straight, slightly curved on umbilical side. Umbilicus moderately wide, covered by a bulla extending around equatorial margin and having a thickened lip or rim; 2-3 infralaminal apertures around the bulla spanning umbilical sutures, or at the edge of the bulla on the equatorial margin. Where the bulla has broken the primary aperture can be seen as an umbilical-extraumbilical arch at the base of the last chamber, surrounded by a lip.

Size: Holotype maximum diameter 0.29 mm, breadth 0.24 mm, thickness 0.15 mm.

ETYMOLOGY.— Named *atlanticus* because of its discovery and more common occurrence in the equatorial Atlantic Ocean.

DISTINGUISHING FEATURES.— *Globorotaloides atlanticus* differs from *Globorotaloides stainforthi,* from which it evolved, in having a distinctive umbilical-to-equatorial bulla that extends around the peripheral margin, an equatorially directed primary aperture and more numerous chambers in the final whorl. The bulla in *Globorotaloides stainforthi* is more strictly umbilical. *Globorotaloides atlanticus* is distinguished from *Protentelloides primitivus*, to which it gave rise, by having straight sutures on the spiral side, compared with recurved or sigmoidal sutures in *Protentelloides,* more inflated chambers and a flattened umbilical-to-equatorial bulla.

DISCUSSION.— *Globorotaloides atlanticus* forms part of the plexus of Oligocene bullate *Globorotaloides*. The most important diagnostic feature of this morphotype is the position of the bulla that extends from the umbilicus around to the equatorial margin. In this respect we view *G. atlanticus* as being transitional between *G. stainforthi*, where the bulla is umbilical, to *Protentelloides* spp., where the bulla forms on the equatorial margin. It is unclear whether or not *Globorotaloides atlanticus* and contemporaneous *G. hexagonus* and *Protentelloides* were spinose. The type material of *G. atlanticus* shows signs of dissolution and recrystallization, including contact dissolution around other biogenic sediment particles such as sponge spicules (linear impressions in Pl. 4.4, Figs. 1, 9 and 11). This obscures any evidence for or against spines.

PHYLOGENETIC RELATIONSHIPS.— *Globorotaloides atlanticus* evolved from *Globorotaloides stainforthi* by extension of the bulla towards the equatorial margin. It gave rise to *Protentelloides primitivus*, which is supported both by morphological similarities and similar pore densities between *G. hexagonus* and *P. primitivus*.

TYPE LEVEL.— Upper Oligocene Zone O7, ODP Hole 667A, Sierra Leone Rise, eastern equatorial Atlantic Ocean.

STRATIGRAPHIC RANGE.— The range of *G. atlanticus* has been determined at equatorial Atlantic Ocean DSDP Site 354 and ODP Site 667 as upper Oligocene Zone O7 to lower Miocene Zone M3. This is supported by more sporadic occurrences at South Atlantic Ocean DSDP Site 526 and rare appearances at equatorial Indian Ocean Site 709. These limits are based on the biostratigraphies of Spezzaferri (1994) and new observations made during this study. *Globorotaloides atlanticus* appears to be most common in O7, where all the examples shown on Plate 4.4 are from.

GEOGRAPHIC DISTRIBUTION.— Low latitude, equatorial. The best-described records are from the equatorial Atlantic Ocean (Spezzaferri, 1994), but it has also been observed in the equatorial Pacific (Quilty, 1976) and Indian Oceans (Spezzaferri, 1995).

Plate 4.4 *Globorotaloides atlanticus* Spezzaferri and Coxall, new species

1-3 (holotype 32509, Natural History Museum of Fribourg), upper Oligocene, Zone O7, ODP Hole 667A/31/4, 24-28 cm, equatorial Atlantic Ocean; **4, 5** (Quilty, 1976, pl. 17, fig. 5, 6), Zone O7, DSDP Hole 320B/2/CC, southeastern Pacific Ocean; **6-8** (paratype 32512), Zone O7, ODP Hole 667A/31/4, 24-28 cm, equatorial Atlantic Ocean; **9-11** (paratype 32511), Zone O7, ODP Hole 667A/31/4, 24-28 cm, equatorial Atlantic Ocean; **12-15** (paratype 32510), upper Oligocene Zone O7, ODP Hole 667A/31/4, 24-28 cm, equatorial Atlantic Ocean. Scale bars: **1-14** = 100 µm, **15** = 20 µm.

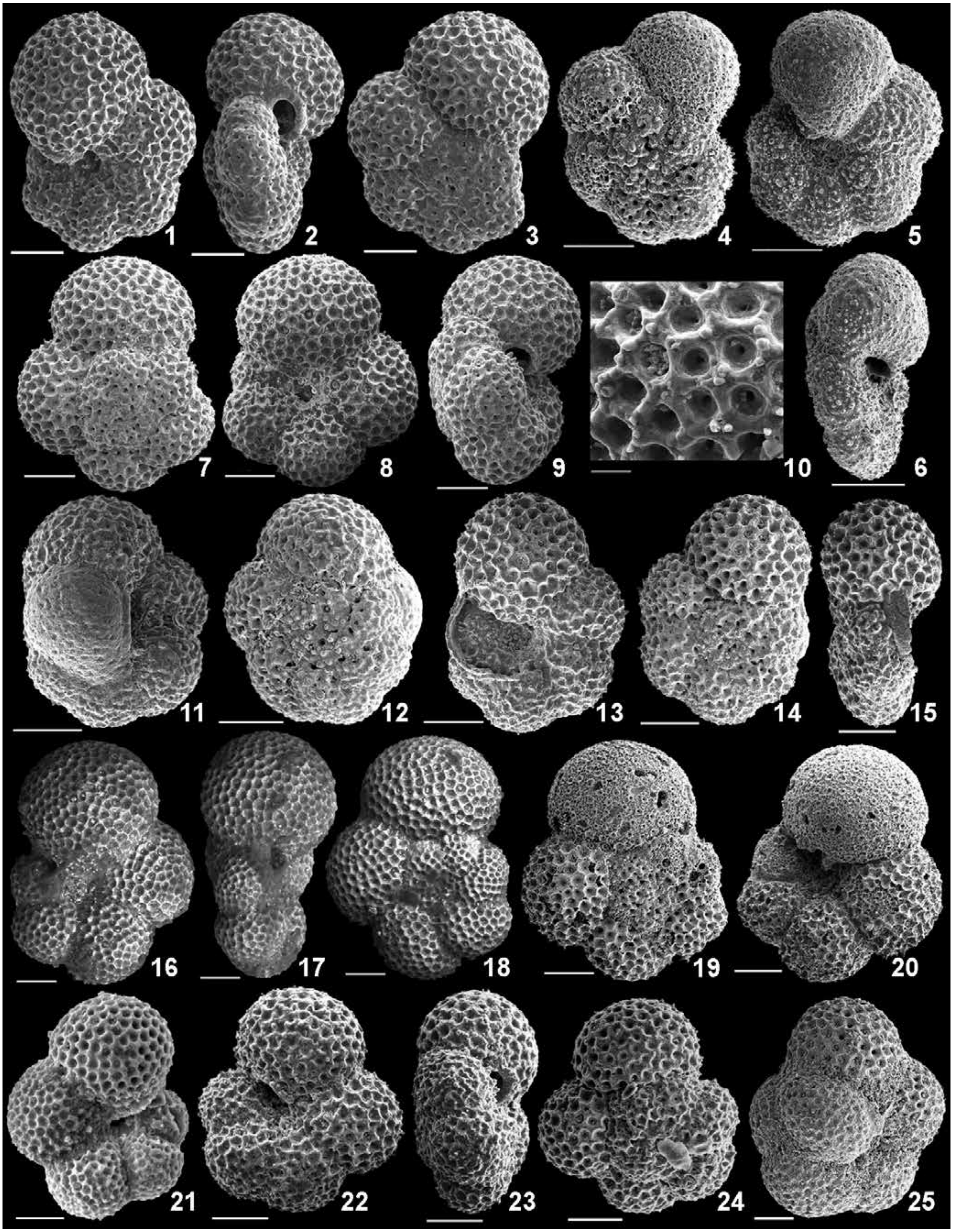

Plate 4.5 *Globorotaloides eovariabilis* Huber and Pearson, 2006

STABLE ISOTOPE PALEOBIOLOGY.— Relatively high $\delta^{18}O$ and low $\delta^{13}C$ compared to other species indicating a deep sub-thermocline habitat (Spezzaferri and Coxall, unpublished) and or life in cool, nutrient rich upwelled water, as has been suggested for *Globorotaloides* sp. from assemblage-based bioprovince analysis (Spezzaferri, 1995).

REPOSITORY.— Holotype (32509) and paratypes (32510, 32511 and 32512) deposited at the Natural History Museum of Fribourg, Switzerland.

Globorotaloides eovariabilis Huber and Pearson, 2006

Plate 4.5, Figures 1-25

Globorotaloides suteri Bolli.—Bolli, 1957:117, pl. 27, figs. 9a-c and 12a-b, *G. suteri* paratypes USNM P5655c and P5655d respectively [lower Oligocene, *Globigerina ampliapertura* Zone, Cipero Fm. Trinidad].—Jenkins and Orr, 1972:1106, pl. 36, figs. 10, 11 [lower Oligocene *Pseudohastigerina barbadoensis* Zone, DSDP Hole 77, eastern equatorial Pacific Ocean].—Poore and Brabb, 1977:260, pl. 1, figs. 11, 12 [lower Oligocene Zone P19-P20, San Lorenzo Fm., Rices Mudstone Member, Santa Cruz Mountains, California].—Krasheninnikov and Basov, 1983:840, pl. 8, figs. 1, 4 [upper Eocene, DSDP Hole 511, Falkland Plateau, South Atlantic Ocean].—Berggren, 1992:564, pl. 4, fig. 4 [upper Eocene *Globorotaloides suteri* Zone, ODP Hole 748B, Kerguelen Plateau, southern Indian Ocean]. [Not Bolli, 1957.]

Globorotaloides variabilis Bolli.—Kennett and Srinivasan, 1983:214, pl. 53, figs. 6-8 [upper Miocene Zone N16, DSDP Hole 289, Ontong Java Plateau, western equatorial Pacific Ocean]. [Not Bolli, 1957.]

Globorotalia munda Jenkins.—Krasheninnikov and Basov, 1983:841, pl. 10, fig. 11 [upper Eocene, DSDP Hole 511, Falkland Plateau, South Atlantic Ocean]. [Not Jenkins, 1965.]

Globorotaloides aff. *G. testarugosa* Jenkins.—Stott and Kennett, 1990:560, pl. 7, fig. 11 [middle Eocene Zone AE4/5, ODP Hole 689B, Maud Rise, sub-Antarctic South Atlantic Ocean].—Huber, 1991:440, pl. 7, figs. 19, 20 [lower Oligocene Zone AE9, ODP Hole 738B, Kerguelen Plateau, southern Indian Ocean]. [Not Jenkins, 1960.]

Globorotaloides sp. 1, Berggren, 1992:568, pl. 4, fig. 11 [upper Eocene *Globorotaloides suteri* Zone, ODP Hole 748B, Kerguelen Plateau, southern Indian Ocean].—Sexton and others, 2006:6, pl. 1, figs. 9, 10 [middle Eocene Zone E13, ODP Site 1052, Blake Nose, western North Atlantic Ocean].

Globorotaloides sp.—Li and others, 2003: pl. 1, fig. 17 [upper Eocene Zone P16, ODP Hole 1126D, Great Australian Bight].

Globorotaloides eovariabilis Huber and Pearson in Olsson and others, 2006a:79-83, pl. 5.4, figs. 1-3, 5-11 [middle Eocene Zone E10-E11, ODP Hole 647A, Labrador Sea], pl. 5.4, fig. 4 [middle Eocene Zone AE7, ODP Hole 690B, Maud Rise, southern Indian Ocean], pl. 5.4, figs. 12-17 [lower Eocene and lower Oligocene Zones AE2 and AO1, ODP Hole 738B, Kerguelen Plateau, southern Indian Ocean].—Pearson and Wade, 2009:206, pl. 5, fig. 7 [upper Oligocene Zone O6 (= O7), Cipero Fm., Trinidad].

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 pores. Possibly spinose (modified from Olsson and others, 2006a).

Test morphology: Test outline lobate, subcircular in axial view, axial periphery rounded to slightly compressed and pinched, 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, 4½-6½ in the final whorl increasing moderately in size; umbilicus shallow to moderately deep and narrow; umbilical sutures moderately depressed, curved, radial; spiral sutures initially indistinct, later weakly depressed, radial; aperture a low umbilical-extraumbilical arch extending one-third towards the peripheral margin, surrounded by a broad lip that extends into the umbilical area; tendency to develop an imperforate peripheral band in some Oligocene forms (modified from Olsson and others, 2006a).

Size: Holotype (USNM 523429) maximum di-

Plate 4.5 *Globorotaloides eovariabilis* Huber and Pearson, 2006

1-3 (holotype USNM 521865, Olsson and others, 2006a, pl. 5.4, figs. 1-3), Zone E10-E11, ODP Sample 647/50R/5, 101 cm, Labrador Sea; **4-6**, Zone AO2, ODP Sample 1137A/17R/CC, Kerguelen Plateau, southern Indian Ocean; **7-10**, Zone O1, ODP Sample 647A/28R/4, 74.5-76 cm, Labrador Sea; **11-15**, Zone O1, ODP Sample 647A/28R/1, 48.5-50 cm, Labrador Sea, (11-12 bullate specimen, 13-15, specimen with broken bulla); **16-18**, paratype of *Globorotaloides suteri* Bolli (USNM 5655b), *Globigerina ampliapertura* Zone, Cipero Fm., Trinidad; **19**, **20**, Zone AO2, ODP Sample 1137A/17R/CC, Kerguelen Plateau, southern Indian Ocean; **21**, Zone O5, Istra More-3 well, cuttings sample 968-974, Adriatic Sea, transitional to *G. hexagonus* (?); **22-24**, Zone O1, ODP Sample 647/28R/1, 96.5-98 cm, Labrador Sea; **25**, Zone O7, IODP Sample U1335B/39H/CC, equatorial Pacific Ocean. Scale bars: **1-3** = 40 µm, **4-9**, **11-25** = 50 µm, **10** = 10 µm.

ameter 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 mm, breadth 0.93 mm.

DISTINGUISHING FEATURES.— *Globorotaloides eovariabilis* differs from *Globorotaloides quadrocameratus* in having greater than 4 (typically 5 but up to 6½) final whorl chambers that are less inflated and increase more gradually in size; from *Globorotaloides variabilis* by its smaller size and more regular low trochospiral coiling and tendency for axial lateral compression and pinching of the periphery. It differs from *Globorotaloides testarugosus* in the more inflated chambers, lobate periphery, and curving of umbilical sutures and from *Globorotaloides hexagonus*, with which it intergrades, in the smaller size, slightly less inflated chambers and lower stratigraphic range (see discussion above). Where a central umbilical bulla occurs there is a single opening.

