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Chapter 11

TAXONOMY, BIOSTRATIGRAPHY, AND PHYLOGENY OF OLIGOCENE AND LOWER MIOCENE *DENTOGLOBIGERINA* AND *GLOBOQUADRINA*

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ABSTRACT

The taxonomy, phylogeny, and biostratigraphy of Oligocene and lower Miocene *Dentoglobigerina* and *Globoquadrina* are reviewed. Because of the discovery of spine holes in various species assigned to these genera, the entire group is now considered to have been fully or sparsely spinose in life and hence part of Family Globigerinidae. One new species, *Dentoglobigerina eotripartita* Pearson, Wade, and Olsson n. sp., is named. *Dentoglobigerina* includes forms with and without umbilical teeth and species for which the presence or absence of a tooth is a variable feature. A significant finding has been the triple synonymy of *Globigerina tripartita* Koch, *Globigerina rohri* Bolli, and *Globoquadrina dehiscens praedehiscens* Blow, which greatly simplifies part of the taxonomy. The genus *Globoquadrina* is restricted to its type species, *Globigerina dehiscens* Chapman and others. The following species from the time interval of interest are regarded as valid: *Dentoglobigerina altispira* (Cushman and Jarvis), *Dentoglobigerina baroemoenensis* (LeRoy), *Dentoglobigerina binaiensis* (Koch), *Dentoglobigerina eotripartita* Pearson, Wade, and Olsson n. sp., *Dentoglobigerina galavisi* (Bermúdez), *Dentoglobigerina globosa* (Bolli), *Dentoglobigerina globularis* (Bermúdez), *Dentoglobigerina juxtabinaiensis* Fox and Wade, *Dentoglobigerina larmeui* (Akers), *Dentoglobigerina prasaepis* (Blow), *Dentoglobigerina pseudovenezuelana* (Blow and Banner), *Dentoglobigerina sellii* (Borsetti), *Dentoglobigerina taci* Pearson and Wade, *Dentoglobigerina tapuriensis* (Blow and Banner), *Dentoglobigerina tripartita* (Koch), *Dentoglobigerina venezuelana* (Hedberg), and *Globoquadrina dehiscens* (Chapman, Parr, and Collins). The genus *Dentoglobigerina* also comprises other Neogene/Quaternary species not listed, including the living species *Dentoglobigerina* cf. *conglomerata* (Schwager).

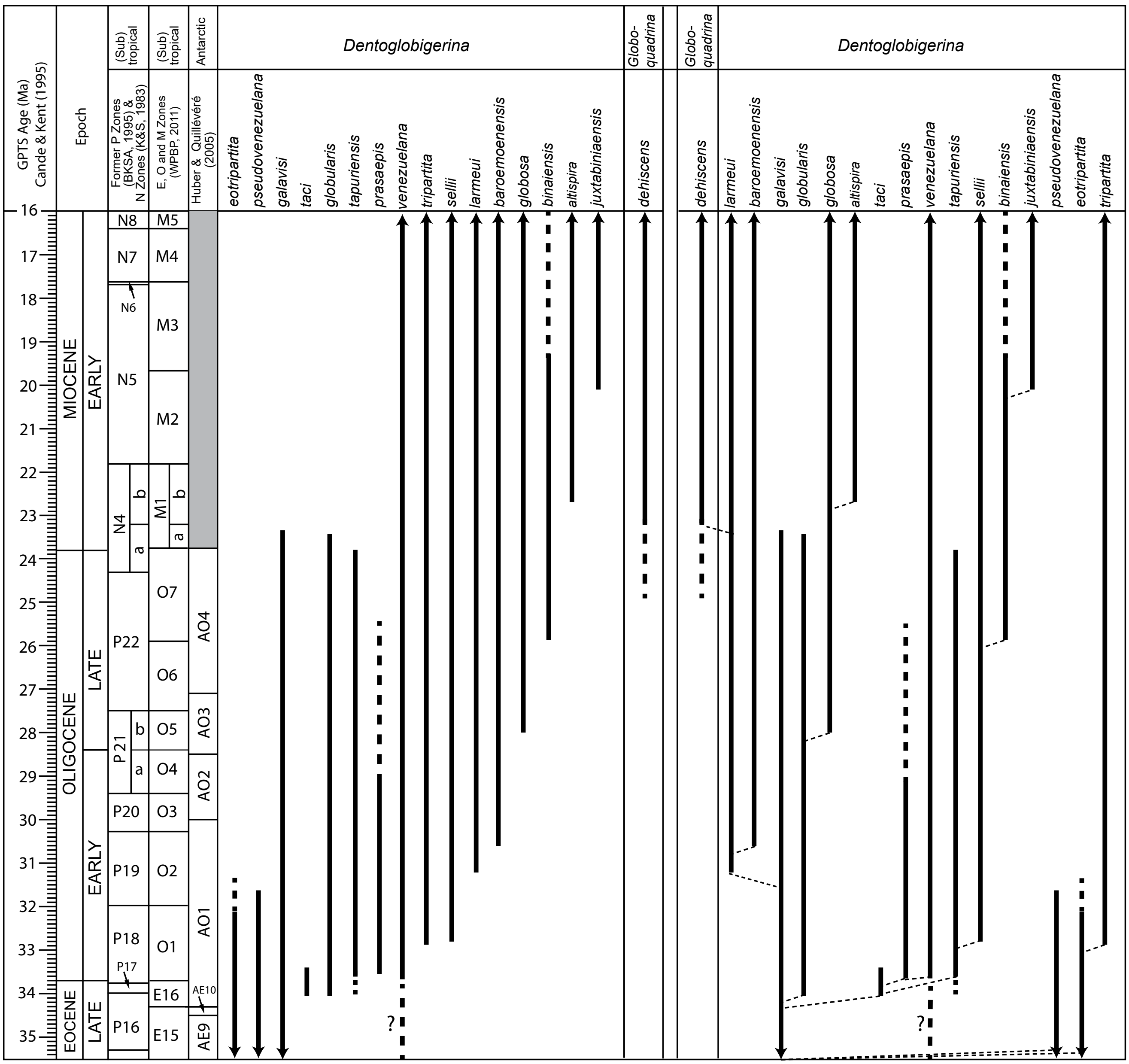

FIGURE 11.1. Stratigraphic ranges and inferred phylogenetic relationships of Eocene to early Miocene species of *Dentoglobigerina* discussed in this chapter. BKSA, 1995 = Berggren and others, 1995; K&S, 1983 = Kennett and Srinivasan, 1983; WPBP, 2011 = Wade and others, 2011.

INTRODUCTION

The dentoglobigerinids are an important group of species that range from the middle Eocene to Recent, but are most diverse in the Oligocene and lower Miocene, where they can dominate the larger size fraction of planktonic foraminiferal assemblages. They are however, a difficult group taxonomically because of their relatively generalized morphology combined with high levels of variation between individuals and evolutionary convergence between species and more distantly related forms in other genera. The taxonomic history of many of the species is, therefore, unusually complex. We hope that by resolving some of these issues we will provide a firm foundation for future use of the group in biostratigraphy, which has hitherto been limited.

Our concept of the group, the species to be included, and its relationship to other groups, has evolved substantially during the course of our research and differs strongly from the original concept of *Dentoglobigerina* as articulated by Blow (1979). He essentially used it as a convenient form-genus – for planktonic foraminifera of generally globigeriniform morphology, possessing an umbilical tooth – and consequently included within it a variety of only distantly related species, while at the same time excluding closely related forms that lack a tooth. According to our concept, *Dentoglobigerina* is an evolving clade of species united by large globular test construction, a tendency for closely appressed chambers that lean towards the umbilicus in edge view, and a distinctive cancellate-pustulose and sparsely spinose to fully spinose wall texture. Despite the etymology, species may or may not possess an umbilical tooth and in some species the presence or absence of a tooth varies between individuals.

No treatment of the *Dentoglobigerina* group can avoid the fact that repetitive evolutionary trends and high levels of homeomorphy occur in different parts of the evolutionary radiation. The taxonomy presented here, is based not only on careful consideration of the morphologies and wall textures of the various species, but also an appreciation of the often high levels of intraspecific variability, and how populations change stratigraphically helping to trace out lineages through time. The main evolutionary trends that occur in this group are in some instances parallel (occurring at similar times) or iterative (occurring at different times). These often involve increasing size, sphericity of the test, and/or angularity of the chambers.

The species level range chart and phylogenetic relationships of late Eocene through early Miocene *Dentoglobigerina* and *Globoquadrina* are shown in Figure 11.1. All the main lineages have their ultimate origin in the ancestral form *D. galavisi*, which is a relatively small and generalized form, although it possesses the typical degree of chamber compression and appression that characterizes almost the whole group. The main lineages we observe are as follows:
galavisi-pseudovenezuelana-eotripartita-tripartita; showing an increase in size and a trend to more spherical morphology.

galavisi-taci-prasaepis-venezuelana; similarly showing an increase in size and sphericity.

galavisi-taci-tapuriensis-sellii-binaiensis-juxtabinaiensis; showing initially an increase in size and sphericity, and in the later part an increase in the angularity of the chambers and flattening of the apertural face.

galavisi-globularis-globosa-altispira; becoming larger, more angular, higher spired and developing a more open umbilicus.

galavisi-larmeui-baroemoenensis; becoming larger, more angular and with a more open umbilicus.

galavisi-larmeui-dehiscens; developing a flattened apertural face and more prominent tooth.

Stable isotope data indicate dentoglobigerinids were consistent in their relatively deep thermocline habitat, although some species (e.g., *D. venezuelana*) may have lived in shallower depths during the pre-adult phase. There is no evidence to date of a photosymbiotic association in Oligocene dentoglobigerinids. Hence, it is likely that the group specialized in carnivorous predation of arthropods around the level of the deep chlorophyll maximum. Variations in apertural morphology may be related to differences in feeding strategy. The group has its highest diversity in oligotrophic tropical waters. *Dentoglobigerina* is a living genus with a single species alive today, *D.* cf. *conglomerata* (Schwager).

SYSTEMATIC TAXONOMY

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

DISCUSSION.— In the *Atlas of Eocene Planktonic Foraminifera* (Pearson and others, 2006), the genus *Dentoglobigerina* was included in the Family Globoquadrinidae Blow, 1979, because it was believed to have been nonspinose in life, and it was postulated that it may have descended from Eocene *Acarinina* (Olsson and others, 2006). The Miocene genus *Globoquadrina* is widely thought to have been closely related to the *Dentoglobigerina* (including by us; see discussion below, under that genus), and *Globoquadrina* has been regarded as another nonspinose form; indeed Steineck and Fleisher (1978) upheld it as the type example of their cancellate nonspinose wall texture. However, the Working Group investigations have produced evidence for spines or spine holes in many species of *Dentoglobigerina* as discussed in the appropriate sections below (see also Pearson and Wade, 2015). We now regard the entire group as belonging to the spinose Family Globigerinidae, and likely descended from the spinose genus *Subbotina* in the Eocene. We note that the spinosity of the wall can be incredibly variable, some groups of *Dentoglobigerina* may have been sparsely spinose or even lost their spines during their evolution. In should also be noted that in SEM images of many modern spinose species (e.g., *Globigerinoides ruber*, *Globigerinella siphonifera*), spine holes are not always evident due to gametogenic calcite. One group that may have lost its spines is the lineage leading to Miocene *Globoquadrina dehiscens*, although the absence of spines is difficult to demonstrate because it relies on negative evidence and could always be disproven by a counter-example. Because of these observations we now include Family Globoquadrinidae Blow, 1979 in synonymy with Family Globigerinidae Carpenter, Parker, and Jones, 1862 (see Chapter 4, this volume).

Genus *Dentoglobigerina* Blow, 1979

TYPE SPECIES.— *Globigerina galavisi* Bermúdez, 1961.

DESCRIPTION.

Type of wall: Cancellate, normal perforate, probably spinose or sparsely spinose in life, commonly pustulose in umbilical region.

Test morphology: Trochospiral, globular, rounded to lobulate in outline, final chamber leaning towards the umbilicus with an ill-defined apertural face in most species; weakly to coarsely pustulose with a concentration of pustules commonly seen around the umbilicus. Primary aperture umbilical, narrow to wide, commonly hidden in umbilical view, often with pustulose apertural lip or an asymmetrical triangular tooth, but in some species no tooth occurs, a bulla may be present, and is more common in late Oligocene and early Miocene forms.

DISTINGUISHING FEATURES.— *Dentoglobigerina* is distinguished from *Globoquadrina* by the more globular morphology, and by lacking the highly compressed chambers and quadrate test shape of that genus. *Dentoglobigerina* is distinguished from *Subbotina* by its less lobulate equatorial outline, more compressed chambers and commonly pustulose umbilical shoulders. According to Pearson and Wade (2015:17) “the chief difference is that the chambers [in *Dentoglobigerina*] are generally more compressed and more closely appressed than in *Subbotina*, with the test as a whole more tightly coiled. Characteristically, in edge view, the final chamber frequently appears flattened and leans over the umbilicus. There is also a much greater tendency toward pustulose wall texture, especially in the umbilical region”. The aperture in *Dentoglobigerina* is almost always (but not exclusively) umbilical, whereas many *Subbotina* species have an intra-extraumbilical aperture. In addition, the sutures in *Dentoglobigerina* are generally more weakly defined than in *Subbotina*.

DISCUSSION.— As discussed under Family Globigerinidae above, the Working Group now regards *Dentoglobigerina* as having been spinose in life, at least in its primitive condition. Fox and Wade (2013) illustrated spine holes in the Miocene species *D. juxtabinaiensis* and Pearson and Wade (2015) illustrated spine holes or possible spine holes in *D. galavisi*, *D. pseudovenezuelana*, *D. taci*, *D. tapuriensis*, and *D.* cf. *tripartita* (= *D. eotripartita* n. sp. in this work). Here we present additional evidence for spine holes in *D. baroemoenensis*, *D. larmeui*, and *D. binaiensis*. Species for which spine holes have not yet been observed are: *D. globosa*, *D. globularis*, *D. prasaepis*, *D. sellii*, *D. tripartita*, *D. venezuelana* and *Globoquadrina dehiscens*. It seems that some species in the genus may have been quite densely spinose in life while others were sparsely spinose or even secondarily nonspinose (i.e., lost spines during their evolution).