DISCUSSION.— *Globorotaloides eovariabilis* is a small but distinctive species that occurs frequently in the <150 μm size fraction (although the holotype is slightly larger). It is long-ranging and most abundant in high latitude Eocene to early Oligocene or equatorial assemblages. It is possible that it is a junior synonym of *Globorotaloides hexagonus,* which was described from the Recent of California (Natland, 1938), however, we separate the two because of the typically larger size of *G. hexagonus* and the possibility that the Paleogene species had a spinose wall, whereas modern *G. hexagonus* does not (see discussion above). Eocene *Globorotaloides eovariabilis* usually does not have a bulla, however, we have observed in Oligocene populations from different localities (e.g., ODP Site 647, North Atlantic Ocean, and Site 1137, southern Indian Ocean) times when bullate and non-bullate forms co-occur (Plate 4.5, Figs. 11, 12). Removal or natural breakage of the bulla reveals the typical *G. eovariabilis* morphology beneath (Plate 4.5, Figs. 13).

PHYLOGENETIC RELATIONSHIPS.— *Globorotaloides eovariabilis* evolved from *Globorotaloides quadrocameratus* (Olsson and others, 2006a).

TYPE LEVEL.— Middle Eocene Zone E10-E11.

STRATIGRAPHIC RANGE.— Lower Eocene (Olsson and others, 2006a) to upper Oligocene Zone O7 (Pearson and Wade, 2009), possibly extending into the lower Miocene (recorded as *Globorotaloides permicrus* at DSDP Sites 360, 26, 563 and 516, Spezzaferri, 1994), although difficult to determine because of the close similarities with *G. hexagonus*. The holotype and paratype are from the middle Eocene of ODP Hole 647A, southern Labrador Sea, which was assigned to calcareous nannofossil Zone NP16 by Firth (1989) and dated as 40.2 Ma on the revised Site 647 biomagnetochronology of Firth and others (2013).

GEOGRAPHIC DISTRIBUTION.— Global, including low and mid-latitudes. Can be common in southern and northern high latitudes. There may be an affinity with high productivity conditions.

STABLE ISOTOPE PALEOBIOLOGY.— *Globorotaloides eovariabilis* exhibits relatively positive $\delta^{18}O$ and negative $\delta^{13}C$ compared to other species suggesting that it occupied a sub-thermocline planktonic habitat similar to *Catapsydrax* (Coxall, unpublished).

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

Globorotaloides hexagonus (Natland, 1938)

Plate 4.6, Figures 1-16
(Pl. 4.6, Figs. 1-3 new SEMs of the holotype of *Globigerina hexagona* Natland)

Globigerina hexagona Natland, 1938:149, pl. 36, figs. 3a-c, holotype [seafloor sample collected off Long Beach, California, 33°27', 20'N; 118°19'00''W, 884 m water depth].

Globoquadrina hexagona (Natland).—Parker, 1962:244, pl. 8, figs. 5a-c [Recent, seafloor sediment, Downwind BG 114, 18°20' S., 79°20.5' W, low latitude south western Pacific Ocean].

Globorotaloides hexagona (Natland).—Lipps, 1964:128 (placed in *Globorotaloides* for first time; no illustration).—Poore, 1981:429, pl. 1, figs. 1-3 [middle Miocene Zone N11, DSDP Hole 470, off Baja California, east Pacific Ocean].—Chaisson and Leckie, 1993:163, pl. 9, fig. 4 [upper Miocene Zone N16/17a, ODP Hole 806B, Ontong Java Plateau, western equatorial Pacific Ocean].

Globorotaloides hexagonus (Natland).—Hemleben and others, 1989:27, pl. 2.6, figs. n-p [Recent].—Spezzaferri, 1994:46, pl. 36, fig. 3a-c [upper Oligocene Zone P22, ODP Hole 667A, equatorial Atlantic Ocean].

Globorotaloides aff. *hexagonus* (Natland).—Spezzaferri, 1994:47, pl. 36, fig. 1a-c [upper Oligocene Zone P22, ODP Hole 667A, equatorial Atlantic Ocean].

Globorotalia extans Jenkins, 1960 (partim,'microspheric' form, not holotype): 360, pl. 4, figs. 5a-c [paratype, lower Miocene "*Globoquadrina dehiscens dehiscens*" Zone, Lakes Entrance oil shaft, Victoria, southeast Australia]. [Not Jenkins, 1960.]

Globorotaloides permicrus (Blow and Banner).—Spezzaferri and Premoli Silva, 1991:250, pl. 10, figs. 1a-c [lower Oligocene Subzone P21a, DSDP Site 538, Gulf of Mexico].—Spezzaferri, 1994:250, pl. 35, figs. 2a-c [specimen reproduced from Spezzaferri and Premoli Silva, 1991]. [Not Blow and Banner, 1962.]

Clavatorella aff. *C. oveyi* Buckley.—Spezzaferri, 1994:50, pl. 36, fig. 2a-c [upper Oligocene Zone P22, ODP Hole 667A, equatorial Atlantic Ocean]. [Not Buckley, 1973.]

DESCRIPTION.

Type of wall: Nonspinose. Normal perforate, coarsely cancellate, *sacculifer*-type wall texture, with a distinctly honeycomb appearance.

Test morphology: Test outline lobate to strongly lobate, axial periphery rounded, biconvex, oval to egg-shaped in edge view; 3-3½ whorls of inflated chambers arranged in a flattened trochospire; 11-14 chambers in adult tests, 4½-6½ in the final whorl increasing gradually in size; umbilicus shallow to moderately deep and narrow; umbilical sutures depressed, radial and slightly curved; spiral initially indistinct, later weakly depressed, radial sutures; aperture a low umbilical-extraumbilical arch surrounded by a broad lip that extends into the umbilical area. Relict apertural lips often preserved as teeth within umbilical region.

Size: Holotype maximum diameter 0.39 mm, breadth 0.33 mm, thickness, 0.18 mm.

DISTINGUISHING FEATURES.— Differs from *Globorotaloides eovariabilis* by the larger size, slightly more inflated chambers and nonspinose wall. It differs from *G. variabilis*, from which it was probably descended, by the more rounded chambers, wider umbilicus and typically the lack of a bulla-like final chamber. Note that the flattened area in the umbilical region of the holotype of *G. hexagonus* (Pl. 4.6, fig. 1) we believe is an adhering coating or glue and not a small umbilical bulla as could be perceived.

DISCUSSION.— We take Blow's (1979:176) view that *Globorotaloides hexagonus* descended from *G. variabilis* in the mid- to late Oligocene (Fig. 4.1). We note, however, that this is only a tentative model because *G. variabilis* and *G. hexagonus* morphotypes are rare at that time and the number of specimens available for comparison is very limited. Moreover, there is a large degree of morphological similarity between *Globorotaloides hexagonus* and *G. eovariabilis* such that *G. eovariabilis* could be the true ancestor of *G. hexagonus* and *G. variabilis* a phylogenetic side branch. As discussed above, it is possible that *G. hexagonus* might be the senior synonym of *G. eovariabilis*, although, as illustrated on Plate 4.6, late Oligocene *G. hexagonus* morphotypes are considerably larger than Eocene to lower Oligocene *G. eovariabilis*. Living *G. hexagonus* has occasionally been observed with a bulla.

Among the living *Globorotaloides* there appear to be two species, *G. hexagonus* and a less well known morphotype that can be assigned to '*Globorotalia* (*Clavatorella*) *oveyi*' Buckley, 1973 (M. Kučera, personal communication). We follow Kennett and Srinivasan (1983) in considering the latter morphotype as belonging to *Globorotaloides*. *Globorotaloides oveyi* differs from *G. hexagonus* in having distinctly curved sutures, more numerous chambers in the final whorl and pronounced apertural lips (reminiscent of *Clavatorella bermudezi* Lipps, 1964). We find no evidence of *Globorotaloides oveyi* in the Oligocene. In both modern species of *Globorotaloides*, tooth-like corners of relict apertural lips project into the umbilicus. Based on the presence of these 'tooth-like projections', Parker (1962) placed *hexagonus* in genus *Globoquadrina*. As discussed by Lipps (1964), however, the similarities with *Globoquadrina* end there since *G. hexagonus* always possesses a flattened spiral and typically also has a more highly cancellate wall. Hemleben and others (1989) describe *G. hexagonus* as an 'Indo-Pacific' species, although this restriction is uncertain. Several studies have suggested that the taxon disappeared from the Atlantic Ocean in the Pleistocene, approximately 60,000 years ago B.P. (Pflaumann, 1986; Kučera and others, 2005), whereas other studies have found *G. hexagonus* in core-top samples from the Caribbean (Saunders and others, 1973), and equatorial Atlantic (Weaver and Raymo, 1989), suggesting it does occur in the Holocene. Apparently this species has narrow environmental preferences. Its occurrence is likely linked to temperature and/or nutrient content of sub-thermocline water masses, which it evidently prefers (see Spezzaferri and Premoli Silva, 1991; Ortiz and others, 1996), potentially even at an entire ocean-scale.

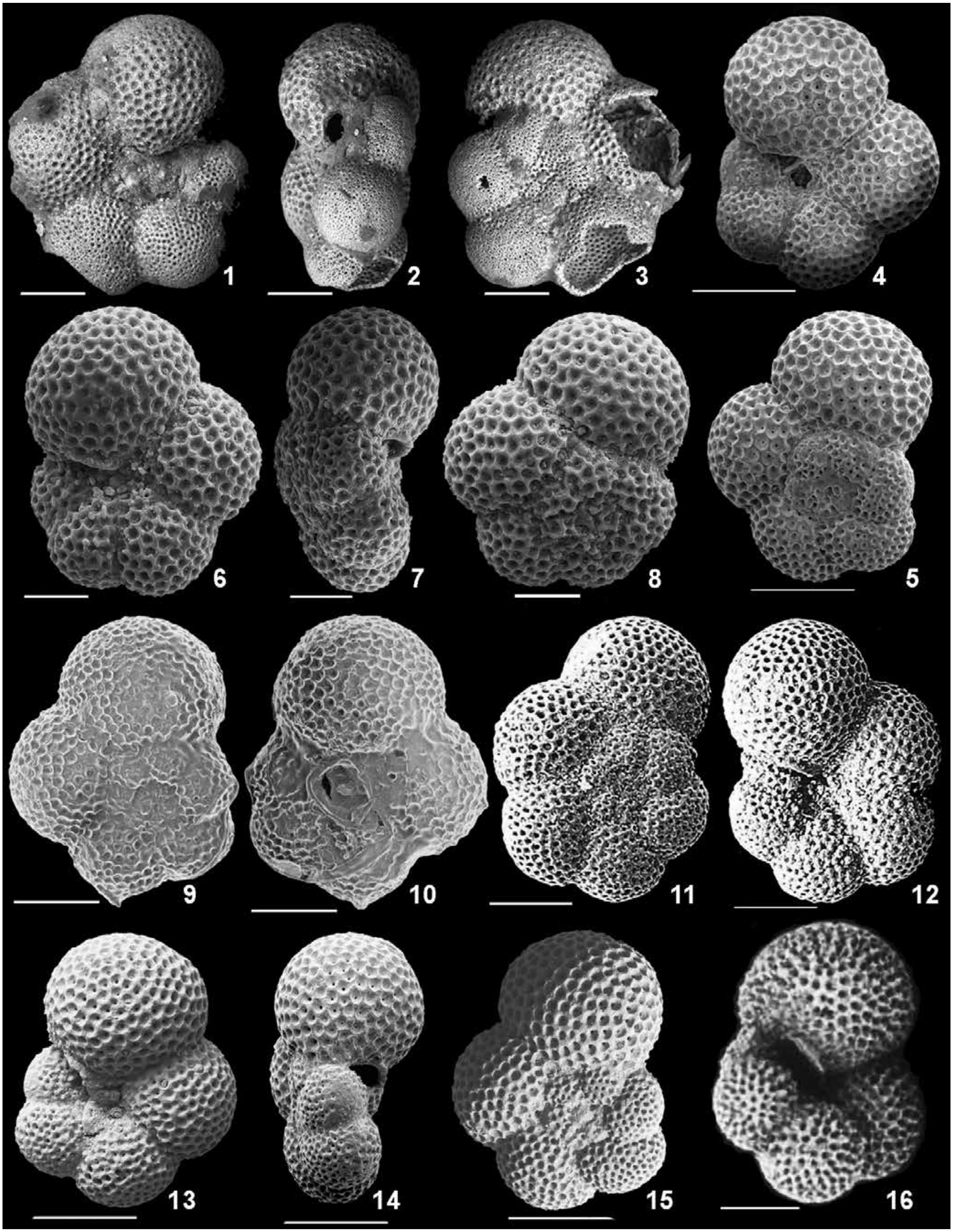

Plate 4.6 *Globorotaloides hexagonus* (Natland, 1938)

PHYLOGENETIC RELATIONSHIPS.—We suggest that *Globorotaloides hexagonus* evolved from *Globorotaloides variabilis* in the uppermost lower Oligocene (Zone O4), rather than *Clavatorella bermudezi* as previously considered (Kennett and Srinivasan, 1983), since its first appearance predates that of *C. bermudezi* by more than 10 million years.

TYPE LEVEL.— Recent. Seafloor sample (see below).

STRATIGRAPHIC RANGE.— Upper Oligocene Zone O4 (rare) (Quilty, 1976; Spezzaferri and Premoli Silva, 1991; Spezzaferri, 1994, this study: Pl. 4.6, Figs. 13-15) to Recent (Hemleben and others, 1989; Ortiz and others, 1996; Kučera and others, 2005). The holotype is from a seafloor sample ("dark green clay with abundant foraminifera") collected off Long Beach, California at a water depth of 884 m. The lowest occurrence of *G. hexagonus* is poorly constrained and is difficult to determine due to a general scarcity of the taxon at the beginning of its range as well as similarities with *G. eovariabilis*. Spezzaferri (1994) illustrated a specimen recorded as "*Globorotaloides* aff. *G. hexagonus"* from Zone P22 (O6/O7) of ODP Site 667 (Spezzaferri, 1994, pl. 36, figs. 1a-c) that we suggest is attributable to *G. hexagonus*. Table 7 of Spezzaferri's article shows *Globorotaloides* aff. *G. hexagonus* ranging from Subzone P21a (O4) to lower Miocene Zone N5 (M2) at this Atlantic Ocean Site. At DSDP Site 354, also in the low latitude Atlantic Ocean, this taxon is recorded as first appearing in Zone P22. Although some of Spezzaferri's *Globorotaloides* aff. *G. hexagonus* can now be placed in *G. atlanticus*, new observations confirm that Subzone P21a (Zone O3/O4) marks the lowest occurrence. Today, *G. hexagonus* is described as an "Indo-Pacific species", having reportedly become extinct in the Atlantic approximately 60,000 years ago B.P. (Pflaumann, 1986; Hemleben and others, 1989; Kučera and others, 2005).

GEOGRAPHIC DISTRIBUTION.— Today as in the past it occurs in subtropical and equatorial environments. It is typically rare. Higher abundance levels may be associated with high nutrient systems, including the Arabian Sea (Kucera, unpublished) and California Current (Ortiz and others, 1996). Based on distribution patterns *Globorotaloides hexagonus* has been identified as an indicator of Oligocene to Miocene upwelling (Spezzaferri, 1995).