Whereas Olsson and others (2006) suggested that *Dentoglobigerina* was derived from the muricate

Eocene genus *Acarinina*, we now think an origin in the spinose genus *Subbotina* is much more likely (see discussion under Family Globigerinidae above), as suggested previously for example by Blow (1979) and Bolli and Saunders (1985) (see also Pearson and Wade, 2015). The ancestral form could have been *Subbotina yeguaensis*, which frequently has an umbilical tooth, and could have given rise to *D. galavisi* in the middle Eocene (Zone E12).

According to Blow's (1979) original definition, the genus requires a globigeriniform morphology and the presence of an umbilical tooth, hence the name *Dentoglobigerina*. However, observations of modern species e.g., *Dentoglobigerina* cf. *conglomerata* and the unrelated *Neogloboquadrina dutertrei* show that a tooth can vary greatly between individuals and is not always present. As discussed by Pearson and Wade (2015), Blow's definition would unite a variety of unrelated species and exclude some potentially closely related forms. Some *Dentoglobigerina* species (e.g., *galavisi*) consistently have a very prominent umbilical tooth, while in other species the tooth is generally absent (e.g., *tapuriensis*). Here we emphasize that the umbilical tooth is a variable character and should not be part of the generic diagnosis although it can help in identifying species. We follow Pearson and Wade (2015) by allowing forms without a tooth within the genus *Dentoglobigerina* but restricting it to *D. galavisi* and its likely descendants. We exclude various toothed forms with inflated, spherical chambers, which are better placed in *Subbotina* (see Chapter 10, this volume).

Several species of *Dentoglobigerina* are distinctly pustulose, particularly on the umbilical face, with a concentration of pustules in the umbilical region and on the umbilical shoulders. The pustules can be large and abundant, particularly in the species *D. sellii*.

PHYLOGENETIC RELATIONSHIPS.— The genus was probably derived from *Subbotina* in the middle Eocene, possibly *S. yeguaensis*, which shows closest morphological similarity to *D. galavisi*. The genus gave rise to *Globoquadrina* in the early Miocene.

STRATIGRAPHIC RANGE.— Middle Eocene (Zone E12) to Recent.

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

***Dentoglobigerina altispira* (Cushman and Jarvis, 1936)**

Globigerina altispira Cushman and Jarvis, 1936:5, pl. 1, fig. 13a-c [Miocene Bowden Marl, Jamaica].

DISCUSSION.— *Dentoglobigerina altispira* is a very common component of Miocene and Pliocene assemblages, first appearing in lower Miocene Subzone M1b (Kennett and Srinivasan, 1983; Chaisson and Leckie, 1993; Spezzaferri, 1994). This species descended from *D. globosa* in the earliest Miocene, and is distinguished from its ancestor by typically fewer chambers, a higher spire, a deeper umbilicus and slightly more angular chambers. We defer discussion of this species to future work on Neogene planktonic foraminifera but include it on the stratigraphic range-charts for completeness.

***Dentoglobigerina baroemoenensis* (LeRoy, 1939)**

Plate 11.1, Figures 1-16

Globigerina baroemoenensis LeRoy, 1939:263, pl. 6, figs. 1, 2 [holotype, Miocene, Rokan, Tapanoeli area, Sumatra, Indonesia].

Globoquadrina baroemoenensis (LeRoy).—Blow, 1969:340-341, pl. 28, fig. 8 [upper Oligocene Zone N3 = P22, Cipero Fm., Trinidad], pl. 28, fig. 4 [lower Miocene Zone N8, Cipero Fm., Trinidad].—Poore, 1979:470, pl. 18, figs. 8, 9 [lower Miocene Zone N7, DSDP Site 408, North Atlantic Ocean], figs. 10-12 [middle Miocene Zone N9-N11, DSDP Site 408, North Atlantic Ocean].—Blow, 1979, pl. 28, fig. 4 (reproduced from Blow, 1969, pl. 28, fig. 4).—Kennett and Srinivasan, 1983:186, pl. 46, figs. 1-3 [upper Miocene Zone N16, DSDP Site 289, western equatorial Pacific Ocean].—Berggren and others, 1983, pl. 1, fig. 12 [lower Miocene Zone N5, DSDP Site 516, Rio Grande Rise, southwest Atlantic Ocean].—Chaisson and Leckie, 1993:159 (partim), pl. 9, fig. 7 [lower Pliocene, ODP Hole 806B, Ontong Java Plateau, western equatorial Pacific Ocean].

Dentoglobigerina baroemoenensis (LeRoy).—Blow, 1979:763, 1300, pl. 28, fig. 8 (reproduced from Blow, 1969, pl. 28, fig. 8).—Spezzaferri and Premoli Silva, 1991:237, pl. 2, fig. 4a-c [lower Oligocene Subzone P21a, DSDP Hole 538A, Gulf of Mexico].—Spezzaferri, 1994:40, pl. 40, fig. 1a-c (reproduced from Spezzaferri and Premoli Silva, 1991, pl. 2, fig. 4a-c).—Fox and Wade, 2013:379, figs. 5.1, 5.2 [lower Miocene Zone Subzone M5a, IODP Hole U1338B, equatorial Pacific Ocean].

Globigerina baroemoenensis var. *quadrata* LeRoy, 1944:39, pl. 3, figs. 34-35; pl. 7, figs. 37-39 [lower and middle

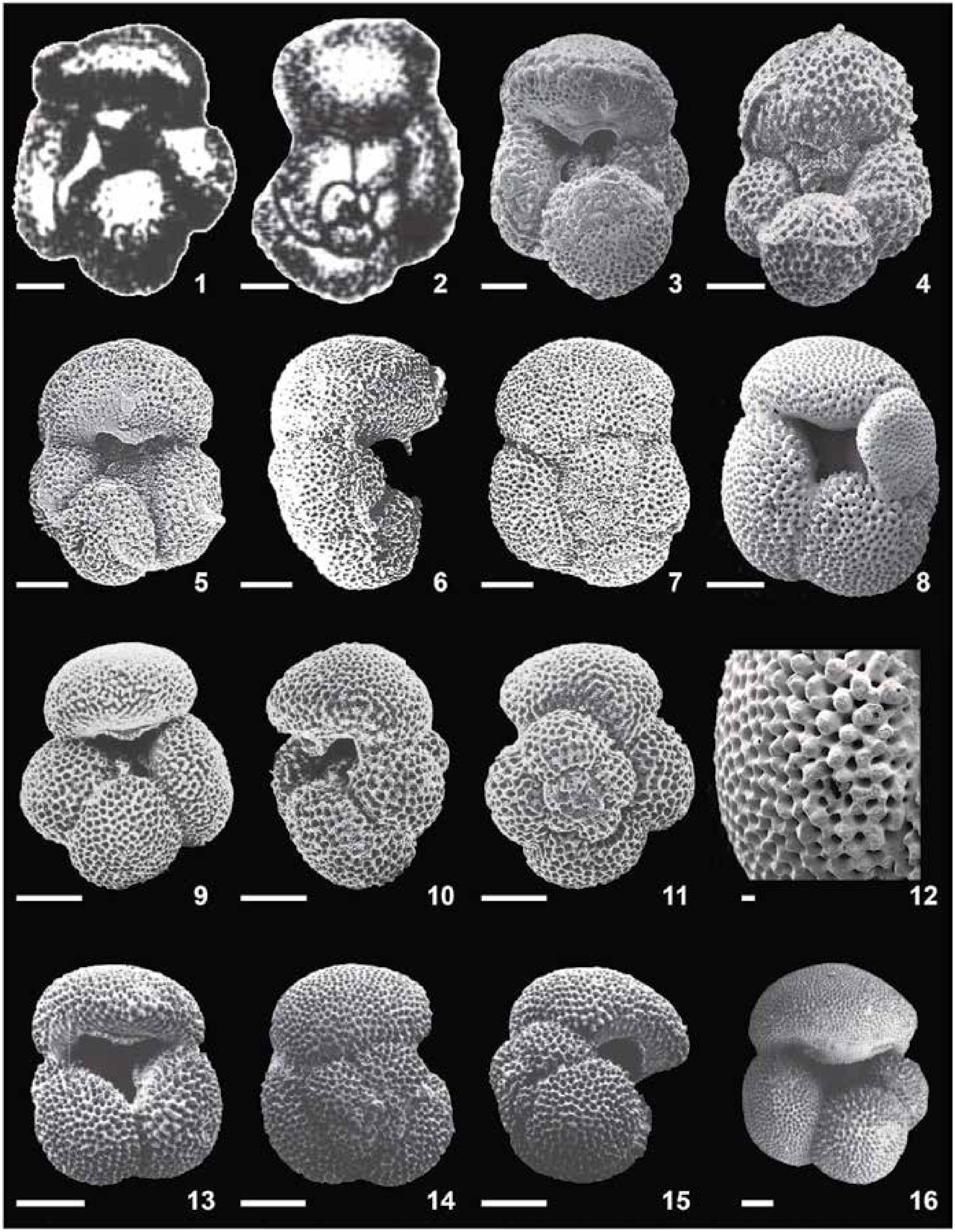

Plate 11.1 *Dentoglobigerina baroemoenensis* (LeRoy, 1939)

Miocene Telisa Fm., Sumatra, Indonesia].

Dentoglobigerina galavisi Bermúdez / *Globoquadrina baroemoenensis* (LeRoy) transition.—Spezzaferri and Premoli Silva, 1991:237, pl. 2, fig. 3a-c [lower Oligocene Subzone P21a, DSDP Hole 538A, Gulf of Mexico].

DESCRIPTION.

Type of wall: Normal perforate, cancellate, spinose in life.

Test morphology: Test a low trochospiral, trapezoidal in outline; in spiral view 4 (rarely 3) flattened, slightly reniform chambers, increasing gradually in size, sutures straight, weakly depressed; in umbilical view 3½-4 subspherical to slightly reniform chambers in ultimate whorl increasingly slowly in size, slightly disjunct at the sutures, ultimate chamber of the holotype with distinct sloping or near vertical perforated apertural face, may have a reduced bulla-like final chamber which extends over the umbilicus; umbilicus deep and broad, quadrangular, aperture a low arch set deep in the umbilicus beneath a broad tooth.

Size: Maximum diameter of holotype 0.50 mm (LeRoy, 1939).

DISTINGUISHING FEATURES.— *Dentoglobigerina baroemoenensis* is distinguished from *D. larmeui* by its more angular, disjunct and slightly reniform chambers and more trapezoidal outline, and by the broad, deep umbilicus. This species is distinguished from *Globoquadrina dehiscens* by its less quadrate / rectangular outline, less closely appressed chambers, and lacking the diagonal and mostly imperforate apertural face that is characteristic of that species. Typical of the lower and middle Miocene, it first appears in the upper Oligocene. It persists for many millions of years in assemblages alongside *G. dehiscens*, and the two forms tend to vary in size and degree of surface encrustation, making them sometimes easy and sometimes more difficult to distinguish. Kummerform individuals of *D. binaiensis* may also be easily confused. Kennett and Srinivasan (1983) considered *baroemoenensis* to be synonymous with *Globigerina conglomerata* Schwager (as discussed in Chaisson and Leckie, 1993). The former species, however, can be distinguished by the umbilical flattening of the apertural face and more reniform final chambers. *Dentoglobigerina venezuelana* has a more closed umbilicus and more embracing chambers.

DISCUSSION.— We have identified spine holes in this species (Pl. 11.1, Fig. 12). The holotype was deposited in the collection of the Javanese Geological Survey. It was reported to be present there by Blow (1969) (fide Dr H.S.N. Hartono), but we have been unable to locate it for our investigation, so we base our concept on LeRoy's type illustrations (see Pl. 11.1, Figs. 1, 2) which are similar to the specimens illustrated in Kennett and Srinivasan's (1983) influential Neogene atlas (reproduced in Pl. 11.1, Figs. 9-11). Those specimens, however, are more gracile in overall morphology and slightly less angular than the holotype, with less prominent umbilical teeth.

Blow (1969) illustrated 'early' (pl. 28, fig. 8) and 'phylogenetically advanced' (pl. 28, fig. 4) specimens of *baroemoenensis*. The latter strongly resembles the holotype from the Miocene of Sumatra, while the former is nearly identical to the form illustrated by Spezzaferri (1994; pl. 40, fig. 1a-c) from the upper Oligocene, highlighting the variable nature of this taxon and, possibly, its evolutionary development.

Blow (1969) recognized that the high-spired paratypes deposited in the U.S. National Museum were not conspecific with the holotype, which we have confirmed with new SEMs (which are not shown here but are available at the U.S. National Museum website). Blow (1969) regarded *baroemoenensis* as a descendant of *galavisi*, with which we agree, although we regard *D. larmeui* as an intermediate morphotype. He recorded having observed the phyletic transition in samples from Trinidad, Barbados, Venezuela, Iran, and the Far East. Spezzaferri and Premoli Silva (1991) and Spezzaferri (1994) also described this transition.

LeRoy (1944) named a new subspecies, *Globigerina baroemoenensis quadrata*, from similar

Plate 11.1 *Dentoglobigerina baroemoenensis* (LeRoy, 1939)

1-2 (holotype; LeRoy, 1939, pl. 6 fig. 1, 2); Miocene (?), Telisa Fm., Rokan Tapanoeli area, Sumatra, Indonesia; **3**, **4** (Blow, 1969; pl. 28, figs. 4, 8); Zone N3 [= Zone O6 or lower O7], Cipero Fm., Trinidad); **5-7**, Zone O3/4, Sample DSDP 538A/10/4, 95-97 cm, Gulf of Mexico (Spezzaferri, 1994; pl. 40, figs. 1a-c); **8**, **12** (same specimen), Zone M1, Sample ODP 904/33/3, 34 cm, western North Atlantic Ocean; **9-11**, Zone N16 [= Zone M13, Sample DSDP 289/31/5, 83 cm, western equatorial Pacific Ocean (Kennett and Srinivasan, 1983, pl. 46, figs. 1-3); **13-15**, Zone N9-N11 [= Zone M6-M8], Sample DSDP 408/31/CC, North Atlantic Ocean (Poore, 1979, pl. 18, figs. 10-12); **16**, Zone N18-N19 [= Zone PL1-PL2], Sample ODP 806B/18H, Ontong Java Plateau, western equatorial Pacific Ocean (Chaisson and Leckie, 1993, pl. 9, fig. 7). Scale bar: **1-11**, **13-16** = 100 µm; **12** = 10 µm.

material in Java but here we include this variety in synonymy. The slightly more gracile form illustrated by the specimen in his plate 7, figs. 37-39, is close to the specimens illustrated by Kennett and Srinivasan (1983) as *baroemoenensis*, whereas the other specimen illustrated in his plate 3, figs. 34 and 35 is kummerform with slightly misleading gross morphology.

PHYLOGENETIC RELATIONSHIPS.— This species evolved from *Dentoglobigerina larmeui* by attaining more disjunct and angular chambers, a more trapezoidal outline and a deeper, wider umbilicus, features that seemingly become more pronounced in younger, Miocene age specimens.

STRATIGRAPHIC RANGE.— The oldest illustrated specimen of this species is from Zone O4 of the Caribbean (Spezzaferri and Premoli Silva, 1991) although the same authors recorded it as low as Zone P20 (=Zone O2), as also recorded by Blow (1969). Rögl (1985) restricted its occurrence to the lower Miocene of the Central Paratethys. According to Kennett and Srinivasan (1983) and various authors following their taxonomy, it persists to the end of the Miocene or basal Pliocene (Chaisson and Leckie, 1993), although its highest occurrence has not been studied as part of this investigation.

TYPE LEVEL.— The holotype is from the Neogene (?Miocene) of the Telisa Fm., in the Rokan Tapanoeli region of Sumatra, Indonesia; its precise level requires new study of the type material.

GEOGRAPHIC DISTRIBUTION.— So far identified mainly from tropical latitudes.

STABLE ISOTOPE PALEOBIOLOGY.— No data available.

REPOSITORY.— Deposited with the Javanese Geological Survey (P.S.1076a).

***Dentoglobigerina binaiensis* (Koch, 1935)**

Plate 11.2, Figures 1-16; Plate 11.3, Figures 1-16
(Pl. 11.2, Figs. 2-4: new SEMs of lectotype of *Globigerina binaiensis* Koch)
(Pl. 11.2, Figs. 5-16: new SEMs of paralectotypes of *Globigerina binaiensis* Koch)

Globigerina? *aspera* Koch, 1926:746, figs. 22a-23c [‘Middle Tertiary’ lower *Globigerina* marls, Binai-Atingdunok, Bulongan, East Borneo] (junior homonym of *Globigerina aspera* Ehrenberg).

Globigerina binaiensis Koch, 1935:558, *nomen novum* for *G. aspera* Koch, 1926 [‘Middle Tertiary’ lower *Globigerina* marls, Binai-Atingdunok, Bulongan, East Borneo].—Blow, 1969:316, pl. 13, figs. 1, 2 [uppermost Oligocene or lowermost Miocene Zone N3 (=P22) or basal Zone N4, Bakan Subis, Sarawak, Borneo].—Postuma, 1971:262, pl. on p. 263, 7 figs. [east Java, Indonesia].—Stainforth and others, 1975:254, fig. 106, nos. 1-3 [Oligocene, Sabah, northern Borneo], nos. 4, 5 (reproduced from Blow, 1969, pl. 13, figs. 1, 2), nos. 6a-7c (reproduction of *Globigerina aspera* Koch, 1926; holotype specimen 6a-c, specimen 7a-c designated as lectotype).—Bolli and Saunders, 1985:181, fig. 14, nos. 6-9 [SEMs of ‘topotypes’ = syntypes from the type sample], no. 10 (reillustration of holotype of *Globigerina*? *aspera* Koch, 1926, labeled as ‘holotype’).—Quilty, 1976:637, pl. 1, figs. 16, 17 [upper Oligocene / lower Miocene Zone N4, DSDP Site 320, Nazca Plate, southeastern Pacific Ocean].

Dentoglobigerina tripartita binaiensis (Koch).—Chaproniere, 1981:117, fig. 8Ea-c [upper Oligocene to lower Miocene Zone N3/4, Ashmore Reef No. 1 Well, northwest Australia].

Globoquadrina binaiensis (Koch).—Kennett and Srinivasan, 1983:182, pl. 45, figs. 1-3 [lower Miocene Zone N5, DSDP Site 289, Ontong Java Plateau, southwest Pacific Ocean].—Spezzaferri and Premoli Silva, 1991:248, pl. 9, figs. 6a-c [upper Oligocene Zone P22, DSDP Hole 538A, Gulf of Mexico].—Chaisson and Leckie, 1993:159, pl. 9, fig. 13 [lower to middle Miocene Zone N8/N9, ODP Hole 806B, Ontong Java Plateau, western equatorial Pacific Ocean].—Spezzaferri, 1994:42 (partim), pl. 42, figs. 3a-c (reproduced from Spezzaferri and Premoli Silva, 1991, pl. 9, figs. 6a-c) (not pl. 38, figs. 1a-d, pl. 42, figs. 4a-c (= *Dentoglobigerina juxtabinaiensis*).—Pearson, 1995:48, pl. 1, fig. 20 [lower Miocene Zone N4/5, ODP

Plate 11.2 *Dentoglobigerina binaiensis* (Koch, 1935)

1 (lectotype, reproduced from Koch, 1926, fig. 22a), ‘Middle Tertiary’, Binai-Atingdunok, East Borneo; **2-4** (lectotype), ‘Middle Tertiary’, Binai-Atingdunok, East Borneo; **5-7**, **8-10**, **11-13**, **14-16** (paralectotypes), ‘Middle Tertiary’, Binai-Atingdunok, East Borneo. Scale bar: **1-16** = 100 μm.

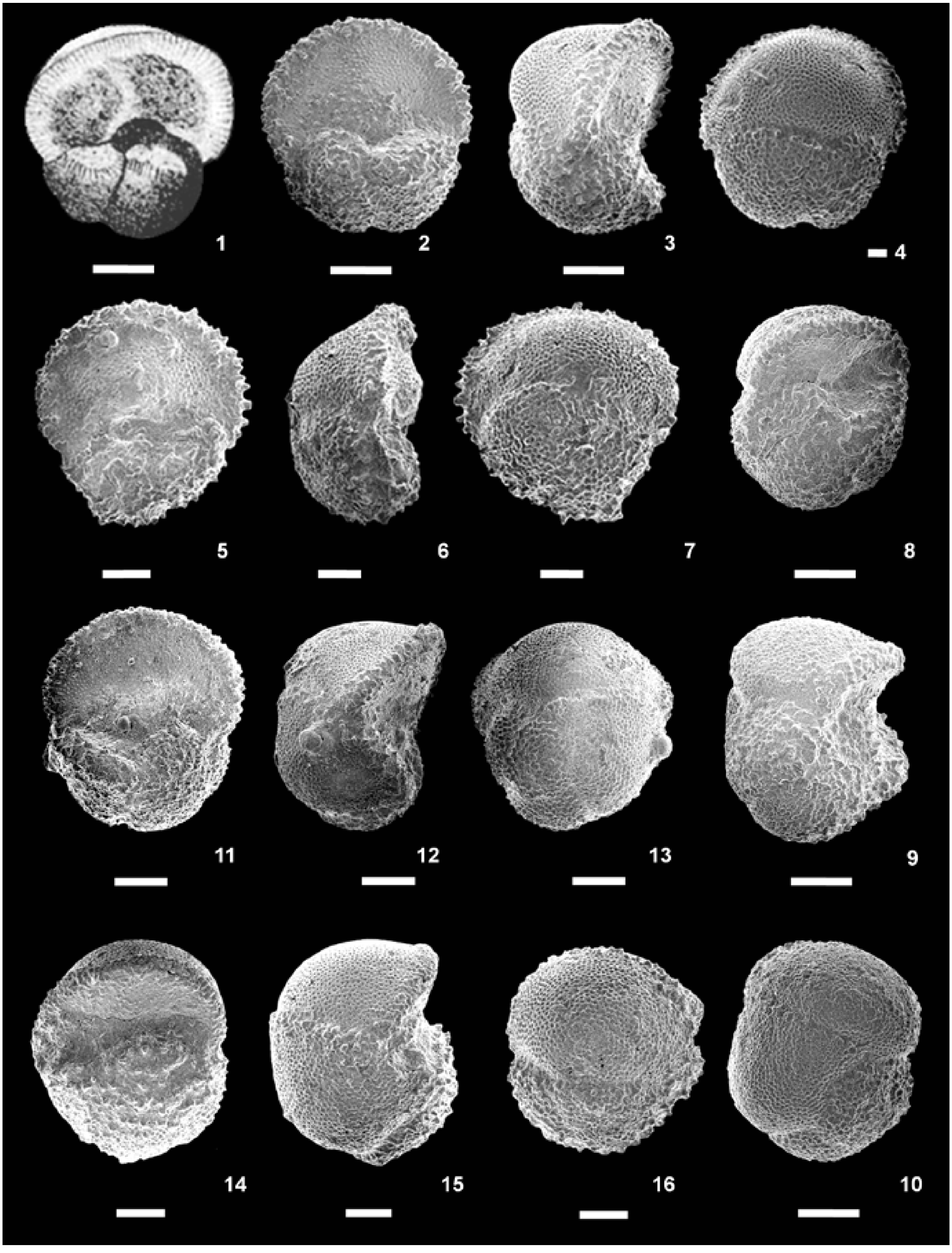

Plate 11.2 *Dentoglobigerina binaiensis* (Koch, 1935)

Hole 871A, Limalok Guyot, Marshall Islands, western equatorial Pacific Ocean].

Dentoglobigerina binaiensis (Koch).—Fox and Wade, 2013:379, figs. 5.3, 5.4 [lower Miocene Subzone M5a, IODP Hole U1338B, equatorial Pacific Ocean].

Not *Globigerina binaiensis* Krasheninnikov and Hoskins, 1973:124, pl. 6, figs. 1-3 (= *Dentoglobigerina juxtabinaiensis* Fox and Wade).

DESCRIPTION.

Type of wall: Normal perforate, weakly cancellate and densely pustulose, probably spinose in life.

Test morphology: Large, almost hemispherical; in umbilical view 3 embracing chambers in the ultimate whorl that rapidly increase in size, especially the final chamber which can be very large with a sharply angled apertural face making up to two-thirds of the test size, commonly with a bulla, smooth or reduced porosity and with a thickened pustulose rim, umbilicus low and broad, restricted, aperture umbilical, a low arch, occasionally with an umbilical tooth or deflection, umbilical sutures depressed, commonly highlighted by thickened pustulose chamber edges; in spiral view 3 embracing, elliptical chambers that rapidly increase in size in ultimate whorl, ultimate chamber makes up half of test size, sutures weakly depressed and sometimes highlighted by pustulose rims of previous chambers; in edge view convexo-concave, rounded spiral side and convex umbilical side. The cut-away shape of the final chamber is very distinctive in edge view.

Size: Maximum diameter of lectotype 0.32 mm.

DISTINGUISHING FEATURES.— *Dentoglobigerina binaiensis* is distinguished from its ancestor *D. sellii* by its larger final chamber and acutely cut-off apertural face as seen in side view, with reduced porosity or smooth areas on the apertural face, and by the enhanced thickened rims on the chamber shoulders. This species is distinguished from *Globoquadrina dehiscens* by being hemispherical in equatorial outline rather than quadrate, and by having 3 rather than 4 chambers per whorl. Kummerform specimens of *binaiensis* (i.e., lacking the large and distinctive final chamber) may resemble *dehiscens* quite closely and are best distinguished by the odd orientation of the final chamber and aberrant stepped sutures (e.g., Pl. 11.2, Figs. 14-16). See also under *D. juxtabinaiensis* for means of distinguishing that species.

DISCUSSION.— This species was first described by Koch (1926) as *Globigerina*? *aspera*. He illustrated two specimens that were deposited in the Natural History Museum, Basel, along with a range of unfigured specimens. These specimens (illustrated and un-illustrated) form the type series with the status of syntypes, because no specimen was specifically designated as a holotype. Koch later realized that the combination *Globigerina aspera* was already taken by Ehrenberg (1854) making it a junior homonym, and so renamed his species *binaiensis* after the type locality at Binai-Atingdunok (Koch, 1935).

According to Bolli quoted in Stainforth and others (1975: footnote on p. 254), one of the two illustrated syntypes had disintegrated hence they designated the other as the lectotype. This act made that specimen the name-bearing type and all other members of the type series (including the broken specimen) paralectotypes. Some ambiguity arises because Stainforth and others (1975) remarked that “the specimen illustrated by Koch as Figure 23a-c and reproduced here as 7a-c is the lectotype” whereas the one they illustrated as their Figure 7a-c is in fact the specimen illustrated by Koch as Figure 22a-c. This ambiguity was clarified by Bolli and Saunders (1985) who published a re-illustration of Koch’s first specimen, labeling it (incorrectly) as ‘holotype’ (should be lectotype), along with some SEMs of ‘topotype’ specimens from the type locality (which are in fact unfigured paralectotypes).

As part of this study we have borrowed the lectotype and additional unfigured paralectotypes of *binaiensis* from Koch’s collection in the Natural History Museum, Basel courtesy of M. Knappertsbusch, which clearly illustrate the nature of the species in SEM and its variability (Pl. 11.2). We note that Koch’s original drawing of the specimen that later became the lectotype (Pl. 11.2, Fig. 1) is slightly misleading in that the suture between the penultimate and antepenultimate chambers seems to be wrongly placed, and similar

Plate 11.3 *Dentoglobigerina binaiensis* (Koch, 1935)

1-4 (same specimen), **9-12** (same specimen), ODP Sample 871A/15H/1, 59-61 cm, Zone O7-M3, Limalok Guyot, western equatorial Pacific Ocean; **5-8** (same specimen), **16**, ODP Sample 871A/15H/2, 59-61 cm, Zone O7-M3, Limalok Guyot, western equatorial Pacific Ocean; **13-15** (same specimen), ODP Sample 871A/14H/2, 125-127 cm, Zone O7-M3, Limalok Guyot, western equatorial Pacific Ocean. Scale bar: **1-3**, **5-7**, **9-11**, **13-16** = 100 µm, **4**, **8**, **12** = 10 µm.