STABLE ISOTOPE PALEOBIOLOGY.— Stable isotopes of *Globorotaloides hexagonus* from plankton tows and a Holocene core-top sample register high $\delta^{18}O$ and low $\delta^{13}C$ compared to other species, indicating a deep sub-thermocline habitat (Ortiz and others, 1996; Birch and others, 2013). This is consistent with observations from depth stratified plankton nets that show this species and *G. oveyi* consistently living below the thermocline and down to at least 800 m water depth (Ortiz and others, 1996; M. Kučera, oral communication). Strong negative $\delta^{13}C$ disequilibrium in this species may be controlled by physiological processes related to slow growth at low temperatures (Ortiz and others, 1996) or enhanced metabolic ^{12}C incorporation due to small test sizes (Birch and others, 2013).

REPOSITORY.— Holotype (USNM 22560) deposited at the Smithsonian Museum of Natural History, Washington, D.C. A set of paratype specimens was deposited at the Scripps Institution of Oceanography, La Jolla, California.

Globorotaloides quadrocameratus Olsson, Pearson, and Huber, 2006

Plate 4.7, Figures 1-16

?*Globigerina fringa* Subbotina, 1953:62, pl. 3, fig. 3 (holotype) [Danian, Pecten horizon, Azov-Black Sea flysch, Anapa, Caucasus].—Olsson and others, 1999:29, pl. 9, figs. 7-9 [re-illustration of holotype].

?*Globorotalia* (*Turborotalia*) *permicra* Blow and Banner, 1962:120, pl. XII, figs. N-P [lower Oligocene *Globigerina oligocaenica* Zone (O1/O2), Lindi area, Tanzania].

Globorotaloides suteri Bolli.—Poore and Brabb, 1977:260, pl. 1, fig. 10, "lobate form" [upper Eocene Zone P15, San Lorenzo Fm., Two Bar Shale Mem., Santa Cruz

Plate 4.6 *Globorotaloides hexagonus* (Natland, 1938)

1-3 (holotype USNM 22560 of *Globigerina hexagona* Natland), Recent sediment, offshore California; **4**, **5**, **6-8**, *Globorotalia kugleri* Zone, Bolli sample 407, Cipero Fm. Trinidad; **9**, **10**, (paratype of *Globorotalia extans* 'microspheric' form) "*Globoquadrina dehiscens dehiscens*" Zone, Lakes Entrance oil shaft, Victoria, southeast Australia; **11**, **12**, (Spezzaferri, 1994; pl. 36, fig. 1a-b) '*Globorotaloides* aff. *hexagonus* (Natland)', Zone P22, ODP Sample 667A/33/2, 129-131 cm, Sierra Leone Rise, equatorial Atlantic Ocean; **13-15**, *Paragloborotalia opima* Zone, Bolli- Sample 381, Trinidad; **16**, *Globorotaloides permicrus* (Blow and Banner) (Spezzaferri and Premoli Silva, 1991; pl. 10, fig. 1a) Subzone P21a (O3/O4), ODP Sample 538A/7/CC, Gulf of Mexico. Scale bars: **1-16** = 100 µm.

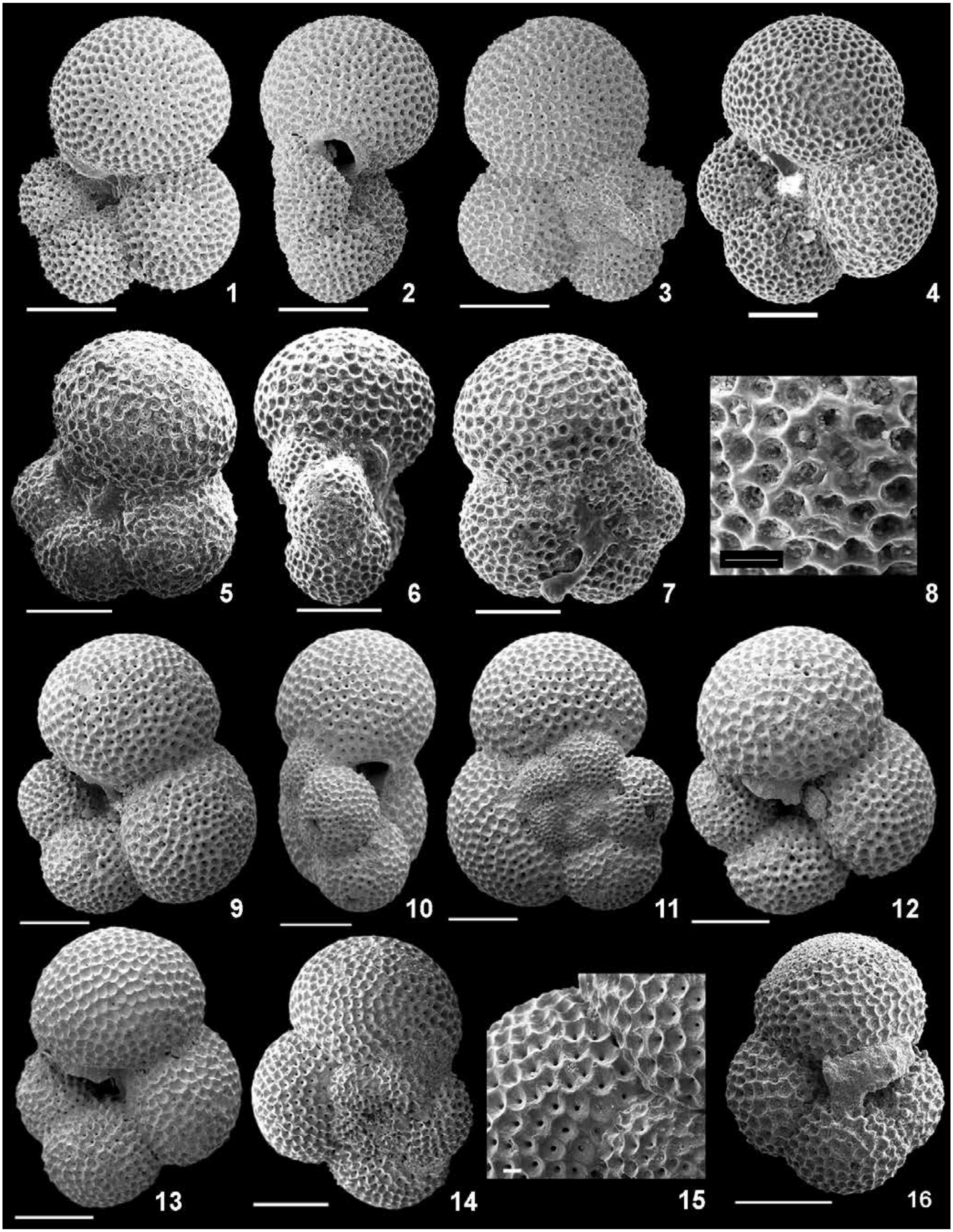

Plate 4.7 *Globorotaloides quadrocameratus* Olsson, Pearson, and Huber, 2006

Mountains, California]. [Not Bolli, 1957.]
Globorotaloides quadrocameratus Olsson, Pearson and Huber, 2006a:83-84, pl. 5.5, figs. 1-3, 5-7 [middle Eocene Zone E11, Guayabal Fm., Tampico, Mexico], figs. 9-11 [lower/middle Eocene Zone E7, TDP Site 2, Kilwa Masoko, Tanzania].

DESCRIPTION.

Type of wall: Spinose (?). Normal perforate, coarsely cancellate, *sacculifer*-type, wall structure.

Test morphology: Test very low trochospiral, 2-2½ whorls, lobate in outline, chambers globular; in spiral view 4 globular, slightly embracing chambers in the ultimate whorl, increasing rapidly in size, sutures moderately depressed, straight; in umbilical view 4 globular, slightly embracing chambers, increasing rapidly in size, ultimate chamber may be directed towards the umbilicus, sutures moderately depressed, straight, umbilicus small, aperture umbilical-extraumbilical a low opening bordered by narrow thickened lip; in edge view chambers globular in shape, slightly embracing (modified from Olsson and others, 2006a).

Size: Maximum diameter of holotype 0.18 mm, breadth 0.10 mm.

DISTINGUISHING FEATURES.— *Globorotaloides quadrocameratus* is characterized by its small, distinctly lobulate test, 4 chambers in the ultimate whorl, the umbilically directed ultimate chamber and rapidly enlarging final whorl chambers. It differs from *Parasubbotina varianta* and *Paragloborotalia griffinoides* by the smaller size, more coarsely cancellate test, more open coiling and flattened spiral side. It differs from *Globorotaloides suteri* in the more open coiling and more rapidly enlarging chambers and from *Catapsydrax unicavus* in the greater number of final whorl chambers and umbilical-extraumbilical position of the aperture and lack of a bulla. *Globorotalia* (*Turborotalia*) *permicra* Blow and Banner is a juvenile form that is probably conspecific with *quadrocameratus* (see Pearson and Wade, 2015, for discussion).

DISCUSSION.— *Globorotaloides quadrocameratus* is a distinctly lobate species of *Globorotaloides*. It intergrades with *Globorotaloides suteri* (Pl. 4.7, Figs. 5-8), to which it gave rise in the middle Eocene (see *Catapsydrax unicavus* and *Globorotaloides suteri* entries for history of synonymy). *Globorotaloides quadrocameratus* lacks a bulla. It is less common in the Oligocene than the Eocene. The relationship of Blow and Banner's (1962) taxon *Globorotalia* (*Turborotalia*) *permicra,* here shown as a questionable prior synonym of *G. quadrocameratus,* is discussed in Pearson and Wade (2015), who conclude it is likely a juvenile and discourage its use.

PHYLOGENETIC RELATIONSHIPS.—The origin of *Globorotaloides quadrocameratus,* and therefore the genus, is uncertain. In their original description of *G. quadrocameratus*, Olsson and others (2006a) suggested that it evolved in the basal Eocene from *Parasubbotina varianta* by flattening of the coil and development of a coarsely cancellate wall. In our current analysis we find similarities between *G. quadrocameratus* and early Paleocene forms referred to *Subbotina cancellata* (see Olsson and others, 1999; pl. 9, figs. 7-9, pl. 25, fig. 7). In particular we see a strong resemblance between *quadrocameratus* and the holotype of '*Globigerina fringa* Subbotina, 1953' (Olsson and others, 1999:29, pl. 9, figs. 7-9), which is quadrate, highly cancellate and laterally flattened. We therefore suggest that the ancestry of *Globorotaloides* lies in the Danian, and that *Globigerina fringa* is a questionable prior synonym of *G. quadrocameratus*. This requires further research that is beyond the scope of this study.

Globorotaloides quadrocameratus is closely allied to *G. eovariabilis*, with which it commonly occurs. The smooth/flattened inner whorl as seen in spiral view, is common to both taxa. *Globorotaloides quadrocameratus* gave rise to *Globorotaloides eovariabilis.*

TYPE LEVEL— Middle Eocene Zone E11.

STRATIGRAPHIC RANGE.— Lower Eocene Zone E2 (Olsson and others, 2006a) to lower Miocene Zone M1 (upper range constrained in this study, see figured specimens and their horizons, pl. 4.7).

Plate 4.7 *Globorotaloides quadrocameratus* Olsson, Pearson, and Huber, 2006

1-3, (holotype USNM 52186, Olsson and others, 2006a) Zone E11, Guayabal Fm., Tampico, Mexico; **4**, Zone O5, Istra More-3 well, Adriatic Sea; **5-8**, *Globigerina ampliapertura* Zone, Cipero Fm. Trinidad, morphology intermediate between *G. quadrocameratus* and *G. suteri*; **9-12**, Zone O6, Atlantic Slope Project corehole 5B, 10F/6-12", western Atlantic Ocean; **13-15**, Zone M1, ODP Hole 904A/35/5, 101-106 cm, New Jersey Slope, North Atlantic Ocean; **16**, Zone AO3, ODP Sample 1137A/17R/CC, Elan Bank, Kerguelen Plateau, southern Indian Ocean. Scale bars: **1-7**, **9-14**, **16** = 100 µm, **8** = 20 µm, **15** = 10 µm.

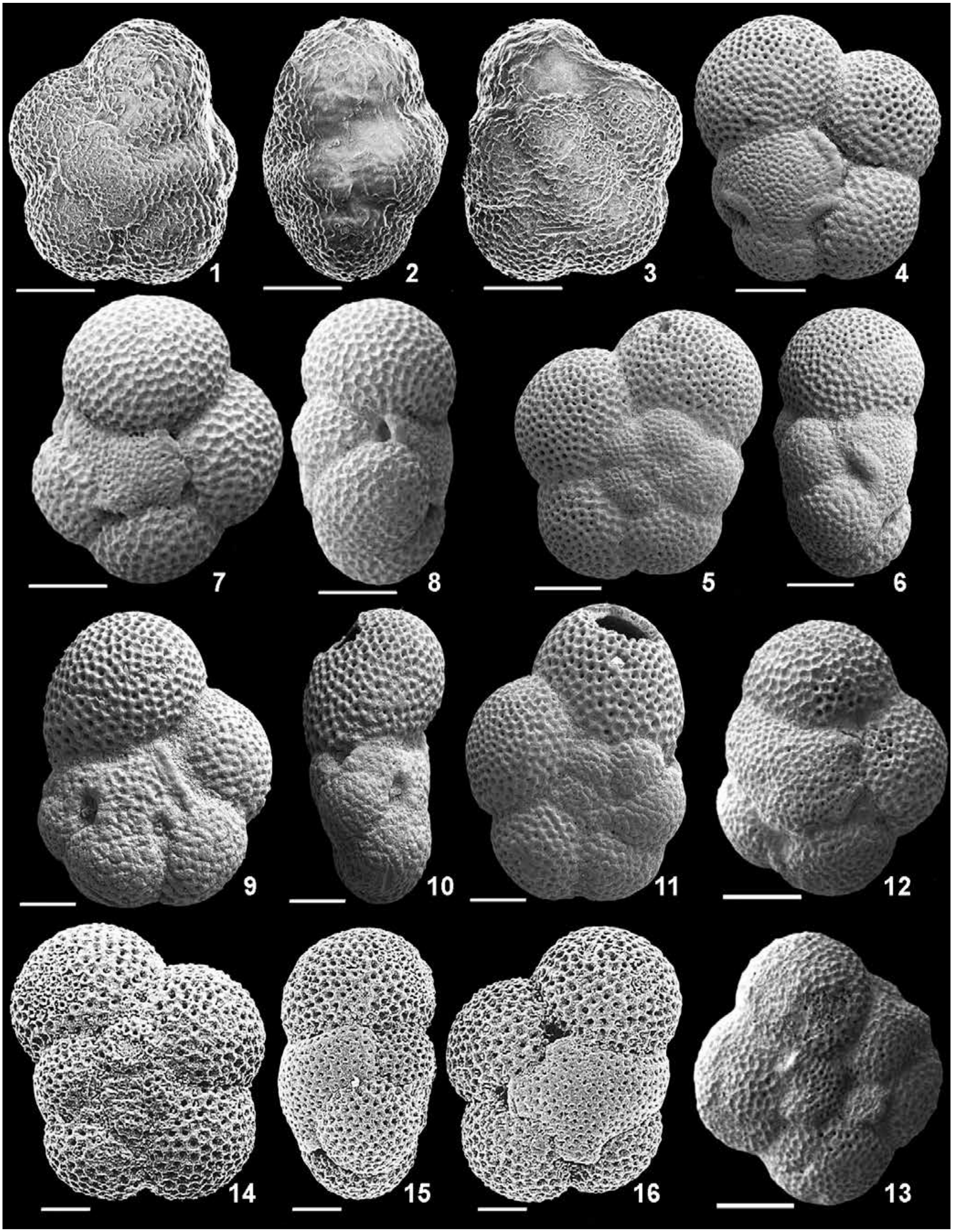

Plate 4.8 *Globorotaloides stainforthi* (Bolli, Loeblich, and Tappan, 1957)

GEOGRAPHIC DISTRIBUTION.— Global, including low and mid-latitudes. Can be common in southern and northern high latitudes. Possible affinity with high productivity conditions.

STABLE ISOTOPE PALEOBIOLOGY.— Stable isotopes suggest that *Globorotaloides quadrocameratus* occupied a sub-thermocline planktonic habitat similar to *Catapsydrax* (Coxall, unpublished data).

REPOSITORY.— Holotype (USNM 521865) and paratype (USNM 521866) deposited at the Smithsonian Museum of Natural History, Washington, D.C.

Globorotaloides stainforthi (Bolli, Loeblich, and Tappan, 1957)

Plate 4.8, Figures 1-16
(Pl. 4.8, Figs. 1-3 new SEMs of the holotype of *Catapsydrax stainforthi* Bolli, Loeblich, and Tappan, 1957)

Catapsydrax stainforthi Bolli, Loeblich, and Tappan, 1957:37, pl. 7, fig. 11, [Miocene *Catapsydrax stainforthi* Zone, Cipero Fm., Trinidad].—Quilty, 1976:641, pl. 7, figs. 12, 13 [upper Miocene Zone N17/N18, DSDP Hole 319, Nazca Plate, southeastern Pacific Ocean].—Kennett and Srinivasan, 1983:26, pl. 3, figs. 4-6 [lower Miocene Zone N7, DSDP Hole 289, Ontong Java Plateau, western equatorial Pacific Ocean].—Bolli and Saunders, 1985:187, pl. 17, figs. 5a-c [holotype re-illustrated].

Globigerinita stainforthi stainforthi (Bolli, Loeblich, and Tappan).—Brönnimann and Resig, 1971:1251, pl. 24, figs. 3, 4 [lower Miocene, DSDP Hole 64, Ontong Java Plateau, western equatorial Pacific Ocean].—Blow, 1979:131, pl. 25, figs. 8-10 [lower Miocene Zone N6, Pozón-El Mene Road traverse, eastern Falcón, Venezuela].

Globigerinita stainforthi (Bolli, Loeblich, and Tappan).—Raju, 1971:29, pl. VI, figs. 4a-c [upper Oligocene/lower Miocene *Globorotalia kugleri/Globigerinoides primordius* Zone, KKL-2 borehole, Cauvery basin, southeast India].

Globorotaloides stainforthi (Bolli, Loeblich, and Tappan).—Jenkins and Orr, 1972:1105, pl. 35, figs. 7-9 [lower Miocene *Catapsydrax dissimilis* Zone, DSDP Hole 77B, eastern equatorial Pacific Ocean].—Spezzaferri, 1994:46, pl. 34, fig. 3a-c [lower Miocene Zone N5, DSDP Hole 151, Beata Ridge, Caribbean Sea].

Globorotaloides suteri Bolli, 1957:117, pl. 27, fig. 12a,b, paratype USNM P5655c of *Globorotaloides suteri* [Miocene, *Catapsydrax stainforthi* Zone, Cipero Fm., Trinidad]. [Not Bolli, 1957.]

Globigerina stainforthi praestainforthi Blow.—Krasheninnikov and Pflaumann, 1977:592, pl. 7, fig. 1a-d [upper Oligocene Zone P21, DSDP Hole 369A, African margin, eastern equatorial Atlantic Ocean]. [Not Blow, 1979.]

Globorotaloides aff. *hexagonus* (Natland).—Spezzaferri, 1994:47, pl. 36, fig. 3a-c [upper Oligocene Zone P22, ODP Hole 667A, equatorial Atlantic Ocean]. [Not Natland, 1938.]

DESCRIPTION.

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

Test morphology: Test very low trochospiral, lobate in outline; axial periphery rounded, 2-2½ whorls, 10-11 chambers, 4-5 subglobular to ovate chambers in the final whorl increasing gradually in size, sutures slightly curved in umbilical view; in spiral view, relatively flattened inner whorl, sutures straight; primary aperture umbilical-extraumbilical, umbilicus covered by a flattened bulla extending to the equatorial periphery with 3-5 small, rimmed, infralaminal accessory apertures, opening over sutures of the final whorl.

Size: Greatest diameter of holotype 0.36 mm; thickness 0.26 mm. Paratypes range from 0.26 to 0.42 mm in diameter.

DISTINGUISHING FEATURES.— *Globorotaloides stainforthi* is distinguished from *Catapsydrax dissimilis* by having a more compressed test, more chambers in the final whorl (4½-5 compared with 4 in *C. dissimilis*), the umbilical to extraumbilical position of the primary aperture and the morphology of the bulla, which extends further towards the equatorial periphery than in *C. dissimilis* and usually has more apertures. It differs from bullate forms of *Globorotaloides eovariabilis* by the larger size and multiple infralaminal apertures. It is distinguished from *Globorotaloides atlanticus* primarily by having fewer chambers in the final whorl (typically 5

Plate 4.8 *Globorotaloides stainforthi* (Bolli, Loeblich, and Tappan, 1957)

1-3 (holotype of *Catapsydrax stainforthi,* USNM 4840) *Catapsydrax stainforthi* Zone (N6), Cipero Fm., Trinidad; **4-6**, **9-11**, Zone O7, ODP Sample 667A/33/1, 60-64 cm, Sierra Leone Rise, equatorial Atlantic Ocean; **7**, **8**, **12**, **13**, 'type *Catapsydrax dissimilis* Zone' (N5), Cipero Fm., Trinidad; **14-16**, (Spezzaferri, 1994, pl. 34, fig. 3a-c) Zone N5, DSDP Sample 151/4/1, 129-131 cm, Beata Ridge, Caribbean Sea. Scale bars: **1-16** = 100 µm.

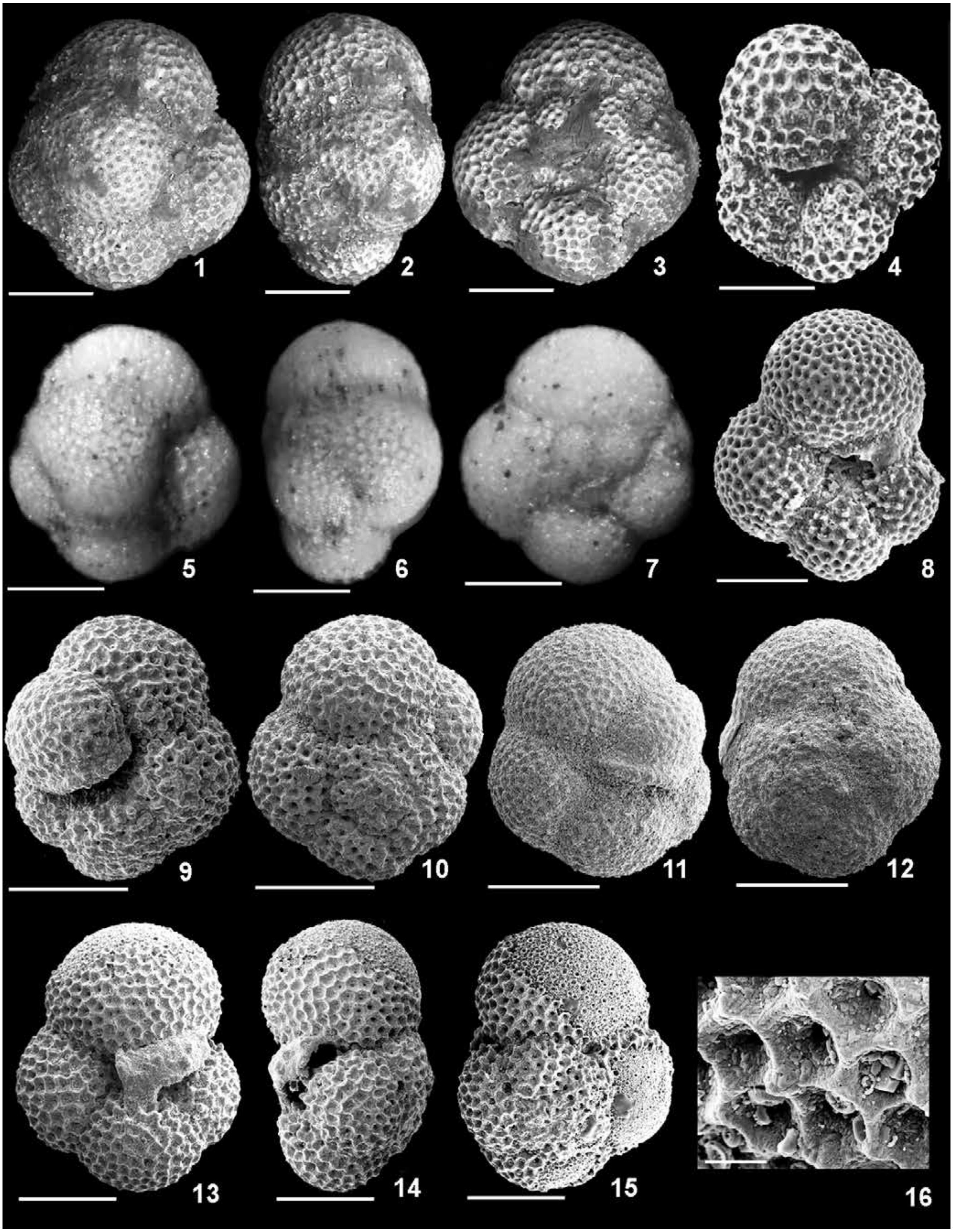

Plate 4.9 *Globorotaloides suteri* Bolli, 1957 (with bulla)

in *stainforthi* compared to 5½ in *atlanticus*). The bulla in *G. atlanticus* also extends around the equatorial periphery whereas in *stainforthi* the bulla is restricted to the umbilical area.

DISCUSSION.— *Globorotaloides stainforthi* is the nominate marker for Bolli's (1957) lower Miocene *'Catapsydrax' stainforthi* Concurrent range zone, which was defined as the interval containing the nominate taxon from the lowest occurrence of *Globigerinatella insueta* to the highest occurrence of *Catapsydrax dissimilis*. These limits now define the top of Zone M3 (base of Zone M4) of Berggren and others (1995). This zone has limited application because the species is relatively rare. Biogeographic distribution patterns suggest *G. stainforthi* to be an indicator of Oligocene to Miocene upwelling (Spezzaferri, 1995). *Tenuitellinata praestainforthi* (Blow, 1969), which also has a bulla and accessory apertures, has a microperforate wall and is thus unrelated to *Globorotaloides stainforthi*.

PHYLOGENETIC RELATIONSHIPS.— *Globorotaloides stainforthi* probably evolved from *Globorotaloides variabilis.* It gave rise to a series of bullate forms including *Globorotaloides atlanticus* n. sp., which was ancestral to the quasi-clavate pseudoplanispiral genus *Protentelloides.*

TYPE LEVEL.— Lower Miocene, Cipero Fm., *Catapsydrax stainforthi* Zone (~N6, M3).

STRATIGRAPHIC RANGE.— Lower Oligocene Zone O4, determined at Atlantic and Indian Ocean sites (Spezzaferri, 1994) to lower Miocene Zone N7 (M4) (Quilty, 1976).

GEOGRAPHIC DISTRIBUTION.— Low latitudes, equatorial. Affinity with high productivity conditions (Spezzaferri, 1995).

STABLE ISOTOPE PALEOBIOLOGY.— Relatively high $\delta^{18}O$ and low $\delta^{13}C$ compared to other planktonic foraminiferal species suggesting that *Globorotaloides stainforthi* preferred sub-thermocline waters similar to *Catapsydrax* and other species of *Globorotaloides* (Poore and Matthews, 1984).

REPOSITORY.— Holotype (USNM 4840) deposited at the Smithsonian Museum of Natural History, Washington, D.C.

Globorotaloides suteri Bolli, 1957

Plate 4.9, Figures 1-16; Plate 4.10, Figures 1-16
(Pl. 4.9, Figs. 1-3 new SEMs of the cleaned holotype of *Globorotaloides suteri* Bolli)
(Pl. 4.9, Figs. 5-7 new reflected light microscope images of the holotype of *Globorotaloides suteri* Bolli)

Globorotaloides suteri Bolli 1957:117 (partim), pl. 27, fig. 13 a-b, holotype, and pl. 27, figs. 9a-c, 11 a-b, paratypes [lower Oligocene *Globigerina ampliapertura* Zone, Cipero Fm. Trinidad].—Raju, 1971:34, pl. VI, figs. 5a,-b [Oligocene, KKL-1 borehole, Cauvery basin, southeast India].—Jenkins and Orr, 1972:1106, pl. 37, figs. 1-3 [lower Oligocene *Pseudohastigerina barbadoensis* Zone, DSDP Hole 77B, eastern equatorial Pacific Ocean].—Fleisher, 1974:1029, pl. 13, fig. 7 [lower Oligocene Zone P18-P19, DSDP Hole 223, Arabian Sea.—Quilty, 1976:649, pl. 17, figs. 3, 4 [lower Oligocene Zone P18, DSDP Hole 321B, Nazca Plate, southeastern Pacific Ocean].—Poore and Brabb, 1977:260, pl. 1, fig. 13 [lower Oligocene Zone P19-P20, San Lorenzo Fm., Santa Cruz Mountains, California].—Krasheninnikov and Pflaumann, 1977:592, pl. 7, figs. 7a-b, 8, 9a-c [upper Oligocene Zone P21, DSDP Hole 369A, African margin, eastern equatorial Atlantic Ocean].—Krasheninnikov and Basov, 1983:840, pl. 8, figs. 2, 3 [upper Eocene, DSDP Hole 511, Falkland Plateau, South Atlantic Ocean].—Bolli and Saunders, 1985:190, fig. 18.10 [holotype illustration reproduced].—Stott and Kennett, 1990:560, pl. 7, fig. 12 [upper Eocene Zone AP11, ODP Hole 690B, Maud Rise, sub-Antarctic South Atlantic Ocean].—Spezzaferri and Premoli Silva, 1991:248, pl. 1, fig. 6a-c [lower Oligocene Subzone P21a, ODP Hole 538A, Gulf of Mexico], pl. 10,

Plate 4.9 *Globorotaloides suteri* Bolli, 1957 (with bulla)

1-3, (holotype of *Globorotaloides suteri,* USNM P5654) *Globigerina ampliapertura* Zone, Cipero Fm. Trinidad (new SEM image taken after cleaning, see text); **4**, (Chaisson and Leckie, 1993, pl. 9, fig. 3) Subzone N4b, ODP Sample 806B/72X/2, 30-32 cm, Ontong Java Plateau, western equatorial Pacific Ocean; **5-7**, light microscope images of the holotype of *Globorotaloides suteri* (after cleaning); **8**, Zone O5, Istra More-3 well, Adriatic Sea; **9**, **10**, Zone AO3, ODP Sample 1137A/15R/CC, Kerguelen Plateau, southern Indian Ocean; **11**, **12**, Zone O6, IODP Sample U1336A/21H/CC, equatorial Pacific Ocean (poorly preserved specimen); **13-16**, Zone AO3, ODP Sample 1137A/17R/CC, Kerguelen Plateau, southern Indian Ocean, shows peeling of wall. Scale bars: **1-15** = 100 µm, **16** = 10 µm.