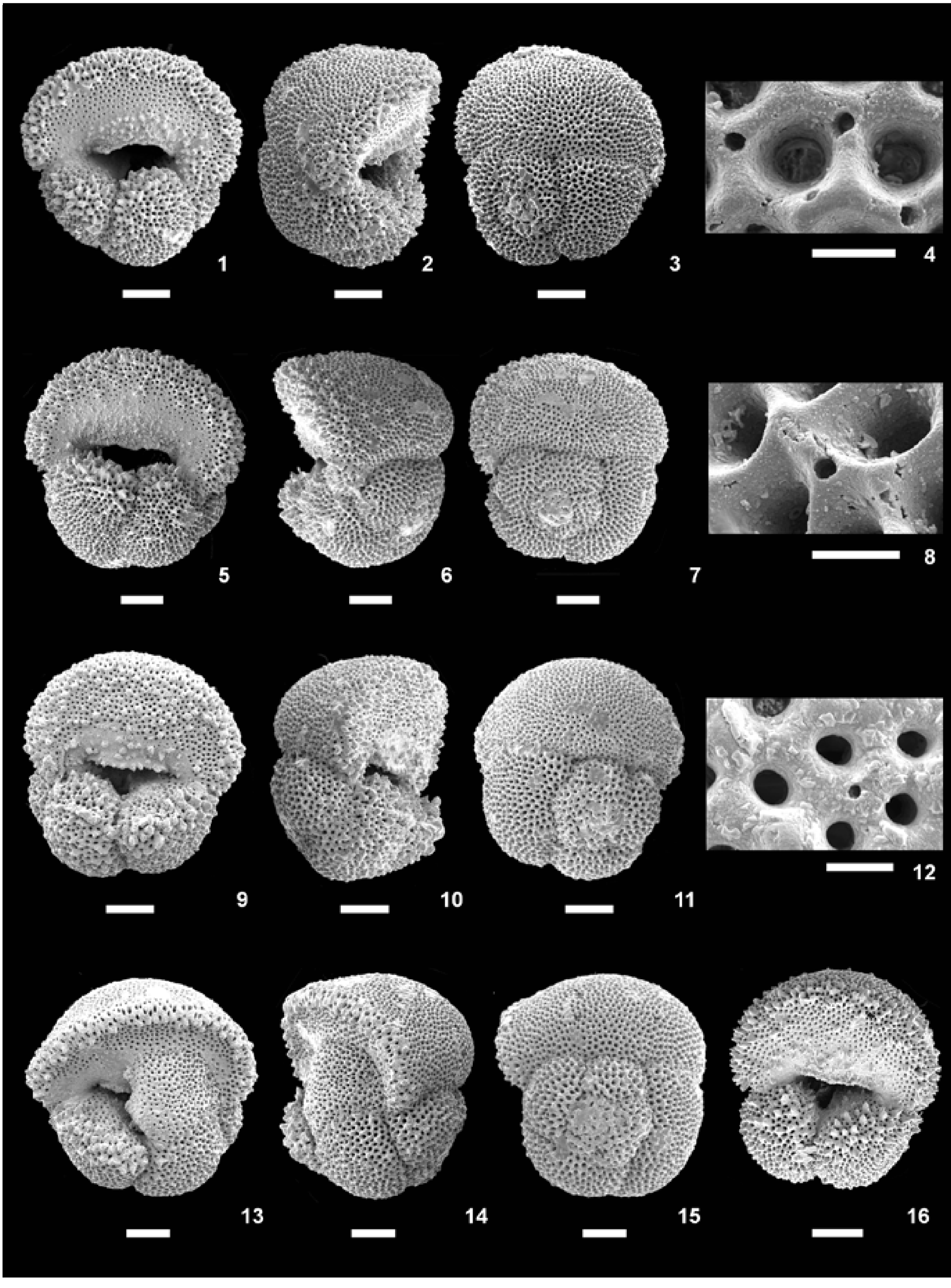

Plate 11.3 *Dentoglobigerina binaiensis* (Koch, 1935)

problems exist with the sutures on the spiral side drawing (not reproduced here). Despite this, the illustrations provided a reasonable idea of the species and formed the basis of a stable species concept for subsequent workers. The aperture is filled with sediment but its shape is faithfully represented in the illustration. The newly illustrated paralectotypes include two slightly kummerform individuals (Pl. 11.2, Figs. 8-10, 14-16) that are broadly homeomorphic with *Globoquadrina dehiscens*.

The type series and our new illustrations of specimens from the tropical Pacific Ocean (Pl. 11.3) show the variability of the aperture, which, like some other species of *Dentoglobigerina*, can vary from a simple unadorned arch to having an inflected pustulose rim or even a pointed tooth. Bullate specimens (e.g. Pl. 11.3, Figs. 13-15) are quite common if not frequently illustrated in the literature. There is no strong preference in coiling direction.

Dentoglobigerina binaiensis is a tightly coiled form with three chambers in the final whorl. Four chambered morphotypes referred by authors to this species that are more loosely coiled with a more open umbilicus are more appropriately referred to *Dentoglobigerina juxtabinaiensis* Fox and Wade (2013).

PHYLOGENETIC RELATIONSHIPS.— According to Blow (1969) and subsequent authors, this species evolved from *Dentoglobigerina sellii*, with which it intergrades in the upper Oligocene, as also observed in the studies of the Working Group.

STRATIGRAPHIC RANGE.— The lowest occurrence of this species is in upper Oligocene Zone N3 (=Zones O6/O7 of this work), as indicated by Blow (1969), Postuma (1971), and Bolli and Saunders (1985), among others. Spezzaferri (1994) recorded its lowest occurrence at the same level as the lowest occurrence of *Paragloborotalia pseudokugleri*, equivalent to the base of Zone O7 of this work. The highest occurrence has traditionally been recorded as within lower Miocene Zone N5 (=M2/M3) (e.g. Blow, 1969:316; Chaisson and Leckie, 1993); see also Spezzaferri (1994:43). At Ceara Rise, Pearson and Chaisson (1997) recorded its highest occurrence in the equivalent of Zone M3 (see also Wade and others, 2011) but noted it was "one of the least successful datums for correlation…a function of the extreme rarity of the species in the higher part of its range" (Pearson and Chaisson 1997:39). It is regrettable that such a distinctive species should make such a poor zone fossil.

TYPE LEVEL.— Described from the 'middle Tertiary' lower *Globigerina* marls of Borneo. According to Blow (1969), a 'near topotype' is 'from high Zone N3 (= P22) or basal Zone N4' = Zone O7 to Zone M1 of this work, hence probably close to the Oligocene/Miocene boundary.

GEOGRAPHIC DISTRIBUTION.— According to Blow (1969, caption to pl. 13) this species is restricted to the Indo-Pacific (see also Kennett and Srinivasan, 1983) but subsequent studies in the Atlantic Ocean and Gulf of Mexico (Spezzaferri and Premoli Silva, 1991; Pearson and Chaisson, 1997) show that it is global in low latitudes.

STABLE ISOTOPE PALEOBIOLOGY.— Pearson and Shackleton (1995) analyzed two samples of *D. binaiensis*, finding them to have oxygen isotope ratios significantly more positive than *Trilobatus trilobus* and *D. altispira*, indicating a thermocline depth habitat.

REPOSITORY.— Lectotype and paralectotypes deposited at the Natural History Museum, Basel, Switzerland.

***Dentoglobigerina eotripartita* Pearson, Wade, and Olsson, new species**

PLATE 11.4, FIGURES 1-15

Globigerina tripartita Koch.—Blow and Banner, 1962:96 (partim), pl. 10, figs. D-F [upper Eocene *Cribrohantkenina*

Plate 11.4 *Dentoglobigerina eotripartita* Pearson, Wade, and Olsson, new species

1-5, (holotype, NHMUK PM PF 71285), Zone E15/E16, Sample TDP12/42/1, 36-46 cm (Pearson and Wade, 2015, fig. 21.4a-e); **6-7**, (paratype, NHMUK PM PF 71286), Zone E15/E16, Sample TDP12/36/2, 66-70 cm (Pearson and Wade, 2015, fig. 21.6a-b); **8-10**, (paratype, NHMUK PM PF 71287), Zone E15/E16, Sample TDP12/42/1, 36-46 cm (Pearson and Wade, 2015, fig. 21.7a-c); **11**, (paratype, NHMUK PM PF 71288), Zone E16, Shubuta Clay, Wayne County, Mississippi; **12**, (Olsson and others, 2006, pl. 13.3, fig. 8), Zone E15/E16, Stakishari, Tanzania; **13**, (Pearson and Wade, 2015, fig. 21.5), Zone E15/16, Stakishari, Tanzania; **14**, (Blow, 1969, pl. 16, fig. 6), Zone P15, Tanzania; **15**, (Blow, 1979, pl. 244, fig. 4), Zone P16, Tanzania. Scale bar: **1-3**, **6-15** = 100 μm, **4**, **5** = 10 μm.

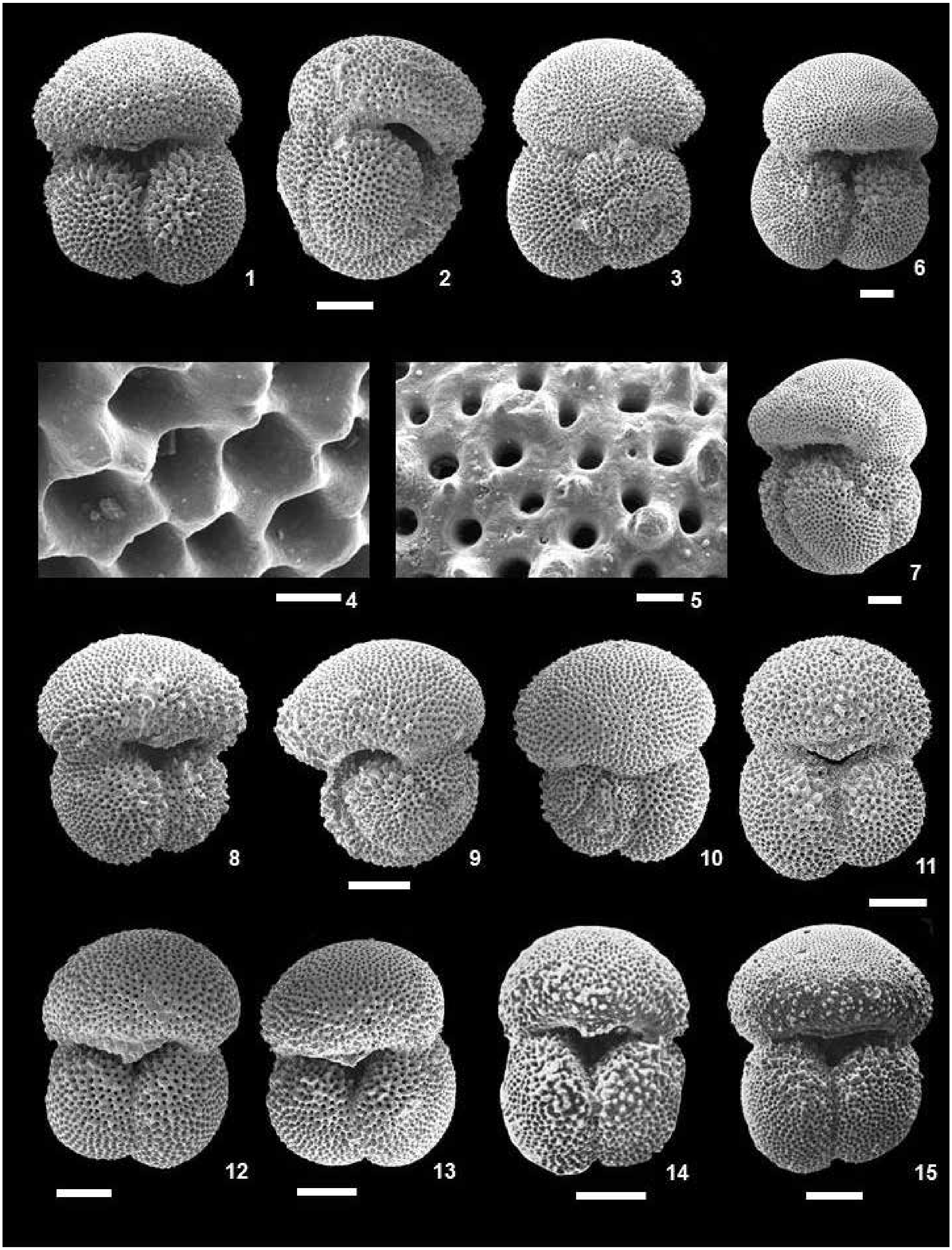

Plate 11.4 *Dentoglobigerina eotripartita* Pearson, Wade, and Olsson, new species

danvillensis Zone, Lindi area, Tanzania].—Blow, 1969:322, pl. 16, fig. 6 [upper Eocene Zone P15, Lindi area, Tanzania].—Stainforth and others, 1975:325, 328 (partim), fig. 148, nos. 1, 6 [upper Eocene *Globigerinatheka semi-involuta* Zone, Navet Fm., Trinidad] (not fig. 148, nos 2-5, 7, 8 = *Dentoglobigerina tripartita*). [Not Koch, 1926.]

Dentoglobigerina tripartita (Koch).—Blow, 1979:1310, pl. 244, figs. 3, 4 [upper Eocene Zone P16, Lindi area, Tanzania].—Olsson and others, 2006:408-410 (partim), pl. 13.3, figs. 4, 15 [upper Eocene Zone E16, Nanggulan Fm., Java], fig. 5 (reproduced from Blow, 1979, pl. 244, fig. 3), fig. 6 (reproduced from Blow, 1969, pl. 16, fig. 6), figs. 7, 8 [upper Eocene Zone E15/16, TDP Site 11, Tanzania], figs. 9-11 [upper Eocene Zone E15/E16, Shubuta Clay, Mississippi], fig. 14 [upper Eocene Zone E15, Istra More-4 well, Adriatic Sea] (Not pl. 13.3, figs. 1-3 = holotype; not pl. 13.3, figs. 12, 16 = *Dentoglobigerina galavisi*). [Not Koch, 1926.]

Dentoglobigerina cf. *tripartita* (Koch).—Pearson and Wade, 2015:20, fig. 21.1 (reproduced from Blow, 1969, pl. 16, fig. 6), fig. 21.2 (reproduced from Blow, 1979, pl. 244, fig. 4), fig. 21.3a-b (reproduced from Olsson and others, 2006, pl. 13.3, figs. 7, 8), fig. 21.4a-7f [upper Eocene Zone E15/16, TDP Site 12, Tanzania] (Note fig. 21.4a-e = holotype designated here, NHMUK PM 71285; fig. 21.6a-b = paratype designated here, NHMUK PM 71286; fig. 21.7a-c = paratype designated here, NHMUK PM 71287).