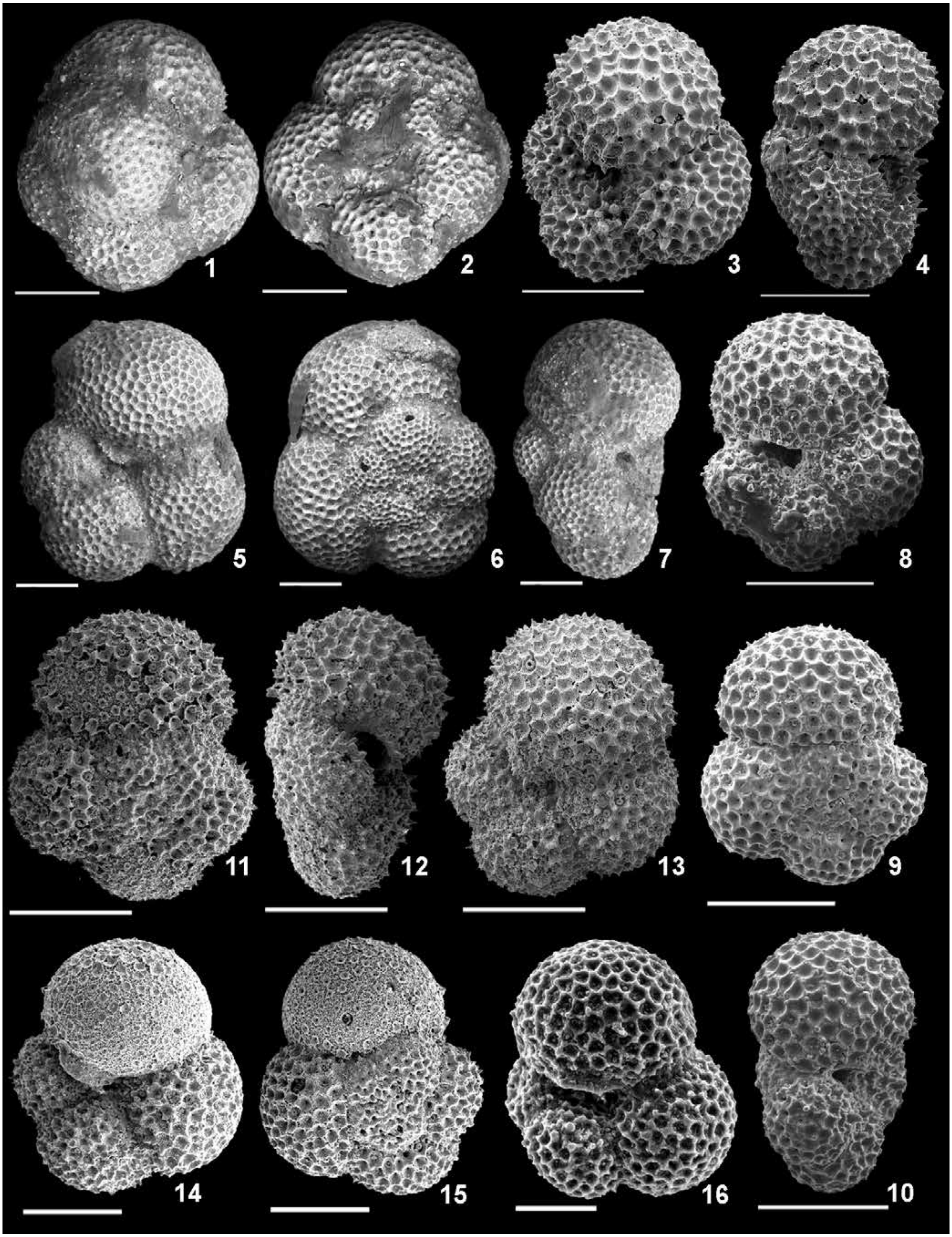

Plate 4.10 *Globorotaloides suteri* Bolli, 1957 (without bulla, and holotype shown again for comparison)

figs. 4a-d [lower Oligocene Zone P20, ODP Hole 538A, Gulf of Mexico].—van Eijden, 1991:112, pl. 4, figs. 18-20 [upper Oligocene Zone P22, ODP Hole 758A, eastern Indian Ocean].—Chaisson and Leckie, 1993:164, pl. 9, fig. 2 [lower Miocene Subzone N4b, ODP Hole 806B, Ontong Java Plateau, western equatorial Pacific Ocean].—Leckie and others, 1993:124, pl. 3, fig. 18 [upper Oligocene Zone P22, ODP Site 628, Little Bahama Bank, Caribbean Sea].—Cicha and others, 1998:104, pl. 40, figs. 16, 18 [upper Oligocene, Moravia, Czech Republic].

Globorotaloides cf. *G. suteri* Bolli.—Leckie and Webb, 1986:1117, pl. 15, figs. 3, 4. [upper Oligocene-lower Miocene, DSDP Site 270, Ross Sea, Antarctica].

Globigerinita unicava primitiva Blow and Banner.—Hooyberghs and De Meuter, 1972:33, pl. 11, fig. 3a-c [upper Oligocene, Edegem Sands, Belgium].—Blow, 1979:1322, pl. 25, figs. 1, 2 [lower Oligocene Zone P18, JOIDES Core -3, Blake Plateau, North Atlantic Ocean]. [Not Blow and Banner, 1962.]

Globigerinita unicava unicava (Bolli, Loeblich, and Tappan).—Hooyberghs and De Meuter, 1972:33, pl. 11, fig. 4a-c [upper Oligocene, Edegem Sands, Belgium]. [Not Bolli, Loeblich, and Tappan.]

Globigerinita martini scandretti Blow and Banner.—Blow, 1979:1342-1343, pl. 24, figs. 6, 7 [lower Oligocene Zone P19, Lindi area, Tanzania]. [Not Blow and Banner, 1962.]

Catapsydrax unicavus Blow and Banner.—Olsson and others, 2006a:75, pl. 5.3, figs. 9-11 [SEM of holotype of *Globorotaloides suteri*], fig. 13 [middle Eocene Zone E8, TDP Site 2, Kilwa, Tanzania]. [Not Blow and Banner, 1962.]

DESCRIPTION.

Type of wall: Nonspinose (?). Normal perforate, coarsely cancellate, *sacculifer*-type wall texture, with a distinctly honeycomb appearance.

Test morphology: Low trochospiral, equatorial periphery lobate, axial periphery rounded; chambers ovate to spherical, 11-14, arranged in 2-2½ whorls, 3½-4 chambers in the final whorl increasing gradually in size; spiral view reveals flattened 'globorotalid' inner whorl, spiral sutures slightly curved, radial, depressed; umbilical sutures straight, radial, depressed, umbilicus small, open in some specimens, in others (including the holotype) completely or partially covered by a bulla extending from the equatorial margin; primary aperture a low interiomarginal umbilical-extraumbilical arch surrounded by beak-like lip, infralaminal aperture slit-like and bordered by a lip.

Size: Holotype maximum diameter 0.35 mm.

DISTINGUISHING FEATURES.— *Globorotaloides suteri* is distinguished from *Globorotaloides quadrocameratus* by the more compact coiling, more gradually enlarging and radial flattening of the final whorl (especially the final chamber) and less lobate peripheral outline. It differs from *Catapsydrax unicavus* in having 4 chambers in the final whorl compared to 3 or 3½ in *C. unicavus*. It differs from *Globorotaloides eovariabilis* in having only 4 chambers in the final whorl and from *Globorotaloides testarugosus* in radial orientation of the spiral sutures and more lobed peripheral outline. Bullate and non-bullate varieties occur, when bullate having a single infralaminal aperture.

DISCUSSION.— An important aspect of our revised taxonomy is the resurrection of *Globorotaloides suteri* Bolli 1957. In the *Atlas of Eocene Planktonic Foraminifera*, *Globorotaloides suteri* was considered a junior synonym of *Catapsydrax unicavus* (Olsson and others, 2006a) based on similarities between the available holotype SEM images. This, however, would leave a range of four-chambered forms of *Globorotaloides* that do not fit in *G. quadrocameratus*, without a name. New SEM and reflected light microscope images (Pl. 4.9, Figs. 1-3, 5-7) made after cleaning of the *G. suteri* holotype (removal of gum tragacanth layers, B. Huber) reveals a typical *Globorotaloides* morphology comprising a flattened *Globorotalia*-like inner whorl. This feature is also visible in spiral views of the four paratypes of *G. suteri*. Based on this new evidence we here reinstate *Globorotaloides suteri* as a compact, four-chambered form that may or may not possess a bulla (see Plates 4.9 and 4.10, respectively). Applying the revised definition of the taxon, we retain two of Bolli's *G. suteri* paratypes in *G. suteri* (Bolli 1957: pl. 27, figs. 9a-c, USNM P5655a and pl. 27, figs. 11a-b, USNM P5655c), while the other two have been reclassified as *Globorotaloides eovariabilis* (Bolli, 1957:117, pl. 27, figs. 10a-b, USNM P5655b and

Plate 4.10 *Globorotaloides suteri* Bolli, 1957 (without bulla)

1-2 (holotype of *Globorotaloides suteri,* USNM P5654), *Globigerina ampliapertura* Zone, Cipero Fm. Trinidad (new SEM image taken after cleaning, see text); **3-4**, Zone O1, ODP Sample 647A/27R/1, 47-49 cm, southern Labrador Sea; **5-7**, (paratype of *Globorotaloides suteri,* USNM P5665a) *Globigerina ampliapertura* Zone, Cipero Fm., Trinidad; **8-10**, Zone O1, ODP Sample 647A/28R/4, 74.5-76 cm, southern Labrador Sea; **11-13** (same specimen), **14**, **15**, Zone AO3, ODP Sample 1137A/17R/CC, Kerguelen Plateau, southern Indian Ocean; **16**, Istra More-3 well, Adriatic Sea, Cuttings sample 1285. Scale bars: **1-16** = 100 µm.

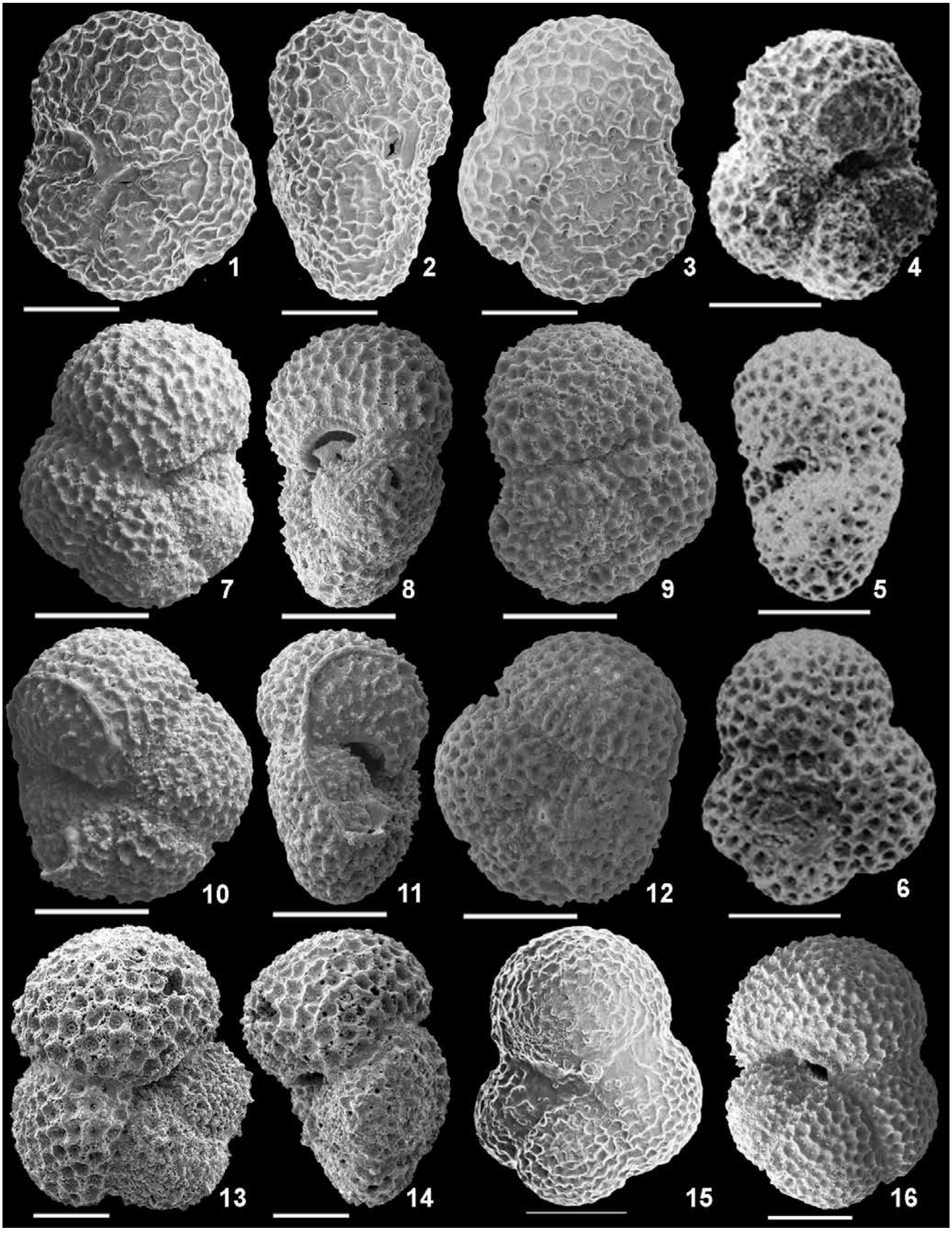

Plate 4.11 *Globorotaloides testarugosus* (Jenkins, 1960)

pl. 27, figs. 12a-b, USNM P5655d) because they have more evolute coiling and 5 chambers in the final whorl. *Globorotaloides suteri* is the most common Oligocene to Miocene *Globorotaloides* morphotype. This is consistent with Bolli's original concept of the holotype and its subsequent usage (see extensive synonym list), although narrower in the sense that we include only four chambered forms.

PHYLOGENETIC RELATIONSHIPS.— *Globorotaloides suteri* probably evolved from *Globorotaloides quadrocameratus*.

TYPE LEVEL.— Lower Oligocene *Globigerina ampliapertura* Zone (O1-O2 of Wade and others, 2011), Cipero Fm., Trinidad.

STRATIGRAPHIC RANGE.— Middle Eocene Zone AP10 (Huber, 1991) (=AE7 Huber and Quillévéré, 2005) to lower-middle Miocene Zone N8 (Kennett and Srinivasan, 1983) (Zone M5 of Wade and others, 2011).

GEOGRAPHIC DISTRIBUTION.— Distribution is global, including low and mid-latitudes. It can be common in southern and northern high latitudes regions. It shows affinities with high productivity conditions.