Dentoglobigerina pseudovenezuelana (Blow and Banner).—Olsson and others, 2006:404-408 (partim), pl. 13.2, figs. 9, 12 [upper Eocene Zone E15/16, Shubuta Clay, Wayne County, Mississippi]. [Not Blow and Banner, 1962.]

DESCRIPTION.

Type of wall: Normal perforate, cancellate, pustulose, probably spinose in life.

Test morphology: Test, compact, globular, chambers arranged in a tight, low trochospiral, subcircular to subquadrate in equatorial outline, moderately lobate; in spiral view 3-3½ ovoid compressed chambers in ultimate whorl, increasing rapidly in size, sutures straight or slightly curved, depressed; in umbilical view 3 ovoid chambers in ultimate whorl, increasing rapidly in size, sutures straight and incised, umbilicus moderate in size, aperture centered deep in the umbilicus, bordered by a thin, irregular, subtriangular-shaped lip or tooth which tends to point down the opposing suture; in edge view test oval in outline, chambers ovoid in shape, ultimate chamber projects above and bends over the umbilicus.

Size: Maximum diameter of holotype 0.42 mm, minimum diameter 0.34 mm, thickness 0.41 mm.

ETYMOLOGY.— *Eo* = dawn; *tripartita* = in three parts, the name of Koch's taxon with which this species has previously been confused; *eotripartita* = the '*tripartita*' typical of the Eocene.

DISTINGUISHING FEATURES.— *Dentoglobigerina eotripartita* is distinguished from *D. galavisi* by its more compact morphology with 3 tightly coiled, more rapidly increasing chamber size in the final whorl and by possessing a more overarching and compressed final chamber. This species differs from *D. tripartita* by its smaller size, and less spherical, less compressed/reniform overall morphology, and from *D. pseudovenezuelana* by more tightly coiled chambers and tooth pointing down the opposing suture.

DISCUSSION.— This species was initially identified in the *Atlas of Eocene Planktonic Foraminifera* (2006) as *D. tripartita* (Koch). At that time, an SEM of the *tripartita* holotype was unavailable and identification relied on a drawing of the holotype by Blow and Banner (1962), which was interpreted as a slightly deformed specimen, so we followed the well defined concept of this species set out by Blow (1969, 1979). The new holotype SEM of *tripartita* (Koch) (Pl. 11.14, Figs. 1-3) clearly shows, however, the large, robust, subspherical, test of this species, which is typical of the Oligocene, but is different from the specimens illustrated by Blow, and from *D.* cf. *tripartita* (Pearson and Wade, 2015). *Dentoglobigerina eotripartita* n. sp. is thus described to represent this smaller more compact morphotype typical of the Eocene, which was probably ancestral to the more robust *tripartita* sensu stricto.

PHYLOGENETIC RELATIONSHIPS.— *Dentoglobigerina eotripartita* n. sp. descended from *D. galavisi* in the middle Eocene (Olsson and others, 2006) and probably gave rise to *D. tripartita* in the lower Oligocene (Pearson and Wade, 2015).

STRATIGRAPHIC RANGE.— The first appearance is in upper Eocene Zone E14 according to Olsson and others (2006) although the oldest figured specimen is from Zone E15 (Olsson and others, 2006, pl. 13.3, fig. 4). This form probably developed gradually into *D. tripartita* by becoming larger and more spherical. All of our illustrated specimens are from the upper Eocene, but the *eotripartita* like morphology persists in the record until at least the upper Oligocene Zone O7 (see the dissections of Blow, 1969, pl. 29, figs. 3 and 5, and the discussion under *tripartita*). Our youngest confirmed occurrence is from Zone O1.

TYPE LEVEL.— Holotype and paratypes from upper Eocene Zone E15/E16 (Zone E16 equivalent) of Tanzania Drilling Project Site 12, in the Kilwa Group of Tanzania (Pearson and Wade, 2015).

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

STABLE ISOTOPE PALEOBIOLOGY.— Stable isotope data indicate a thermocline habitat, becoming deeper with increasing test size (Wade and Pearson, 2008, recorded as *D. tripartita*; see also Pearson and Wade, 2015).

REPOSITORY.— Holotype (NHMUK PM PF 71285) and paratypes (NHMUK PM PF 71286 to 71288) deposited at the Natural History Museum, London.

Dentoglobigerina galavisi (Bermúdez, 1961)

Plate 11.5, Figures 1-16

Globigerina galavisi Bermúdez, 1961:1183, pl. 4, fig. 3 [upper Eocene Jackson Fm., Mississippi].—Blow, 1969:319, pl. 5, figs. 1-3 (reillustration of holotype), pl. 16, fig. 4 [upper Eocene Zone P16, upper Jackson Fm., Mississippi], pl. 16, fig. 5 [upper Eocene Zone P16, Lindi area, Tanzania].—Brönnimann and Resig, 1971, pl. 8, figs. 2, 3 [upper Eocene Zone P16, DSDP Hole 64.1, Ontong Java Plateau, western equatorial Pacific Ocean].—Krasheninnikov and Hoskins, 1973:122, pl. 8, figs. 3-5 [middle Eocene *Orbulinoides beckmanni* Zone, DSDP Site 202, western North Pacific Ocean].

Globoquadrina galavisi (Bermúdez).—Fleisher, 1975:758, pl. 1, figs. 1, 2 [lower Oligocene *Cassigerinella chipolensis-Pseudohastigerina barbadoensis* Zone, DSDP Site 305, central North Pacific Ocean].

Dentoglobigerina galavisi (Bermúdez).—Blow, 1979:1301-1305 (partim), pl. 5, figs. 1-3 (holotype, reproduced from Blow, 1969), pl. 16, fig. 4 (reproduced from Blow, 1969, pl. 16, fig. 4), pl. 16, fig. 5 (reproduced from Blow, 1969, pl. 16, fig. 5) (not pl. 177, figs. 8, 9, ?= *Subbotina tecta*, pl. 186, figs. 8, 9, ?= *Subbotina projecta* n. sp., pl. 244, figs. 1, 2 = *Subbotina tecta*).—Poore and Bybell, 1988:16, pl. 4, figs. 6, 9 [upper Eocene Zone E16, ACGS Borehole, New Jersey].—Spezzaferri and Premoli Silva, 1991:243, pl. 2, figs. 1a-c [upper Oligocene Zone P22, DSDP Hole 538A, Gulf of Mexico].—Nishi and Chaproniere, 1994:259, pl. 5, figs. 10-12 [upper Eocene, ODP Hole 841B, Tonga Trench, South Pacific Ocean].—Poag and Commeau, 1995:149, pl. 6, fig. 8 [upper Eocene Zone E14, Chickahominy Fm., USGS Exmore Core, Virginia].—Olsson and others, 2006:403-405, pl. 13.1, figs. 1-3 (reillustration of holotype in SEM), figs. 4-7, 12-16 [Zone E15/16, Shubuta Clay, Wayne County, Mississippi], figs. 8, 11 [upper Eocene Zone E16, Nanggulan Fm, Java], figs. 9, 10 [Zone E15/16, Istra More-4 well, Adriatic Sea].—Pearson and Wade, 2015:17-18, fig. 15.1a-c (reillustration of holotype in SEM, from Olsson and others 2006), fig. 15.2-3, 5a-6, 8a-b [upper Eocene Zone E15/16, TDP Site 12, Tanzania], fig. 15.4 [upper Eocene Zone E15/16, TDP Site 17, Tanzania], fig. 15.7 [lower Oligocene Zone O1, TDP Site 12, Tanzania].

?*Dentoglobigerina galavisi* (Bermúdez).—Blow, 1979:1301-1305 (partim), pl. 191, figs. 8, 9 (unknown specimens, showing features transitional between *Subbotina* and *Dentoglobigerina*; considered here possible phylogenetically primitive *galavisi*).

Dentoglobigerina galavisi (Bermúdez) / *D. baroemoenensis* (LeRoy) transition.—Spezzaferri and Premoli Silva, 1991:243, pl. 2, figs. 2a-c [upper Oligocene Zone O6, DSDP Hole 538A, Gulf of Mexico], pl. 2, figs. 3a-c [lower Oligocene Zone O4, DSDP Hole 538A, Gulf of Mexico].

Globoquadrina larmeui Akers.—Jenkins, 1960:355 (partim), pl. 3, figs. 1a-1c [Oligocene Zone 2-3, overlapping with range of *Paragloborotalia opima*, Lakes Entrance Oil Shaft, Victoria, Australia]. [Not Akers, 1955.]

Globigerina yeguaensis yeguaensis Weinzierl and Applin.—Blow and Banner, 1962:99, pl. 13, figs. k-m (partim, not figs. h, j) [lower Oligocene *Globigerina oligocaenica* Zone, Lindi area, Tanzania]. [Not Weinzierl and Applin, 1929.]

Globigerina winkleri (Bermúdez).—Quilty, 1976:639, pl. 4, figs. 15, 16 [Zone N4, DSDP Site 320, Nazca Plate, southeastern Pacific Ocean]. [Not Bermúdez, 1961.]

Not *Globigerina galavisi* Bermúdez.—van Eijden and Smit, 1991:110, pl. 2, fig. 17 (= *Turborotalia ampliapertura*).

DESCRIPTION.

Type of wall: Cancellate, honeycomb, normal perforate, probably spinose in life.

Test morphology: Test trochospiral, globular, oval to quadrate in equatorial outline, chambers globular; in spiral view 3½ ovoid chambers in ultimate whorl, increasing rapidly in size, sutures moderately depressed, straight to slightly curved; in umbilical view 3-3½ ovoid chambers increasing rapidly in size, sutures deeply incised, straight; umbilicus small, enclosed

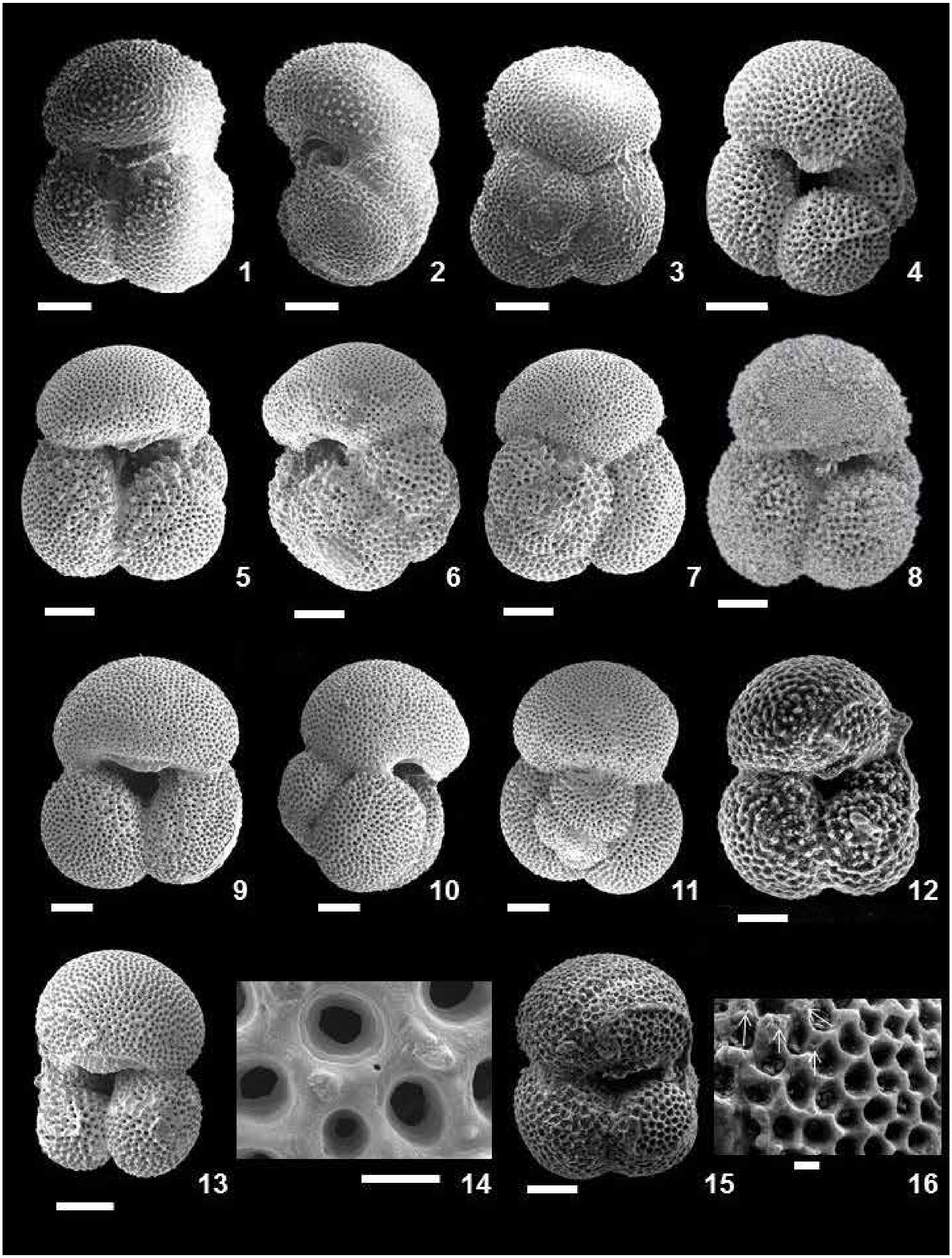

Plate 11.5 *Dentoglobigerina galavisi* (Bermúdez, 1961)

by surrounding chambers, aperture centered over the umbilicus, bordered by a thin irregular, triangular-shaped lip that is centered below an ill-defined apertural face; in edge view chambers ovoid in shape, projecting over the umbilicus, ultimate chamber shows a distinct bending and flattening into the umbilicus forming an indistinct umbilical face (modified from Olsson and others, 2006).

Size: Maximum diameter of holotype 0.46 mm, thickness 0.40 mm.

DISTINGUISHING FEATURES.— It is the root-stock of the evolutionary radiation of dentoglobigerinids: see under *eotripartita*, *globularis*, *larmeui*, *pseudovenezuelana*, and *taci*, for means of distinguishing those species. It is distinguished from most species of *Subbotina* by its more quadrate shape, more appressed and radially compressed chambers, and the tendency for the final chamber to bend over the umbilicus (features which it shares with most other *Dentoglobigerina*).

DISCUSSION.— Bermúdez (1961) described this species from the upper Eocene of Mississippi, and also recorded having observed it in coeval formations of Cuba, Trinidad and Mexico. Brönnimann and Resig (1971) recorded it from the Pacific Ocean for the first time, pointing out some of its distinctive features such as the flattened spiral side, radially compressed chambers, and thin, plate-like lip. However, other authors (e.g., Stainforth, 1974, and Bolli and Saunders, 1985) regarded it as a synonym of *Globigerina yeguaensis* Weinzierl and Applin, which we include here in *Subbotina*. Blow (1979) first recognized it as a distinct and important morphotype within a wider taxonomic scheme, but he operated a very broad taxonomic concept, including in it very globular specimens we now assign to various species of *Subbotina*. A more stable and restricted morphological concept was applied by Olsson and others (2006) and Pearson and Wade (2015). According to this taxonomy, *Dentoglobigerina galavisi* was probably the first species of the genus to evolve, in the middle Eocene, and it is also the name-bearing type. It gave rise to a range of other forms from the middle Eocene through to the Oligocene. Whereas Olsson and others (2006) regarded it as nonspinose, and suggested a possible ancestry in *Acarinina*, Pearson and Wade (2015) illustrated a possible spine hole in a specimen from Tanzania (reproduced in Plate 11.5, Fig. 14), and we here show another specimen (Plate 11.5, Fig. 16) from the Adriatic Sea with possible spine stumps in spine bases, hence we now consider it more likely that *galavisi* evolved from a spinose subbotinid ancestor. Blow (1979, pl. 191, figs. 8, 9) illustrated two unusual specimens that show transitional features between the genera *Subbotina* and *Dentoglobigerina* from middle Eocene Zone P13 (= E12) of Tanzania. Despite searching, we have not been able to find similar specimens in our own material of approximately this age; we tentatively regard them as possible phylogenetically primitive *galavisi*. The occurrence and diversity of the earliest dentoglobigerinids in the middle Eocene requires further study, and there is an intriguing possibility that the genus evolved during the climatic perturbation of the Middle Eocene Climatic Optimum.

PHYLOGENETIC RELATIONSHIPS.— This species may have evolved from a subbotinid ancestor (possibly *Subbotina yeguaensis*) in in the middle Eocene and became the rootstock of a minor evolutionary radiation, giving rise to several other species.

STRATIGRAPHIC RANGE.— *Dentoglobigerina galavisi* first occurs in the middle Eocene, probably Zones E10/E11, though further work is required to constrain its evolutionary first occurrence. This species was illustrated from middle Eocene Zone E12 by Krasheninnikov and Hoskins (1973), who recorded its first appearance at that level. It was also questionably recorded from the same zone by Blow (1979, pl. 191, figs. 8, 9) (see discussion above). Miller and others (1991) calibrated the first occurrence to Chron C16n (upper Eocene) at DSDP Site 612, northwest Atlantic Ocean; and it is from the upper Eocene and Oligocene that most reliable occurrences have been recorded.

Plate 11.5 *Dentoglobigerina galavisi* (Bermúdez, 1961)

1-3 (holotype, USNM 638941; Olsson and others, 2006, pl. 13.1-3) Zone E15/16, Upper Jackson Fm., Frost Bridge, Sample PJB-6, Mississippi; **4**, Zone M1, ODP Site 904/33/1 - 44", western North Atlantic Ocean; **5-7**, Zone E15/16, Sample TDP12/46/2, 56-66 cm (Pearson and Wade, 2015, Fig. 15.3a-c); **8**, Zone O1, Sample U1367B, 3H-1, 5-7 cm, South Pacific Ocean; **9-11** (same specimen), Zone E15/16, Sample TDP12/27/1, 35-45 cm (Pearson and Wade, 2015, Fig. 15.5a-c); **12**, Zone E16/O1, 1280 m, Istra More-3 well, Adriatic Sea; **13-14**, Zone O1, Sample TDP12/7/1, 0-10 cm (14, detail of wall showing possible spine hole) (Pearson and Wade, 2015, Fig. 15.7a-b); **15-16**, Zone O2, 1191.4 m, Istra More-3 well, Adriatic Sea (16, detail of wall showing possible spine holes). Scale bar: **1-13**, **15** = 100 µm; **16** = 20 µm; **14** = 10 µm.

The uppermost datum may be difficult to define precisely because of intergradation with *D. larmeui*, which has been regarded as a closely related species since the work of Bermúdez (1961) and Brönnimann and Resig (1971). Krasheninnikov and Hoskins (1973) suggested a highest occurrence in the 'middle' Oligocene *Paragloborotalia opima* Zone. Spezzaferri and Premoli Silva (1991) recorded a range extending to the upper part of Zone P22, overlapping with the range of *Paragloborotalia pseudokugleri* (= upper Oligocene Zone O7) (see also Spezzaferri, 1994). Pearson and Chaisson (1997) recorded a range into the lower Miocene at Ceara Rise, Atlantic Ocean, but no specimens were illustrated. Here we show a specimen (Pl. 11.5, Fig. 4) from lower Miocene Zone M1 from ODP Site 904, western North Atlantic Ocean.

TYPE LEVEL.— From a sample described by Bermúdez (1961) from Frost Bridge, Wayne County, Mississippi, from the upper part of the Jackson Formation (uppermost Eocene, probably referable to Zone E16).

STABLE ISOTOPE PALEOBIOLOGY.— Oxygen and carbon isotope data indicate a deep-dwelling habitat for this species (Pearson and others, 2001; Wade and Pearson, 2008). Earlier reports of relatively negative $\delta^{18}O$ (Douglas and Savin, 1978; Poore and Matthews, 1984; van Eijden and Ganssen, 1995) may refer to a different species concept. Eocene $\delta^{11}B$ data (Pearson and Palmer, 1999) confirm a thermocline dwelling habitat.

REPOSITORY.— Holotype (USNM 638941) deposited at the Smithsonian Museum of Natural History, Washington, D.C.

Dentoglobigerina globosa (Bolli, 1957)

Plate 11.6, Figures 1-16
(Pl. 11.6, Figs. 1-3: new SEMs of holotype of *Globoquadrina altispira globosa* Bolli)
(Note: This synonymy list is restricted to taxonomically important works and Oligocene occurrences)

Globoquadrina altispira globosa Bolli, 1957:111, pl. 24, figs. 9a-10c [lower Miocene *Catapsydrax dissimilis* Zone, Cipero Fm., Trinidad].—Stainforth and others, 1975:245, 248, fig. 101, no. 1-5 [lower Miocene *Catapsydrax dissimilis* Zone, Cipero Fm., Trinidad], fig. 101, no. 6a-c (reproduction of holotype of *Globoquadrina altispira globosa* Bolli from Bolli, 1957, pl. 24, fig. 9a-c.), fig. 101, no. 7a-c (reproduction from Blow, 1959, pl. 11, fig. 52a-c).

Dentoglobigerina altispira globosa (Bolli).—Kennett and Srinivasan, 1983:89 (partim), pl. 44, fig. 4, pl. 46, figs. 7, 9 [lower Miocene Zone N8, DSDP Site 289, western equatorial Pacific Ocean] (not pl. 46, fig. 8 = *Dentoglobigerina altispira*).—Spezzaferri and Premoli Silva, 1991:237, pl. 3, fig. 4a-c [upper Oligocene Zone P22, DSDP Hole 538A, Gulf of Mexico].—Spezzaferri, 1994:40, pl. 40, fig. 3 [upper Oligocene Subzone P21b, ODP Hole 709B, Mascarene Plateau, equatorial Indian Ocean].

Globoquadrina pozonensis Blow, 1959:184-185, pl. 10, figs. 54a-56 [? Pliocene *Globigerina bulloides* Zone, Pozón Fm., Venezuela].

Dentoglobigerina cf. *D. altispira* (Bolli).—Chaisson and Leckie, 1993:155, pl. 9, fig. 12 [lower Miocene Zone N5, ODP Hole 806B, Ontong Java Plateau, western equatorial Pacific Ocean].

DESCRIPTION.

Type of wall: Cancellate, probably spinose in life.

Test morphology: Moderately elevated trochospiral, globular, lobulate; in spiral view 5-6 globular, slightly embracing chambers in final whorl increasing slowly in size, ultimate chamber may be reduced in size, sutures straight, moderately depressed; in umbilical view 5-6 globular, slightly embracing chambers in final whorl increasing slowly in size, may have a reduced final chamber, umbilicus open, medium size, aperture umbilical, usually bordered by a sharp triangular shaped umbilical tooth, sutures straight, moderately depressed; in edge view very moderately elevated trochospiral, oval, rounded in outline.

Size: Maximum diameter of holotype 0.44 mm, minimum diameter 0.39 mm, thickness 0.32 mm.

Plate 11.6 *Dentoglobigerina globosa* (Bolli, 1957)

1-3 (holotype, USNM P5626), *Catapsydrax dissimilis* Zone, Cipero Fm., Trinidad; **4**, **12**, Zone O6, Sample ODP 872C/16H/1, 20-22 cm, Lo-En Guyot, western Pacific Ocean; **5-7**, (paratype, USNM P5627) *Catapsydrax dissimilis* Zone, Cipero Fm., Trinidad; **8**, Zone N8 [=Zone M5], Sample DSDP 289/52/5, 76 cm, Ontong Java Plateau, western Pacific Ocean, (Kennett and Srinivasan, 1983, pl. 46, fig. 9); **9**, **10**, Zone O6, Sample ODP 925A/27R/5, 75-77 cm, Ceara Rise, western equatorial Atlantic Ocean; **11**, Zone M1, Sample ODP 904/33/2 - 43", western North Atlantic Ocean; **13**, Zone N5 [=Zone M2/M3], ODP Site 806, Ontong Java Plateau, western equatorial Pacific Ocean, (Chaisson and Leckie, 1993, pl. 9, fig. 12); **14-16**, Zone O6, Atlantic Slope Project corehole 5, 5A/0-6", western Atlantic Ocean, showing transition to *D. globularis*. Scale bar: **1-16** = 100 μm.

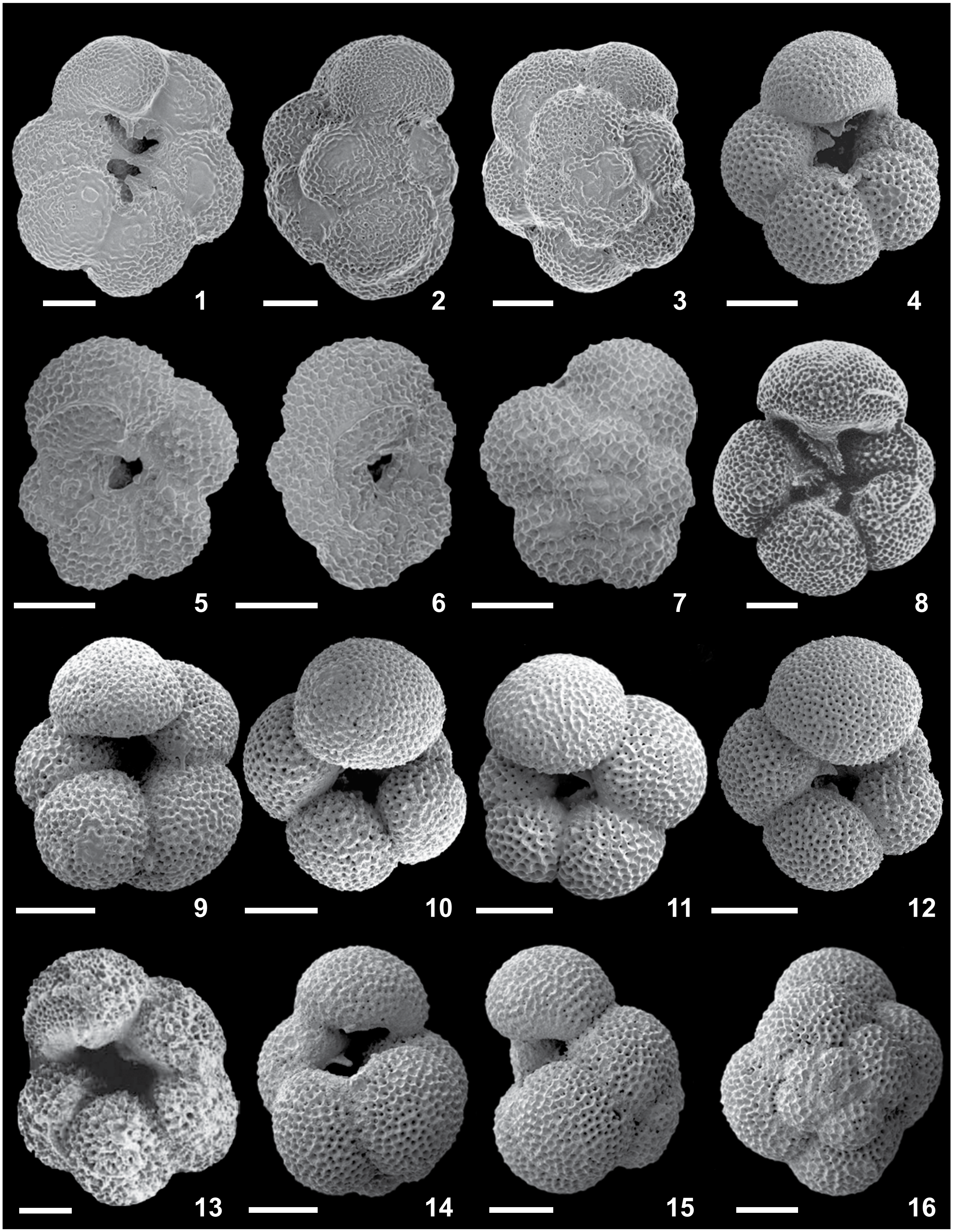

Plate 11.6 *Dentoglobigerina globosa* (Bolli, 1957)

DISTINGUISHING FEATURES.— This species is distinguished from *D. globularis* by having more chambers in the final whorl leading to a more lobulate outline, a wider umbilicus, and from *D. altispira* by its more rounded chambers.

DISCUSSION.— The holotype of *D. globosa* is from the lower Miocene, and Bolli's original concept was that *globosa* was a more globular subspecies of *D. altispira*. The paratype (Pl. 11.6, Figs. 5-7) appears to be a juvenile specimen and may not belong to this species. Fleisher (1974) suggested that *D. globosa* was the ancestral form to *altispira*, and was itself derived from *globularis* in the Oligocene. We regard *Globoquadrina pozonensis* Blow as a junior synonym.