STABLE ISOTOPE PALEOBIOLOGY.— Relatively high $\delta^{18}O$ and low $\delta^{13}C$ compared to other species suggest that *Globorotaloides suteri* occupied a sub-thermocline planktonic habitat similar to *Catapsydrax* (Poore and Matthews, 1984; Barrera and Huber, 1991; Coxall, unpublished). The middle Eocene morphotype recorded as '*Globorotaloides* sp. 1', by Sexton and others (2006), and which we here assign to *G. suteri*, similarly shows $\delta^{18}O$ and low $\delta^{13}C$ indicative of a thermocline habitat.

REPOSITORY.— Holotype (USNM P5654) and paratypes (USNM 5655a-d) deposited at the Smithsonian Museum of Natural History, Washington, D.C.

Globorotaloides testarugosus (Jenkins, 1960)

Plate 4.11, Figures 1-16
(Pl. 4.11, Figs. 1-3: new SEMs of the holotype of *Globorotalia testarugosa* Jenkins, 1960)
(Pl. 4.11, Fig. 15: new SEM of the holotype of *Globorotalia extans* Jenkins, 1960)

Globorotalia testarugosa Jenkins, 1960:368, pl. 5, figs. 8a–c [upper Oligocene "pre-*Globoquadrina dehiscens dehiscens* Zone", Lakes Entrance Oil Shaft, Victoria, Australia].

Globorotaloides testarugosa (Jenkins).—Jenkins, 1971:190 pl. 22, figs. 652, 653 [upper Oligocene *Globigerina euapertura* Zone, type Whaingaroan, Raglan Harbor section, south western Australia].—Jenkins, 1985:279, figs. 7, 3a-b [re-illustration of holotype].—Spezzaferri, 1994:47, pl. 35, figs. 1a-c, 4a-c [upper Oligocene Zone P22, DSDP Site 593, South Pacific Ocean], fig. 3a-c [lower Oligocene Subzone P21a, DSDP Hole 516F, eastern South Atlantic Ocean].—Pearson and Wade, 2009:206, pl. 5, fig. 6 [upper Oligocene Zone O6 (= O7 this study), Cipero Fm., Trinidad].

Globorotalia extans Jenkins, 1960:360 (partim, 'megalospheric form'), pl. 4, figs. 5a-c [lower Miocene, "*Globoquadrina dehiscens dehiscens*" Zone, Lakes Entrance oil shaft, Victoria, southeast Australia].

Globorotaloides sp.—Stewart and others, 2004: pl. A.1, figs. 19-21 [lower Miocene Subzone M1b, Lindi, Tanzania].

DESCRIPTION.

Type of wall: Nonspinose (?). Normal perforate, coarsely cancellate, *sacculifer*-type wall texture, with a distinctly honeycomb appearance.

Test morphology: Test outline compact, continuous equatorial periphery very slightly quadrilobate, axial periphery rounded; 3-3½ whorls of inflated chambers, arranged in a trochospire, flattened on the spiral side; 11-12 chambers in adult tests, 4½-6 in the final whorl increasing moderately in size; umbilicus shallow to moderately deep and narrow; umbilical sutures, straight, radial, depressed and somewhat grooved, spiral sutures initially indistinct, later depressed, distinctly straight, tangential; spiral aperture a low interiomarginal um-

Plate 4.11 *Globorotaloides testarugosus* (Jenkins, 1960)

1-3 (holotype CPC4207 of *Globorotalia testarugosa*) "Pre-*Globoquadrina dehiscens dehiscens* Zone", Lakes Entrance Oil Shaft, Victoria, Australia; **4-6**, (Stewart and others, 2004, '*Globorotaloides* sp', pl. A.1, figs. 19-21) Subzone M1b, outcrop sample RAS99-42, Tanzania, Lindi; **7-9**, Zone P22, DSDP Sample 593/50X/5, 140-142 cm, Tasman Sea; **10-12**, Zone P22, DSDP Sample 593/50X/5, 140-142 cm, Tasman Sea; **13-14**, Zone AO3, ODP Site 1137A/17R/CC, Kerguelen Plateau, southern Indian Ocean; **15**, (holotype CPC4193 *Globorotalia extans* 'megalospheric' form) "*Globoquadrina dehiscens dehiscens*" Zone, Lakes Entrance Oil Shaft, Victoria, Australia; **16**, Zone P22, DSDP Hole 593, Tasman Sea. Scale bars: **1-16** = 100 µm.

bilical-extraumbilical arch surrounded by a narrow lip.

Size: Holotype maximum diameter 0.3 mm.

DISTINGUISHING FEATURES.— Differs from other species of *Globorotaloides* by the more compact coiling, less lobate peripheral outline, a highly rugose wall, more restricted umbilicus and distinctly straight sutures, which are grooved on the umbilical side and tangential on the spiral side.

DISCUSSION.—We change the species name to its masculine form to accord with Article 31.2 of the ICZN ("a species-group name, if it is or ends in a Latin or latinized adjective or participle in the nominative singular, must agree in gender with the generic name with which it is at any time combined"). Thus *Globorotaloides testarugosa* becomes *G. testarugosus*. We recognize *Globorotaloides testarugosus* as a distinct morphotype with angular chambers and a highly rugose wall that occurs in the mid-Oligocene to lower Miocene. Importantly our concept of the taxon has been broadened to encompass *Globorotalia extans* Jenkins, 1960, which was described at the same time from the same locality (Lakes Entrance Oil Shaft). According to Jenkins, *testarugosus* s.s. is restricted to Jenkins' local "pre- *Globoquadrina dehiscens dehiscens* zone", while the *extans* morphotype extends stratigraphically above *testarugosus* into the "*Globoquadrina dehiscens dehiscens*" and "*Globigerina woodi*" zones (Jenkins, 1993). These zones are approximately equivalent to Zones O6-M3 of Wade and others (2011).

According to Jenkins (1960), *G. extans* differs from *G. testarugosus* by being more loosely coiled and in the greater degree of chamber inflation. He recognized two variants; i) *extans* 'megalospheric forms', having a relatively large proloculus and 4 chambers in the final whorl, and (ii) *extans* 'microspheric forms', which has a relatively small proloculus, 5 chambers in the final whorl and extends stratigraphically above the megalospheric forms. Micro- and megalospheric forms are not generally recognized in the planktonic foraminifera, so these morphotypes likely belong to different species. The 'megalospheric' form (and holotype of *extans*) we refer to *G. testarugosus* (Pl. 4.11, Fig. 15), such that *extans* becomes a junior synonym of *testarugosus*. The 'microspheric' form, which is represented by the paratype of *extans*, we here assign to *Globorotaloides hexagonus* (Pl. 4.6, Figs. 9, 10). Technically *extans* should be the senior synonym because it has page priority. However, we chose to retain *G. testarugosus* as the working name because of the confusion with the micro- and megalospheric type examples of *extans*, and since the concept of *G. testarugosus* is better known and used.

Jenkins (1971) reported a high degree of variability in populations of *G. testarugosus* from the New Zealand Whaingaroan type sample (N55/545), with some specimens having a bulla-like final chamber. Forms described as *Globorotaloides* aff. *G. testarugosus* (Jenkins) from the subantarctic Atlantic and Indian Oceans by Stott and Kennett (1990; Huber, 1991) we suggest are closer to *G. eovariabilis* (and synonymized as such). Although not commonly recorded outside of the Austral realm, *G. testarugosus* has been described from Trinidad (Pearson and Wade, 2009) and Tanzania (Stewart and others, 2004, figured as *Globorotaloides* sp.), suggesting a global, geographic range.

PHYLOGENETIC RELATIONSHIPS.— *Globorotaloides testarugosus* probably evolved from *Globorotaloides eovariabilis* in the mid-Oligocene.

STRATIGRAPHIC RANGE.— Based on the originally reported stratigraphic range of *G. testarugosus* and *G. extans* 'megalospheric' (Jenkins, 1960), in combination with records of this taxon from elsewhere we report the range of *G. testarugosus* as mid-Oligocene Subzone P21a (O3/O4) (Premoli Silva and Spezzaferri, 1990; Spezzaferri, 1994) to lower Miocene Zone N4 (O7/M1) (Spezzaferri, 1994).

TYPE LEVEL.— Upper Oligocene, "pre-*Globoquadrina dehiscens dehiscens* zone" (Jenkins, 1960), referable to Zone O4/O5 (Wade and others, 2011), Whaingaroan sample N55/545, Raglan Harbour section, south western Australia.

GEOGRAPHIC DISTRIBUTION.— Tropical to subtropical. Possibly global. Most common in the Austral realm (southeastern Australia and New Zealand; Jenkins, 1960, 1975) as well as the southeastern Atlantic, South Pacific and Indian Oceans (Premoli Silva and Spezzaferri, 1990; Spezzaferri, 1994; Stewart and others, 2004).

STABLE ISOTOPE PALEOBIOLOGY.— No data available.

REPOSITORY.— Holotype (CPC4207), deposited at the BMR, Canberra, Australia.

Globorotaloides variabilis Bolli, 1957

Plate 4.12, Figures 1-16
(Pl. 4.12, Figs. 1-3: new SEMs of the holotype USNM P5657 of *Globorotaloides variabilis* Bolli)
(Pl. 4.12, Figs. 6-8: new SEMs of the paratype USNM 5658C of *Globorotaloides variabilis* Bolli)
(Pl. 4.12, Figs. 13-14: new SEMs of the paratype USNM 5658D of *Globorotaloides variabilis* Bolli)

Globorotaloides variabilis Bolli, 1957:117, pl. 27, figs. 15a-20c [upper Miocene, *Globorotalia menardii* Zone, Lengua Fm., Trinidad].—Kennett and Srinivasan, 1983:214, pl. 53, figs. 6-8 [upper Miocene, Zone N19, DSDP Hole 289, Ontong Java Plateau, western equatorial Pacific Ocean].—Bolli and Saunders, 1985:190, pl. 18, figs. 7-9 (re-illustration of holotype).—Chaisson and Leckie, 1993:164, pl. 9, fig. 3 [middle Miocene Zone N13, ODP Hole 806B, Ontong Java Plateau, western equatorial Pacific Ocean].—Spezzaferri, 1994:46, pl. 34, figs. 1a-c [lower Miocene Zone N4, Walvis Ridge, southeastern Atlantic Ocean].

Globorotaloides suteri Bolli, 1957.—Hooyberghs and De Meuter, 1972:32, pl. 10, fig. 4a-c [lower Miocene, Houthalen Sands, Belgium].—Kennett and Srinivasan, 1983:214, pl. 53, figs. 3-5 [lower Miocene *Catapsydrax dissimilis* Zone, DSDP Hole 208, southwest Pacific Ocean]. [Not Bolli, 1957.]

Globorotaloides sp. 1.—Premoli Silva and Spezzaferri, 1990:303, pl. 3, figs. 2a-c [upper Oligocene Zone P22, ODP Hole 707A, Mascarene Plateau, equatorial Indian Ocean].

Globigerinita unicava unicava (Bolli, Loeblich, and Tappan), 1957.—Brönnimann and Resig, 1971:1307, pl. 25, fig. 4 [lower Miocene Zone N6, DSDP Hole 64, Ontong Java Plateau, western equatorial Pacific Ocean]. [Not Bolli, Loeblich, and Tappan.]

Globorotaloides hexagona hexagona (Natland).—Quilty, 1976:649, pl. 16, fig. 11 [middle Miocene Zone N12, DSDP Hole 319, southeastern Pacific Ocean]. [Not Natland, 1938.]

DESCRIPTION.

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

Test morphology: Low trochospiral, equatorial periphery lobate, axial periphery rounded; chambers subangular to ovate in early stage, later becoming ovate to globular; 2-2½ whorls; 4½-6 slightly embracing chambers in final whorl, chambers of final whorl increase fairly gradually in size, final chamber typically a bulla or bulla-like, may cover part of or the entire umbilicus; spiral view, sutures distinctly curved to retroflexed in early stage, becoming more radial in the adult stages in some specimens, depressed, inner whorl distinctly flattened; umbilical view, chambers increase rapidly in size, sutures moderately depressed, straight; umbilicus small, primary aperture a slit or low arch, bordered by narrow thickened lip, umbilical-extraumbilical in early stage, later becoming umbilical, in the mature stage this becomes covered by the bulla-like final chamber with one infralaminal aperture. Coiling variable.

Size: Maximum diameter of holotype 0.45 mm.

DISTINGUISHING FEATURES.— *Globorotaloides variabilis* as the name suggests shows some irregularity in its late-stage coiling and other features. The final bulla-like chamber may cover part of or the entire umbilicus. The primary aperture is also umbilical in adult forms, whereas in most other *Globorotaloides* species it is umbilical-extraumbilical, although in forms transitional to *G. hexagonus* the aperture is more extraumbilical. It is distinguished from species of *Catapsydrax* by the flattened spiral side. Forms without the terminal bulla-like chamber can be distinguished from *Globorotaloides hexagonus* and *Globorotaloides eovariabilis* by the more embracing chambers and more umbilical position of the primary aperture. Some specimens lack a bulla, revealing the umbilical position of the primary aperture and a lip (Pl. 4.12, Figs. 13, 14 and 15, 16).

DISCUSSION.— *Globorotaloides variabilis* is not a well known species and the original concept has been only weakly applied. Blow (1969, 1979) treated *Globorotaloides variabilis* as a subspecies of *Globorotaloides hexagonus* (Natland). Kennett and Srinivasan (1983) recognized *G. variabilis* from the late Miocene of the southwestern Pacific Ocean. Their figured specimen (Kennett and Srinivasan, 1983; pl. 53, figs. 6-8, reproduced here on Pl. 4.12, Figs. 15 and 16), which is nonbullate and somewhat pinched around the periphery, has propagated a rather narrow concept of the taxon as being non-bullate and close to *G. hexagonus*. Our assessment of the type material, however, demonstrates greater variability within the taxon, including bullate forms rather similar to Bolli's types and our topotypes (Pl. 4.12, Figs. 5, 9-12), as well as forms closely comparable to Kennett and Srinivasan's examples.