PHYLOGENETIC RELATIONSHIPS.— Descended from *D. globularis* and ancestral to *D. altispira* according to Fleisher (1974) and various subsequent authors.

STRATIGRAPHIC RANGE.— According to Fleisher (1974) this species first appeared in Zone P21. The oldest confirmed illustrated occurrence is from Spezzaferri (1994) from Subzone P21b (Zone O5). It persists through much of the Miocene and possibly part of the Pliocene (e.g., Chaisson and Leckie, 1993); the highest occurrence has not been determined in this study.

TYPE LEVEL.— From a sample on the San-Fernando By-Pass road, western Trinidad, lower Miocene *Catapsydrax dissimilis* Zone, Cipero Fm.

GEOGRAPHIC DISTRIBUTION.— Widespread in low to mid-latitudes, but more common at low latitudes (Spezzaferri, 1994).

STABLE ISOTOPE PALEOBIOLOGY.— No data available.

REPOSITORY.— Holotype (USNM P5626) and paratype (USNM P5627) deposited at the Smithsonian Museum of Natural History, Washington, D.C.

Dentoglobigerina globularis (Bermúdez, 1961)

Plate 11.7, Figures 1-16
(Pl. 11.7, Figs. 1-3: new SEMs of holotype of *Globoquadrina globularis* Bermúdez)

Globoquadrina globularis Bermúdez, 1961:1311, pl. 13, figs. 4-6 ['middle' Oligocene, Tinguaro Fm., Matazanzas Province, Cuba].—Poore 1984:444, pl. 3, figs. 8-10 [upper Oligocene Zone OL4, DSDP Site 522, South Angola Basin, South Atlantic Ocean].

Globoquadrina altispira globularis Bermúdez.—Quilty, 1976:644, pl. 10, figs. 11, 12 [lower Miocene Zone N4, DSDP Site 320, Nazca Plate, southeastern Pacific Ocean].

Dentoglobigerina globularis (Bermúdez).—Spezzaferri and Premoli Silva, 1991:237, pl. 2, figs. 5, 7 [lower Oligocene Subzone P21a, DSDP Hole 538A, Gulf of Mexico], pl. 3, fig. 1 [upper Oligocene Zone P22, DSDP Hole 538A, Gulf of Mexico].—Spezzaferri, 1994:40, pl. 40, figs. 2a-c (reproduced from Spezzaferri and Premoli Silva, 1991).—Hernitz Kučenjak and others, 2006, pl. 3, fig. 4 [lower Oligocene Zone O1, Jihar-5 well, Syria].—Wade and others, 2007:172, pl. 2, figs. f-h [upper Oligocene Zone O5, ODP Hole 1218B, equatorial Pacific Ocean].

Dentoglobigerina globularis / D. altispira globosa transition.—Spezzaferri and Premoli Silva, 1991:237, pl. 3, figs. 3, 6, 7 [upper Oligocene Zone P22, DSDP Hole 538A, Gulf of Mexico].

Subbotina? *eocaena* (Gümbel).—Leckie and others, 1993:125, pl. 2, fig. 10 [uppermost Eocene Zone P17, ODP Hole 628A, Little Bahama Bank, western North Atlantic Ocean], pl. 2, fig. 11 [lower Oligocene Zone P18, ODP Hole 628A, Little Bahama Bank, western North Atlantic Ocean]. [Not Gümbel, 1868.]

Subbotina? *yeguaensis* (Weinzierl and Applin).—Leckie and others, 1993:125, pl. 3, fig. 3 [uppermost Eocene Zone P17, ODP Hole 628A, Little Bahama Bank, western North Atlantic Ocean], pl. 3, fig. 4 [lower Oligocene

Plate 11.7 *Dentoglobigerina globularis* (Bermúdez, 1961)

1-3 (holotype, USNM 639031), 'middle' Oligocene, Tinguaro Fm., Matazanzas Province, Cuba; **4**, Zone O7, Sample 872C/16H/1, 20-22cm, Lo-En Guyot, western Pacific Ocean; **5-7**, Zone O6, Sample ODP 628A/19X/2, 100-102 cm, Little Bahama Bank, western North Atlantic Ocean; **8-9**, Zone P18 [=O1], Sample ODP 628A/35/3, 47-49 cm, Little Bahama Bank, western North Atlantic Ocean, (Leckie and others, 1993; pl. 3, fig. 4; pl. 2, fig. 8); **10**, **11**, Zone O5, Sample ODP 1218B/15/3, 60-62 cm, equatorial Pacific Ocean, (Wade and others, 2007, pl. 2, figs. g, h); **12**, Zone O7, Sample ODP 925A/27R/5, 75-77 cm, Ceara Rise, western equatorial Atlantic Ocean; **13-15**, Zone O6 [= Zone O7 of this study], Sample PP07/T5, Cipero Fm., Trinidad (Pearson and Wade, 2009, pl. 3, fig. 2a-c); **16**, Zone O7, Sample ODP 925A/27R/5, 75-77 cm, Ceara Rise, western equatorial Atlantic Ocean, showing transition to *D. globosa*. Scale bar: **1-16** = 100 µm.

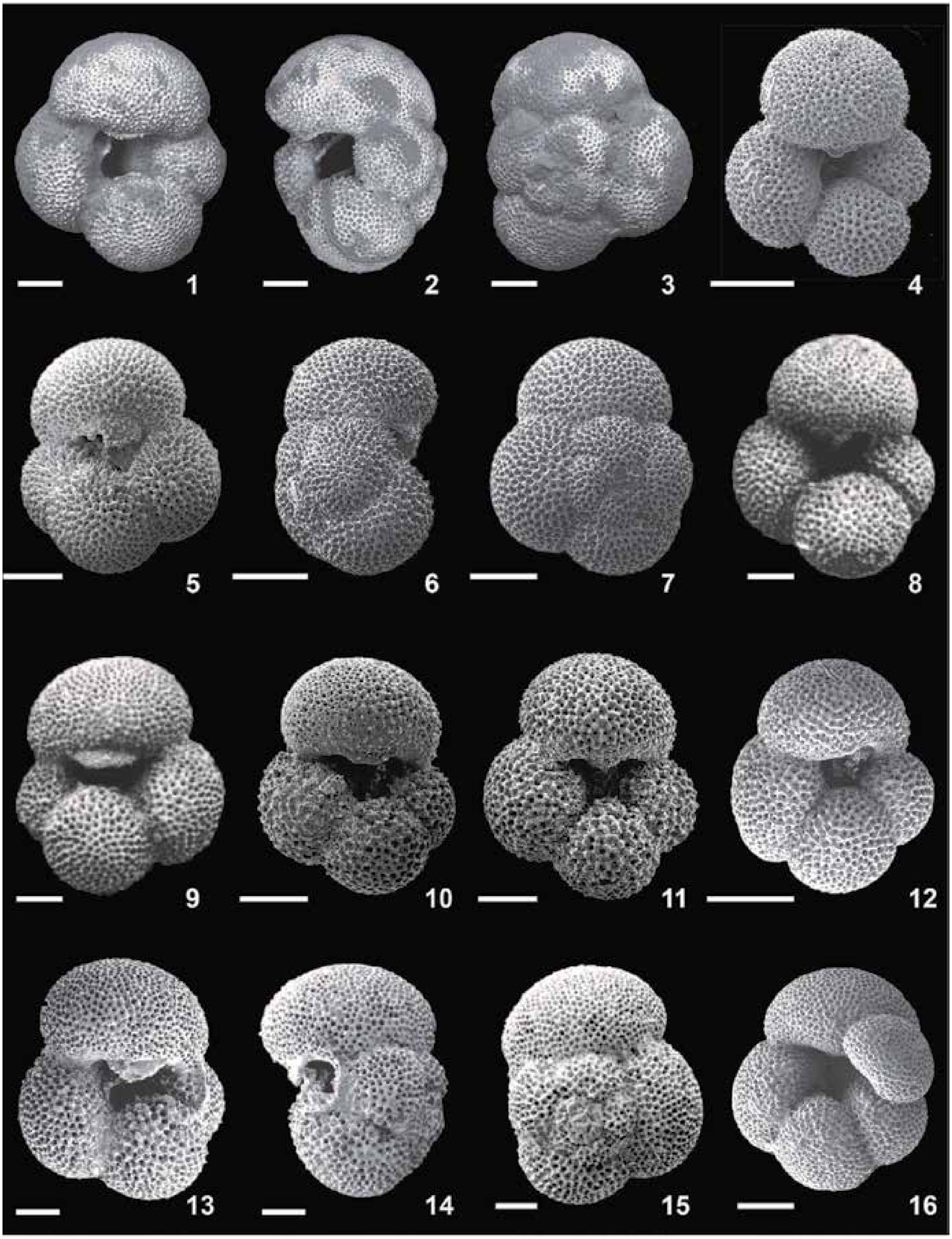

Plate 11.7 *Dentoglobigerina globularis* (Bermúdez, 1961)

Zone P18, ODP Hole 628A, Little Bahama Bank, western North Atlantic Ocean], pl. 3, fig. 5 [upper Oligocene Subzone P21b, ODP Hole 803D, Ontong Java Plateau, western equatorial Pacific Ocean]. [Not Weinzierl and Applin, 1929.]

Dentoglobigerina larmeui (Akers).—Pearson and Wade, 2009:203, pl. 3, figs. 2a-d [upper Oligocene Zone O6 (= O7 of this study), Cipero Fm., Trinidad]. [Not Akers, 1955.]

Not *Globoquadrina altispira globularis* Bermúdez.—Blow, 1969:340, pl. 28, figs. 1, 2 (fig. 1 = ?*Dentoglobigerina globosa*, fig. 2 = uncertain).

Not *Dentoglobigerina altispira globularis* Bermúdez.—Blow, 1979:311, pl. 28, figs. 1, 2 (reproduced from Blow, 1969, pl. 28, figs. 1, 2).

Not *Dentoglobigerina globularis* (Bermúdez).—Li and others, 2003, pl. 3, fig. 5 (=*Ciperoella ciperoensis*, same specimen as pl. 3, fig. 1).

DESCRIPTION.

Type of wall: Normal perforate, probably spinose in life.

Test morphology: Test large, globular, medium trochospiral, lobulate in equatorial outline; in spiral view chambers ovate, 3½-4 in final whorl, increasing moderately in size, sutures moderately depressed, straight; in umbilical view chambers ovate, slightly embracing, 3½-4 in final whorl, sutures moderately depressed, straight, ultimate chamber may be reduced in size, directed over the umbilicus; umbilicus open, square, aperture umbilical; the lip or tooth is highly variable; in edge view, chambers globular to ovate, ultimate chamber directed over umbilicus.

Size: Maximum diameter of holotype 0.62 mm, maximum thickness approximately 0.40 mm.

DISTINGUISHING FEATURES.— *Dentoglobigerina globularis* is distinguished from its ancestral form *D. galavisi* by its larger adult size, more open coiling with 3½-4 chambers in the whorl (compared to 3-3½ in *galavisi*), more open umbilicus, less embracing chambers, and slightly higher spire. This species resembles *D. prasaepis* and *D. pseudovenezuelana* in several of these respects, but *prasaepis* lacks an umbilical tooth and *pseudovenezuelana* has a more compact test, a heavily pustulose umbilical area and ragged, pustulose tooth. It is distinguished from *Subbotina projecta* n. sp. by having more compressed and closely appressed chambers. See under *globosa* for means of distinguishing this species.

DISCUSSION.— The holotype is illustrated here for the first time in SEM. Blow (1969, 1979) illustrated two metatypes from Cuba provided to him by Bermúdez. However, these specimens do not agree well with the type series; here we regard the first as probably referable to *Dentoglobigerina globosa* and the second as uncertain. Fortunately, most subsequent authors seem to have based their concept on the type illustrations. Fleisher (1974:1024) placed *globularis* in taxonomic context by suggesting a phylogenetic transition from *galavisi* to *globularis* to *globosa*, eventually leading to the common Miocene species *altispira*. This lineage has been accepted by several authors, including this study.

PHYLOGENETIC RELATIONSHIPS.— According to Fleisher (1974) and subsequent authors, this species evolved from *galavisi* and gave rise to *globosa*.

STRATIGRAPHIC RANGE.— This species ranges through the entire Oligocene. Although not included in the *Atlas of Eocene Planktonic Foraminifera*, we now consider the first occurrence to have been in the uppermost Eocene (Zone E16 equivalent), as illustrated by Leckie and others (1993) from the western North Atlantic Ocean. The uppermost confirmed occurrence is from lower Miocene Zone M1 (Quilty, 1976).

TYPE LEVEL.— Described from the 'middle' Oligocene Adelina Marl, Tinguaro Fm., Cuba.

GEOGRAPHIC DISTRIBUTION.— Widespread in low to mid-latitudes.

STABLE ISOTOPE PALEOBIOLOGY.— Biolzi (1983) indicated that it was a mixed-layer dweller although the species was not illustrated. Wade and others (2007) showed variable isotopic ratios.

REPOSITORY.— Holotype (USNM 639031) deposited at the Smithsonian Museum of Natural History, Washington, D.C.

Dentoglobigerina juxtabinaiensis Fox and Wade, 2013

Globigerina binaiensis Koch.—Krasheninnikov and Hoskins, 1973:124, pl. 6, figs. 1-3 [lower Miocene *Globigerinatella insueta – Globigerinita dissimilis* Zone, DSDP Site 200, Ita Maitai Guyot, equatorial Pacific Ocean]. [Not Koch, 1935.]

Globoquadrina binaiensis Koch.—Spezzaferri, 1994:42

(partim), pl. 38, figs. 1a-d [lower Miocene Zone N5, ODP Hole 667A, equatorial Atlantic Ocean], pl. 42, figs. 4a-c [lower Miocene Zone N5, ODP Hole 709C, Mascarene Plateau, equatorial Indian Ocean]. [Not Koch, 1935.]

Globoquadrina dehiscens Chapman and others.—Chaisson and Leckie, 1993:159 (partim), pl. 9, fig. 14 [lower Miocene Zone N5, ODP Hole 806B, Ontong Java Plateau, western equatorial Pacific Ocean]. [Not Chapman and others, 1934].