PHYLOGENETIC RELATIONSHIPS.— *Globorotaloides variabilis* probably evolved from *Globorotaloides*

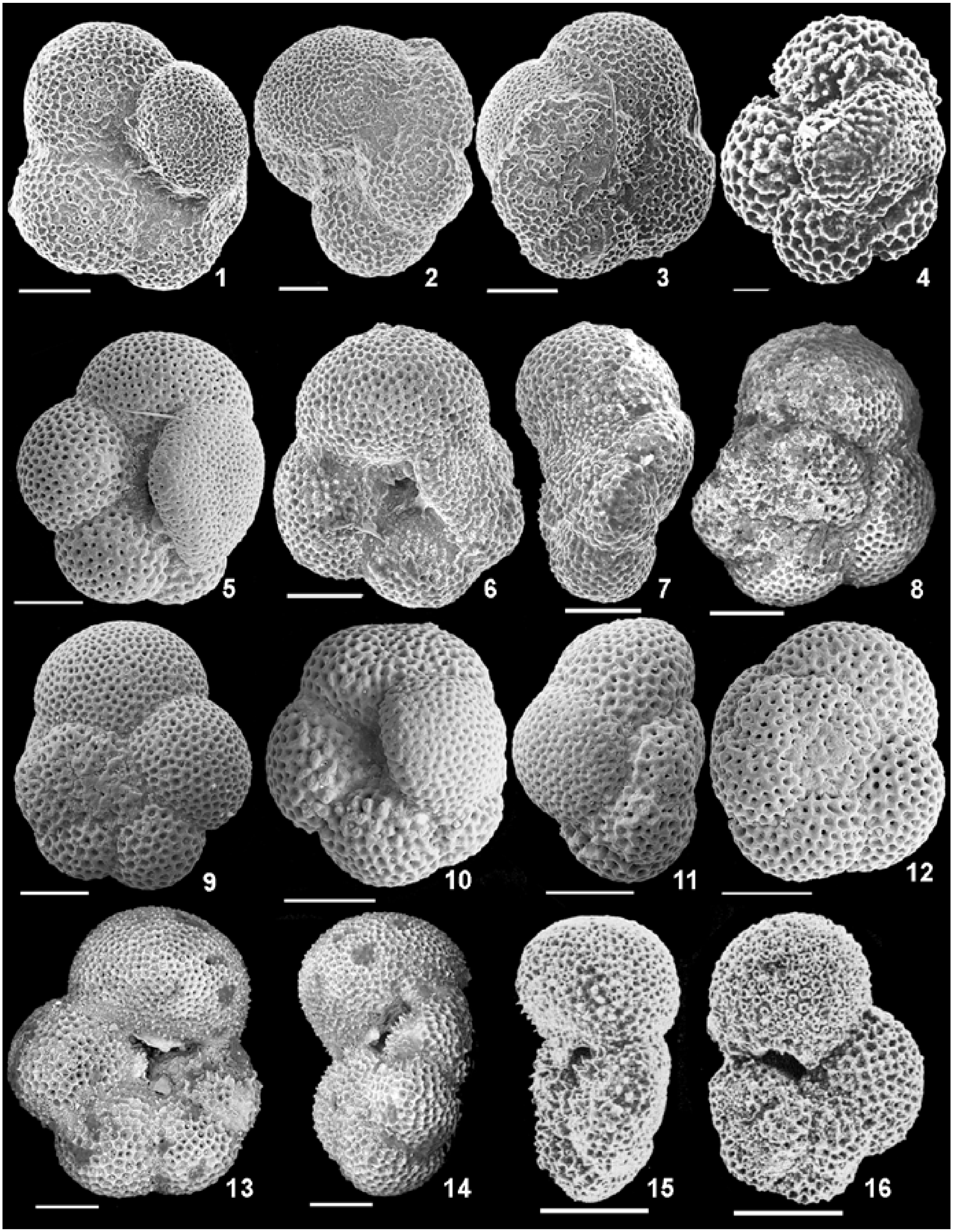

Plate 4.12 *Globorotaloides variabilis* Bolli, 1957

eovariabilis in Zone O3/O4 and was ancestral to *G. stainforthi* and *G. hexagonus.*

TYPE LEVEL.— Upper Miocene, *Globorotalia menardii* Zone = Zone N15 of Blow (1979) (= Zone M12), Lengua Fm., Trinidad.

STRATIGRAPHIC RANGE.— Uncertain due to the variability and scarcity of the morphotype and therefore uncertainty in consistency of positive identifications. Bolli and Saunders (1985) show *G. variabilis* to be restricted to Miocene Zones N8-N17, disappearing prior to the base of the Pliocene. Subsequent constraints extend the first appearance back to lower Oligocene Subzone P21a (Zone O3/O4) (Atlantic Ocean DSDP Sites 17A, 363 and 516, and Indian Ocean ODP Site 707; Spezzaferri, 1994), or possibly Zone P20 (Zone O2) (DSDP Site 94 Gulf of Mexico). Spezzaferri's (1994) best constraint for the highest occurrence of *G. variabilis* is N8-N9 (M5/M6), as seen at DSDP Sites 17A, 363 and 588. Reports of this species in the Pliocene (Poore, 1981: Zone N19) are likely to be a bullate form of *G. hexagonus*.

GEOGRAPHIC DISTRIBUTION.— Global at mid- to low latitudes.

STABLE ISOTOPE PALEOBIOLOGY.— No data available.

REPOSITORY.— Holotype (USNM P5657) deposited at the Smithsonian Museum of Natural History, Washington, D.C.

Protentelloides **Zhang and Scott, 1995**

TYPE SPECIES.— *Protentelloides dalhousiei* Zhang and Scott (1995).

DESCRIPTION.

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

Test morphology: Laterally compressed, low trochospiral/pseudoplanispiral; lobate to strongly lobate, 5-7 chambers in the final whorl, increasing rapidly in size; chambers flatten towards the center of the test; sutures on both sides almost radial, depressed, straight, becoming curved to sigmoidal; final chamber is typically reduced in size, bulla-like, centered at the equatorial margin and highly variable in morphology, ranging from globular and protruding to flattened and unobtrusive; primary aperture highly variable, also equatorially centered, ranging from a low extraumbilical to equatorial, symmetrical or asymmetrical arch, a long equatorial slit extending up the final chamber face, a bi-radiate equatorial arch (with one ray extending into the umbilical region). The aperture is bordered by an imperforate flap-like lip that may fuse to subdivide the primary aperture, or be perforated by one or more circular or elongated accessory apertures, reminiscent of the 'cribrate' supplementary aperture system of late Eocene *Cribrohantkenina*.

DISTINGUISHING FEATURES.— *Protentelloides* is distinguished from *Globorotaloides* in the lateral flattening and spreading of the test and the equatorial positioning of the bulla or bulla-like final chamber, and aperture(s). *Protentelloides* differs from *Clavatorella* and *Protentella* in lacking digitate chambers. *Protentelloides* also has a distinctive bulla-like final chamber, projecting imperforate lip and a cancellate *Globorotaloides*-wall whereas *Protentella* has a more finely 'reticulate' wall. *Protentelloides* differs from *Globigerinella* in having flattened chambers. The system of accessory apertures is reminiscent of the 'cribrate' equatorial aperture of late Eocene genus *Cribrohantkenina*.

DISCUSSION.— The appearance of this short ranging genus (1-2 million years) in the upper Oligocene is a prominent event in the evolution of this group. It may have biostratigraphic potential, however to date, *Protentelloides* has not been recorded outside its type location in the eastern equatorial Atlantic Ocean, Sierra Leone Rise, DSDP Hole 366A (Zhang and Scott, 1995) and ODP Hole 667A (Spezzaferri, 1994). Zhang and Scott (1995) suggested that *Protentelloides dalhousiei* maybe

Plate 4.12 *Globorotaloides variabilis* Bolli, 1957

1-3 (holotype of *Globorotaloides variabilis*, USNM P5657) *Globorotalia menardii* Zone, Lengua Fm., Trinidad; **4**, (Brönnimann and Resig, 1971, pl. 25, fig. 4), lower Miocene Zone N4, DSDP Sample 64.1/3/1, 33-35 cm, Ontong Java Plateau, western equatorial Pacific Ocean; **5-14**, *Globorotalia menardii* Zone, Lengua Fm., Trinidad, (5, 9-12 topotypes); 6-8 paratype USNM 5658C), 9 is the spiral view of 5, 13-14, paratype USNM 5658D; **15**, **16** (Kennett and Srinivasan, 1983, pl. 53, figs. 7, 6), Zone N16, DSDP Sample 289/33/2, 99 cm, Ontong Java Plateau, western equatorial Pacific Ocean. Scale bars: **1-16** = 100 µm

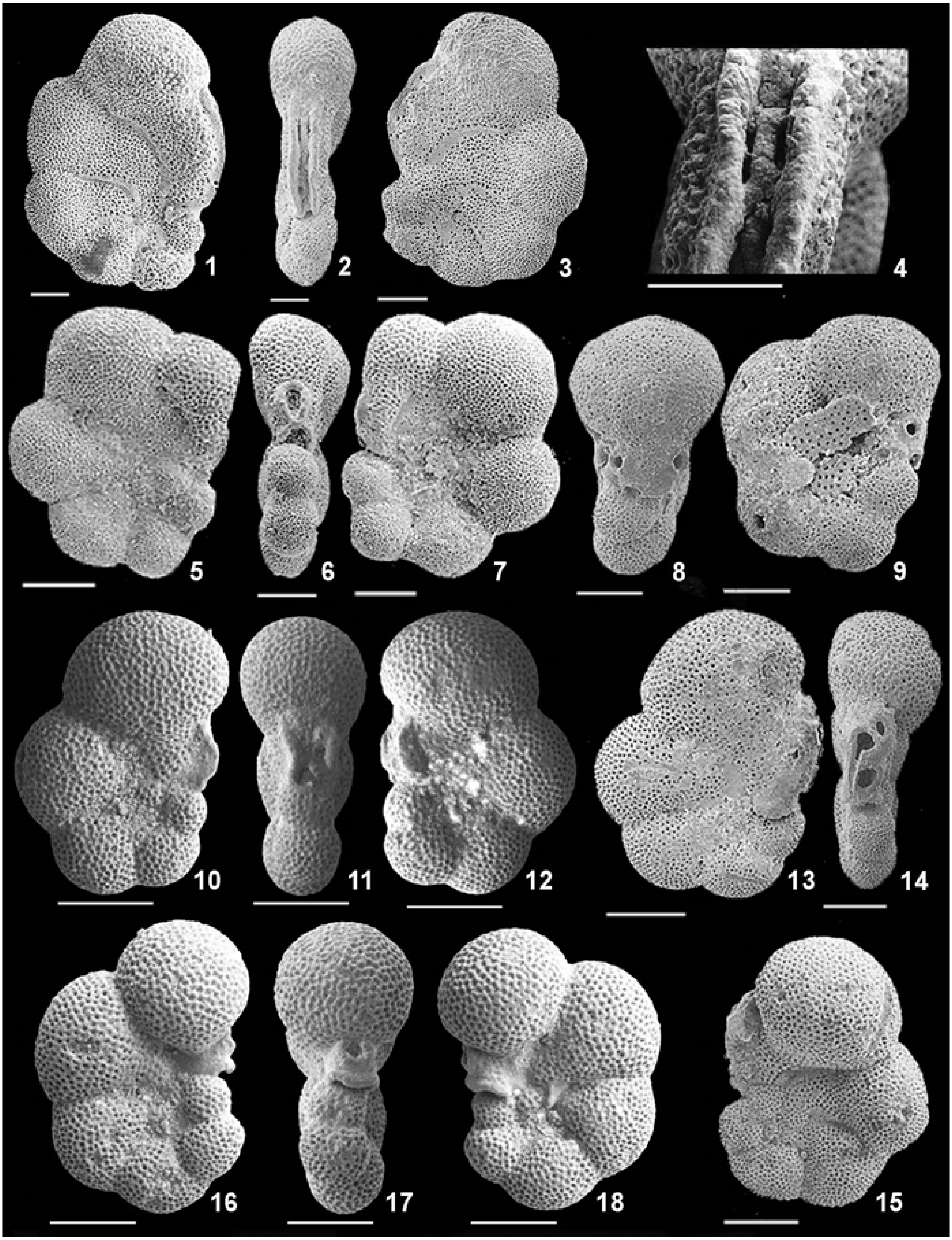

Plate 4.13 *Protentelloides dalhousiei* Zhang and Scott, 1995

the ancestor of *Clavatorella bermudezi*. It is easy to see the morphological resemblance but a direct connection to *C. bermudezi* seems unlikely since that taxon does not appear until the early Miocene, approximately 7 million years after the *Protentelloides* horizon, and intermediates between *Globorotaloides hexagonus* and *C. bermudezi* have been described (Pearson, 1995). We suggest *Protentelloides dalhousiei* represents a sub-clavate homeomorph of *C. bermudezi*.

Protentelloides dalhousiei **Zhang and Scott, 1995**

Plate 4.13, Figures 1-18

Protentelloides dalhousiei Zhang and Scott, 1995:77, pl. 1, figs. 12a-d [upper Oligocene Zone P22, DSDP Hole 366A, eastern equatorial Atlantic Ocean].

Clavatorella aff. *C. oveyi* Buckley, 1974.—Spezzaferri, 1994:50, pl. 36, figs. 5a-c and 6a-c [upper Oligocene Zone P22, ODP Hole 667A, eastern equatorial Atlantic Ocean].

DESCRIPTION.

Type of wall: Normal perforate, coarsely cancellate, *sacculifer*-type to *ruber/sacculifer*-type. Possibly spinose. Pore density: ~40 pores/50 μm^2.

Test morphology: Laterally compressed, evolute, low trochospiral/pseudoplanispiral, strongly lobate; 2-2½ whorls, 5 rounded chambers in the innerwhorl, 5-6 chambers in the final whorl, increasing very rapidly in size, rounded at first with the final 3-4 becoming radially elongate to comma-shaped, final chamber maybe reduced in size, bulla-like, centered at the equatorial margin, variable in morphology; spiral view, sutures depressed, straight between early chambers, becoming curved and later sigmoidal, pre-adult whorls visible, flattened into center; umbilical view, sutures radial, depressed, straight, becoming curved to sigmoidal, small but deep umbilicus; primary aperture equatorial to slightly umbilical, highly variable in morphology: an elongated equatorial slit or low arch at the base final chamber with one ray extending into the umbilicus, bordered by an imperforate rim that may be elongated into a protruding lip; the primary aperture may occur with or without one or more rimmed circular to elongated accessory openings ('cribrate') within the final chamber or apertural lip, or along the equatorial face where converging apertural lips divide the primary opening.

Size: The maximum diameter of the holotype as figured by Zhang and Scott (1995) is 0.675 mm. All new observations of this species and its close relative *P. primitivus* are considerably smaller.

DISTINGUISHING FEATURES.— *Protentelloides dalhousiei* is a rare but conspicuous species. It differs from *Protentelloides primitivus* from which it evolved in the more evolute coiling, near-planispiral coiling, less conspicuous inner whorl, equatorially centered final chamber and primary aperture, and the great variability and complexity of the apertural system, including the tendency to become 'cribrate'. It differs from all other globorotaloidids in the tendency to form a cribrate aperture system. It can also be distinguished from *Globorotaloides hexagonus*, to which some forms bear a close resemblance, by its tendency to possess an equatorial-umbilically positioned bulla-like final chamber. Also by the nature of the primary aperture, which possess distinctive lips, as well as, commonly, accessory apertures. There is a tendency for the final chambers of *P. dalhousiei* to become slightly radially elongate, but as not dramatically as in *Clavatorella bermudezi* Blow, 1965, and *Protentella* Lipps, 1964.

DISCUSSION.— This species exhibits a very wide range of morphological variability in the shape of the final chamber or bulla and the structure and complexity of the aperture system. The test is superficially planispiral (pseudoplanispiral), however, unlike Eocene *Hantkenina* and *Pseudohastigerina* that are truly planispiral (biumbilicate), umbilical and spiral sides are recognizable due to asymmetry of the apertural lip on the two sides, which rotates slightly into the umbilicus. *Protentelloides dalhousiei* has a similar wall texture to *G. atlanticus*. Pore density in *P. dalhousiei* is much lower than in *G. variabilis* and *G. stainforthi.*

Like its ancestor *Protentelloides primitivus*, this taxon has not been recorded since its description in 1995, or outside its type locality in the eastern equatorial

Plate 4.13 *Protentelloides dalhousiei* Zhang and Scott, 1995

1-4 (holotype of *Protentelloides dalhousiei*, Zhang and Scott, 1995, pl. 1, fig. 12a-d) Zone P22 (O7), DSDP Sample 366A/28/6, 133-137 cm, Sierra Leone Rise, equatorial Atlantic Ocean; **5-9**, Zone P22 (O7), DSDP Sample 366A/28/6, 133-137 cm, Sierra Leone Rise, equatorial Atlantic Ocean, (5-7, paratype, Zhang and Scott, 1995, pl. 1, fig. 9a-c, 8-9, paratype, Zhang and Scott, 1995, pl. 1, fig. 4a-c); **10-12**, **16-18**, Zone O6/O7, ODP Sample 667A/33/1, 60-64 cm, Sierra Leone Rise, equatorial Atlantic Ocean; **13-15**, (topotype of *Protentelloides dalhousiei*, Zhang and Scott, 1995, pl. 1, fig. 8a-c). Scale bars: **1-3**, **5-18** = 100 µm, **4** = 50 µm.

Atlantic Ocean. We recognize it as a distinct species that represents a branch of the *Globorotaloides* lineage. Described from DSDP Site 366 (Zhang and Scott, 1995), this morphology was recorded informally as *Clavatorella* aff. *C. oveyi* Buckley by Spezzaferri (1994) from the equivalent level (Zone O7) in ODP Site 667, 150 km to the northeast of Site 366. The Site 366 sequence has been restudied for the purposes of this work. Together with *Protentelloides primitivus, P. dalhousiei* has been suggested as an accessory marker for recognizing the Oligocene/Miocene boundary in tropical settings (Zhang and Scott, 1995) (see below), however, this is of limited use because it has not been found elsewhere (e.g. Leckie and others, 1993; Spezzaferri, 1994; Pearson and Chaisson, 1997). Moreover, Spezzaferri (1994) who recorded this morphotype as *Clavatorella* aff. *C. oveyi* at nearby ODP Site 677, indicate the range of *Protentelloides* (species undifferentiated) to extend sporadically across the Oligocene/Miocene boundary up to Zone N4 (lower Miocene Zone M1 of Berggren and others, 1995).

Zhang and Scott (1995) tentatively suggested *Protentelloides dalhousiei* as the ancestor of *Clavatorella bermudezi* (Bolli). This is based on a single specimen of *C. bermudezi* recorded (not illustrated) occurring 8-9 m above the highest occurrence of *Protentelloides* spp. in DSDP Hole 366A, still within Zone O7 (Zhang and Scott, 1995:82, Table 1). Oligocene to Miocene biostratigraphic studies of DSDP Hole 366A by Krasheninnikov and Pflaumann (1977), however, record '(rare) *C. bermudezi* only' in the upper part of the lower Miocene (*Praeorbulina glomerosa* Zone) (= M4/M5, Berggren and others, 1995), and middle Miocene (*Orbulina suturalis-Globorotalia peripheroronda* and *Globorotalia peripheroacuta* zones = M6), which is consistent with the range of this species based on observations from other sites (Quilty, 1976; Spezzaferri, 1994; Pearson and Chaisson, 1997). The single specimen is described as being "well-preserved…and… thin-walled" (Zhang and Scott, 1995:82). This is inconsistent with the heavily cancellate wall of *Clavatorella* and is instead suggestive of Quilty's (1976) species *Quiltyella nazcaensis* described from the Oligocene (Zones N2-N4 = O4-O7 of Wade and others, 2011) in the equatorial Pacific Ocean (see Chapter 6, this volume). Based on this reasoning we conclude that the range of *Protentelloides* and *C. bermudezi* do not overlap, and thus, that *P. dalhousiei* is not the ancestor of *C. bermudezi* but that Zhang and Scott's (1995) specimen is a rare, protentelloidid homeomorph (as indicated by the higher stratigraphic range of the morphotype recorded at Site 667, Spezzaferri, 1994) or possibly *Quiltyella nazcaensis,* which is related to *Globigerinella* (see Chapter 6, this volume). This trend of becoming digitate, as we presume Zhang and Scott's *C. bermudezi* to be, occurs repeatedly in a variety of Eocene to Recent low latitude tropical taxa (Coxall and others, 2007).

PHYLOGENETIC RELATIONSHIPS.— *Protentelloides dalhousiei* evolved from *Protentelloides primitivus*.

TYPE LEVEL.— Zone O7 (upper P22) (Zhang and Scott, 1995).

STRATIGRAPHIC RANGE.— Zhang and Scott (1995) report a short range for *Protentelloides primitivus* (~0.45 million years) restricted to Zone O7 (Spezzaferri, 1994; Zhang and Scott, 1995). At DSDP Site 366 Zhang and Scott (1995) recorded the first occurrence of *Protentelloides dalhousiei* stratigraphically above the first occurrence of *Protentelloides primitivus* with the two disappearing simultaneously ~0.5 million years before the origin of *Paragloborotalia kugleri*. This led the authors to suggest this bioevent as an accessory marker for recognizing the Oligocene/Miocene boundary in tropical settings (Zhang and Scott, 1995). Spezzaferri (1994), however, recorded this morphotype as *Clavatorella* aff. *C. oveyi* at nearby ODP Site 677, extending the range of *Protentelloides* (species undifferentiated) up to Zone N4 (=lower Miocene Zone M1), i.e. above the first appearance of *Paragloborotalia kugleri*. This is confirmed by our latest studies of this core.

GEOGRAPHIC DISTRIBUTION.— So far found only in the eastern equatorial Atlantic Ocean.

STABLE ISOTOPE PALEOBIOLOGY.— *Protentelloides dalhousiei* registers positive δ^{18}O and negative δ^{13}C compared to other species indicating a deep sub-thermocline habitat (Spezzaferri and Coxall, unpublished) consistent with many other independently evolved flattened, clavate forms (Coxall and others, 2007).

REPOSITORY.— The type reference lists USNM collection numbers for the type specimens (holotype USNM 486366 and 7 paratypes USNM 486367-486375), however, these were not deposited at the Smithsonian Museum of Natural History, Washington, D.C. as intended (B. Huber, pers. comm.).

Protentelloides primitivus Zhang and Scott, 1995

Plate 4.14, Figures 1-18

Protentelloides primitiva Zhang and Scott, 1995:77, pl. 1, figs. 1a-d [upper Oligocene Zone P22, DSDP Hole 366A, eastern equatorial Atlantic Ocean].

DESCRIPTION.

Type of wall: Normal perforate, coarsely cancellate, *sacculifer*-type to *ruber/sacculifer*-type. Possibly spinose. Pore density: ~40 pores/50 μm^2.

Test morphology: Large, lobate to strongly lobate, laterally compressed, low trochospiral/pseudoplanispiral, 2 whorls, axial periphery rounded; internal whorl 4-5 rounded chambers, well-defined and clearly visible in spiral view, 4-6 chambers in the final whorl, increasing rapidly in size, final chamber reduced and bulla-like, variably cantilevered slightly towards the umbilical or spiral side; spiral sutures depressed, straight to curved; umbilical sutures radial, depressed, straight, becoming curved, small umbilicus; primary aperture an elongated slit at the base of the bulla-like final chamber extending from the equatorial margin to the umbilicus, bordered by an imperforate rim or well-defined lip.

Size: The maximum diameter of the holotype as figured by Zhang and Scott (1995) is 0.52 mm.

DISTINGUISHING FEATURES.— Large and distinctive, *Protentelloides primitivus* differs from *Globorotaloides atlanticus* n. sp., from which it evolved, by the more irregularly shaped and inflated chambers, the deeply depressed sutures, more lobate peripheral outline and the distinctly equatorial position of the terminal bulla-like chamber. It differs from *Globorotaloide*s *hexagonus* (Natland) in possession of a bulla and the equatorial-umbilical aperture. It is distinguished from *Protentelloides dalhousiei* in the slightly more involute coiling, the transitional position of the primary aperture, which is umbilical to extraumbilical, and in lacking accessory apertures. It also typically has fewer chambers in the final whorl than *P. dalhousiei.* It differs from *Protentella prolixa* Lipps (1964) in the lower stratigraphic range, possession of a bulla-like final chamber and the coarse cancellate wall. The tendency towards elongation of the final chamber represents another example of evolutionary convergence on a digitate form.

DISCUSSION.— We change the species name to its masculine form to accord with Article 31.2 of the ICZN ("a species-group name, if it is or ends in a Latin or latinized adjective or participle in the nominative singular, must agree in gender with the generic name with which it is at any time combined"). Thus *Protentelloides primitiva* becomes *P. primitivus. Protentelloides primitivus* has a similar wall texture to the proposed ancestor *G. atlanticus*. Pore density is much lower than in *G. variabilis* and *G. stainforthi.* Longer ranging than its descendant, it exhibits a wide range of morphological variability in both the number of final whorl chambers and the nature of coiling. The morphologies assigned to this morphospecies clearly shows overlap with *P. dalhousiei.* We choose to separate the two due to the slightly higher stratigraphic appearance of forms that consistently have near-planispirally coiled and an elaborate aperture system. There are no published occurrences of this taxon since its description in 1995. In our recent studies of Oligocene material we find it in ODP Site 667, which is near to DSDP Site 366, but not outside of the eastern equatorial Atlantic Ocean where these two sites lie.

PHYLOGENETIC RELATIONSHIPS.— *Protentelloides primitivus* evolved from *Globorotaloides atlanticus* n. sp. by compression and radial spreading of the test and migration of the bulla-like chamber from the umbilicus to the equatorial periphery. It gave rise to *Protentelloides dalhousiei* by development of the equatorially centered bulla.

TYPE LEVEL.— Upper Oligocene Zone O7 (= upper P22).

STRATIGRAPHIC RANGE.— Zhang and Scott (1995) report a short range for *Protentelloides primitivus* (~1.3 myr range), restricted to upper Oligocene Zone O7 (upper P22) (Spezzaferri, 1994; Zhang and Scott, 1995). Our recent studies based on ODP Site 667 material suggest this range can be extended into the early Miocene (Zone M1) (Fig. 4.1).

GEOGRAPHIC DISTRIBUTION.— So far found only in the eastern equatorial Atlantic Ocean.

STABLE ISOTOPE PALEOBIOLOGY.— No data available.

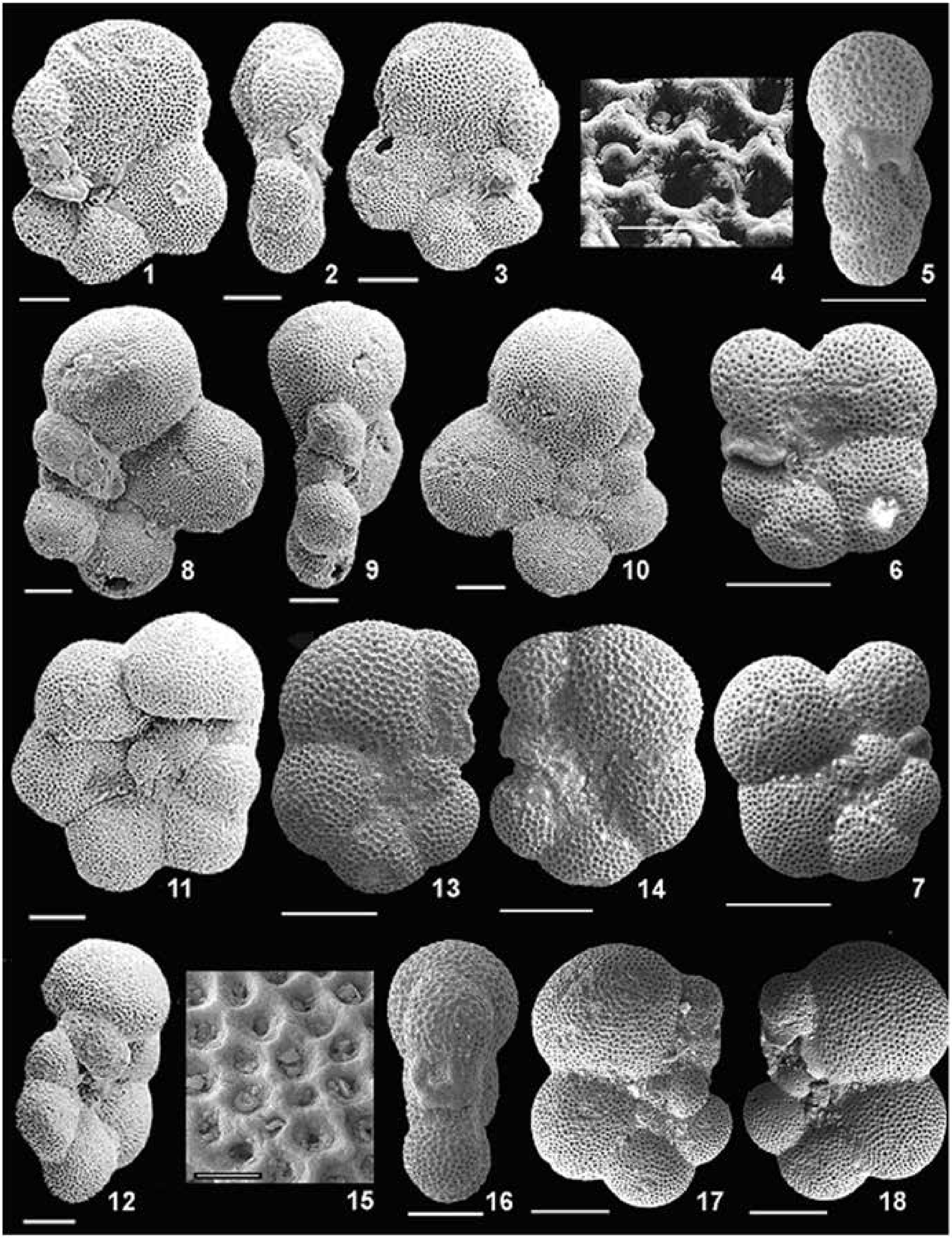

Plate 4.14 *Protentelloides primitivus* Zhang and Scott, 1995

REPOSITORY.— The type reference lists USNM collection numbers for the type specimens (holotype USNM 486363 and paratypes USNM 486364 and 486365), however, these are not in the collection and apparently were not deposited at the Smithsonian Museum of Natural History, Washington, D.C. as intended (B. Huber, pers. comm.). We have been unable to track down the type species via the original author.

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Plate 4.14 *Protentelloides primitivus* Zhang and Scott, 1995

1-4 (holotype of *Protentelloides primitiva,* Zhang and Scott, 1995, pl. 1, fig. 1a-d) Zone P22, ODP Sample 667A/33/1, 60-64 cm, Sierra Leone Rise, eastern equatorial Atlantic Ocean; **5-7**, **13-16**, **17**, **18**, upper Zone P22 (= O7), same sample as holotype; **8-10**, **11**, **12**, (paratypes 1 and 2 respectively of *Protentelloides primitiva,* Zhang and Scott, 1995, pl. 1, fig. 2a-c, and pl. 1. fig. 3a-c), Zone P22, DSDP Sample 366A/28/6, 133-137 cm, Sierra Leone Rise, eastern equatorial Atlantic Ocean. Scale bars: **1-3**, **5-14** and **16-18** = 100 µm, **4** and **15** = 10 µm.

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