Dentoglobigerina juxtabinaiensis Fox and Wade, 2013:399, figs. 6.1-6.5 [lower Miocene Subzone M5a, IODP Hole U1338B, equatorial Pacific Ocean], figs. 7.1, 7.5 [lower Miocene Zone M2/3, IODP Hole U1337A, equatorial Pacific Ocean], figs. 7.2, 7.6 [lower Miocene Zone N6/7, ODP Hole 871A, Limalok Guyot, Marshall Islands, western equatorial Pacific Ocean], fig. 7.3 [lower Miocene Zone M4, IODP Hole U1337A, equatorial Pacific Ocean], fig. 7.4 [lower Miocene Zone N4/5, ODP Hole 871A, Limalok Guyot, Marshall Islands, western equatorial Pacific Ocean].

DISCUSSION.— *Dentoglobigerina juxtabinaiensis* appears to be restricted to the Miocene but is listed here for completeness because it appears on the range-charts. This species is distinguished from *D. binaiensis* (Koch) by having 4 rather than 3 chambers in the final whorl, less rapid chamber expansion and a more open umbilicus. It appears to have been descended from *binaiensis* and survived the extinction of that form.

Dentoglobigerina larmeui (Akers, 1955)

Plate 11.8, Figures 1-16
(Pl. 11.8, Figs. 1-3: new SEMs of holotype of *Globoquadrina larmeui* Akers)

Globoquadrina larmeui Akers, 1955:661, pl. 65, figs. 4a-c [Miocene *Operculinoides* Zone, Shell Godhaux Sugars No. 1 well, Louisiana].—Blow, 1959:183-184, pl. 11, fig. 53a-c [lower Miocene *Globigerinatella insueta* Zone, Pozón Fm., Venezuela].—Jenkins, 1960:355 (partim), pl. 3, figs. 2a-2c [middle Miocene Zone 4-5, Lakes Entrance Oil Shaft, Victoria, Australia].—Jenkins, 1971:167, pl. 17, figs. 522-524 [lower Miocene *G. trilobus trilobus* Zone, New Zealand].—Poore, 1979:470, pl. 18, figs. 1-3 [middle Miocene Zone N12-N14, DSDP Site 407, North Atlantic Ocean].—Berggren and others, 1983, pl. 1, fig. 13 [lower Miocene Zone N5, DSDP Site 516, Rio Grande Rise, southwest Atlantic Ocean].

Globoquadrina larmeui larmeui Akers.—Blow, 1969 (partim), pl. 28, fig. 6 [middle Miocene Zone N11, Venezuela].—Quilty, 1976:644, pl. 11, figs. 1, 2 [middle Miocene Zone N10-N11, DSDP Site 319, Nazca Plate, southeastern Pacific Ocean].

Dentoglobigerina larmeui (Akers).—Spezzaferri and Premoli Silva, 1991:243, pl. 2, figs. 6a-c [Oligocene Subzone P21a, DSDP Hole 538A, Gulf of Mexico].—Spezzaferri, 1994:41, pl. 41, figs. 3a-c (reproduced from Spezzaferri and Premoli Silva, 1991, pl. 2, figs. 6a-c).

Globoquadrina baroemoenensis (LeRoy).—Chaisson and Leckie, 1993:159 (partim), pl. 9, fig. 6 [middle Miocene Zone N9, ODP Hole 806B, Ontong Java Plateau, western equatorial Pacific Ocean]. [Not LeRoy, 1939.]

Not *Globoquadrina larmeui* Akers.—Jenkins, 1960:355, pl. 3, figs. 1a-1c [Oligocene Zone 2-3, overlapping with range of *Paragloborotalia opima*, Lakes Entrance Oil Shaft, Victoria, Australia] (= *D. galavisi*).

Not *Globoquadrina larmeui larmeui* Akers.—Blow, 1969 (partim), pl. 28, fig. 5 [middle Miocene Zone N11, Venezuela] (= unknown species).

Not *Dentoglobigerina* aff. *D. larmeui* (Akers).—Spezzaferri and Premoli Silva, 1991:243, pl. 7, figs. 3a-b [Oligocene Subzone P21a, DSDP Hole 538A, Gulf of Mexico] (?=*Subbotina gortanii*).—Spezzaferri, 1994:41, pl. 41, figs. 1a-c [upper Oligocene Zone P22, DSDP Hole 538A, Gulf of Mexico] (?= *D. baroemoenensis*).

Not *Dentoglobigerina larmeui* (Akers).—Pearson and Wade, 2009:203, pl. 3, figs. 2a-d [upper Oligocene Zone O6 (= O7 of this study), Cipero Fm., Trinidad] (= *D. globularis*).

DESCRIPTION.

Type of wall: Normal perforate, cancellate, probably spinose in life.

Test morphology: Low trochospiral, globular, to subquadrate, slightly lobulate; in spiral view 3½-4 flattened, ovoid-shaped chambers in final whorl increasing rapidly in size, sutures straight, moderately depressed; in umbilical view 3½-4 subspherical chambers in final whorl increasing rapidly in size, final chamber distinctly flattened and sloped toward the umbilicus, may have a reduced bulla-like final chamber which extends over the umbilicus; umbilicus open, broad, aperture umbilical, bordered by a small triangular lip, sutures straight or slightly curved, weakly depressed; in edge view very low trochospiral, oval, rounded in outline, with final chamber extending over the umbilicus.

Size: Maximum diameter of holotype 0.35 mm, minimum diameter 0.28 mm, thickness 0.24 mm.

DISTINGUISHING FEATURES.— *Dentoglobigerina larmeui* (the holotype of which is from the middle Miocene) closely resembles *D. galavisi* (holotype from the upper Eocene) but is distinguished by the slightly wider and more open umbilicus and more distinctly

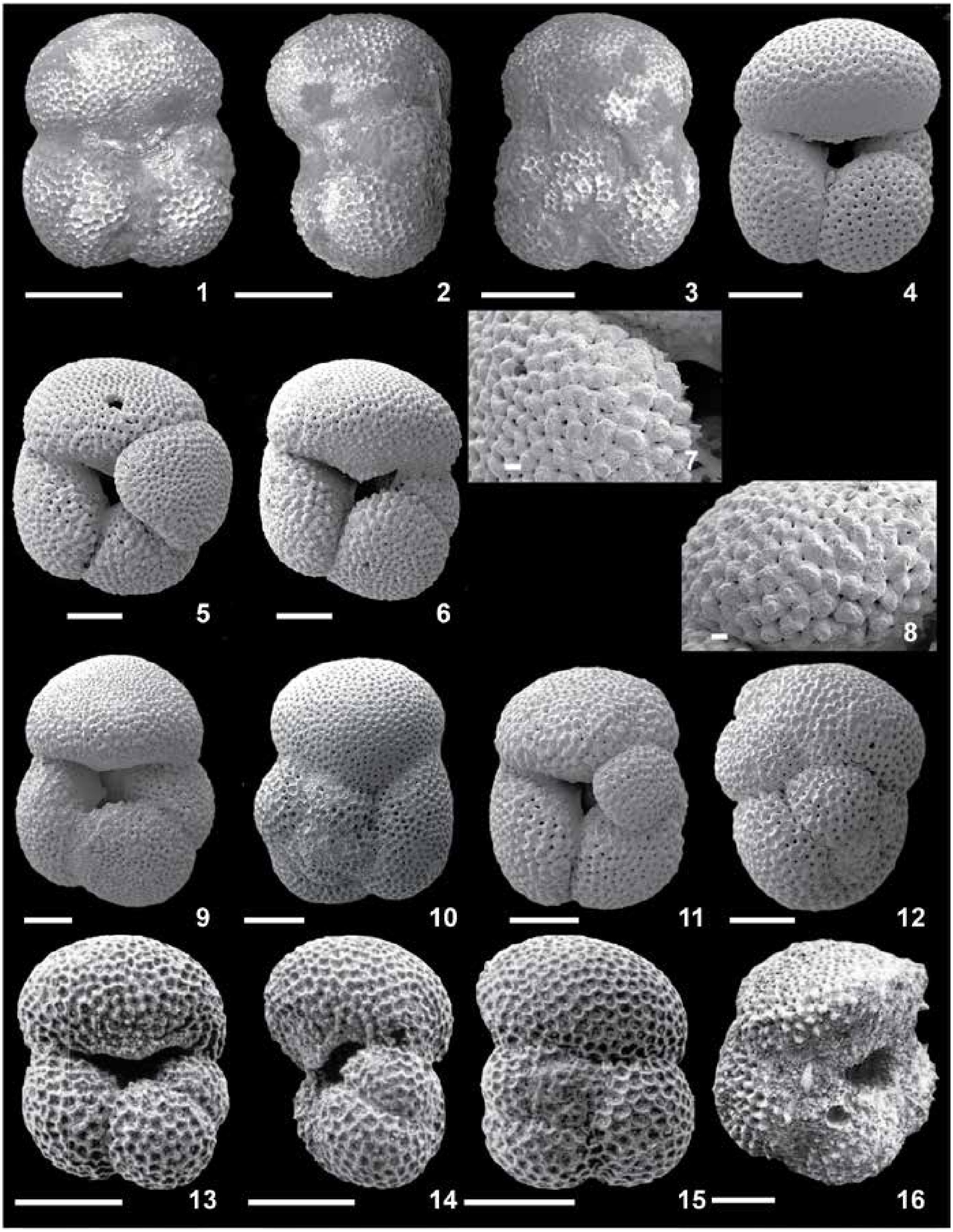

Plate 11.8 *Dentoglobigerina larmeui* (Akers, 1955)

flattened umbilical face to the final chamber, giving rise to a somewhat quadrate form. *Dentoglobigerina larmeui* typically has 3½-4 chambers in the final whorl, compared to 3-3½ in *galavisi*, which tends to produce a more square and symmetrical umbilicus in *larmeui* as opposed to a more triangular, asymmetrical umbilicus that is typical of *galavisi*. The umbilical tooth is usually less well developed in *D. larmeui*, and there is more of a tendency to form a reduced bulla. *Dentoglobigerina larmeui* differs from *D. globularis* by the the more compact and flattened nature of the final whorl chambers. *Dentoglobigerina larmeui* differs from *D. baroemoenensis* by having more embracing chambers, less reniform, more subspherical chambers, and a narrower umbilicus. This species differs from *Globoquadrina dehiscens* by lacking the 'boxy' outline, strongly embracing chambers, and flat, imperforate apertural face of this Miocene taxon. Transitional specimens between to *G. dehiscens* are shown on Plate 11.8.

DISCUSSION.— We illustrate the holotype of *larmeui* in SEM for the first time. This shows that Akers's type illustration in spiral view is slightly misleading as drawn from an oblique angle, giving the outline a more asymmetrical, lobulate appearance than is seen in our more orthodox orientation. *Dentoglobigerina larmeui* is a rather generalized morphologic species that in our taxonomy forms a link between *D. galavisi* (typical of the upper Eocene and Oligocene) and both *D. baroemoenensis* and *Globoquadrina dehiscens* (forms that are typical of the lower to middle Miocene). Its close similarity to *galavisi* was already noted by Bermúdez (1961) and Brönnimann and Resig (1971), and the distinction between these forms can be very subjective, particularly among variable populations, making the highest occurrence of *galavisi* and lowest occurrence of *larmeui* difficult to locate precisely. Jenkins (1960) illustrated two specimens as *larmeui* from the Oligocene and Miocene of the Lakes Entrance Oil Shaft in Victoria, Australia which nicely illustrate the difference between the morphologies, the older one (pl. 3, fig. 1a-c) being assigned to *galavisi* in this study. Transitional stages in the evolution of *D. larmeui* from *D. galavisi* are the development of a broader umbilicus, more flattened apertural face, and a more symmetrical triangular umbilical tooth. These trends become more fully enhanced in the evolution of *Globoquadrina dehiscens*. Iaccarino (1985) noted its similarity to *Globoquadrina langhiana* Cita and Gelati from the type Langhian (middle Miocene) of Italy, although we have not investigated this possible synonymy. We illustrate specimens that show evidence of a true spine and spine collar (Plate 11.8, Figs. 7 and 8).

PHYLOGENETIC RELATIONSHIPS.— This species evolved from *Dentoglobigerina galavisi* and gave rise to both *Globoquadrina dehiscens* and *Dentoglobigerina baroemoenensis*.

STRATIGRAPHIC RANGE.— The oldest illustrated specimen that we assign to this species is from Spezzaferri and Premoli Silva (1991), from Subzone P21a of DSDP Hole 538A, from a sample overlapping the range of *Ciperoella angulisuturalis* in that hole (= Zone O4). It has been recorded as low as Zone P19 (= Zone O1) in Spezzaferri and Premoli Silva (1991), but we have not been able to confirm this. It extends until at least the type level in the middle Miocene, and we have not investigated its highest occurrence, or its possible relationship with *Globoquadrina larmeui obesa* Akers from the Pliocene.

TYPE LEVEL.— Described from the Miocene *Operculinoides* Zone, Shell Godhaux Sugars No. 1 well, Louisiana (middle Miocene).

GEOGRAPHIC DISTRIBUTION.— Cosmopolitan; recorded at 63°N at DSDP Site 407 (Poore, 1979).

STABLE ISOTOPE PALEOBIOLOGY.— This species had an upper thermocline habitat according to Pearson and Wade (2009).

Plate 11.8 *Dentoglobigerina larmeui* (Akers, 1955)

1-3 (holotype, USNM P4756), Miocene *Operculinoides* Zone, Shell Godhaux Sugars No. 1 well, Louisiana; **4**, **11**, **12**, Zone M1, ODP Site 904/33/1 - 44", western North Atlantic Ocean; **5-8**, Zone M1, ODP 904/33/3, 34 cm, western North Atlantic Ocean; **9-10**, Zone M1, ODP 904/33/2, 43 cm, western North Atlantic Ocean; **13-15**, Zone N12-N14 [=M9-M11], DSDP Site 407, North Atlantic Ocean (Poore, 1979, pl. 18, figs. 1-3); **16**, form transitional to *Globoquadrina dehiscens,* Zone N4 [= O7/M1], Sample ODP 803D/35/3, 47-49 cm, Ontong Java Plateau, western equatorial Pacific Ocean (Leckie and others, 1993; pl. 8, fig. 17). Scale bar: **1-6**, **9-16** = 100 µm; **7**, **8** = 10 µm.

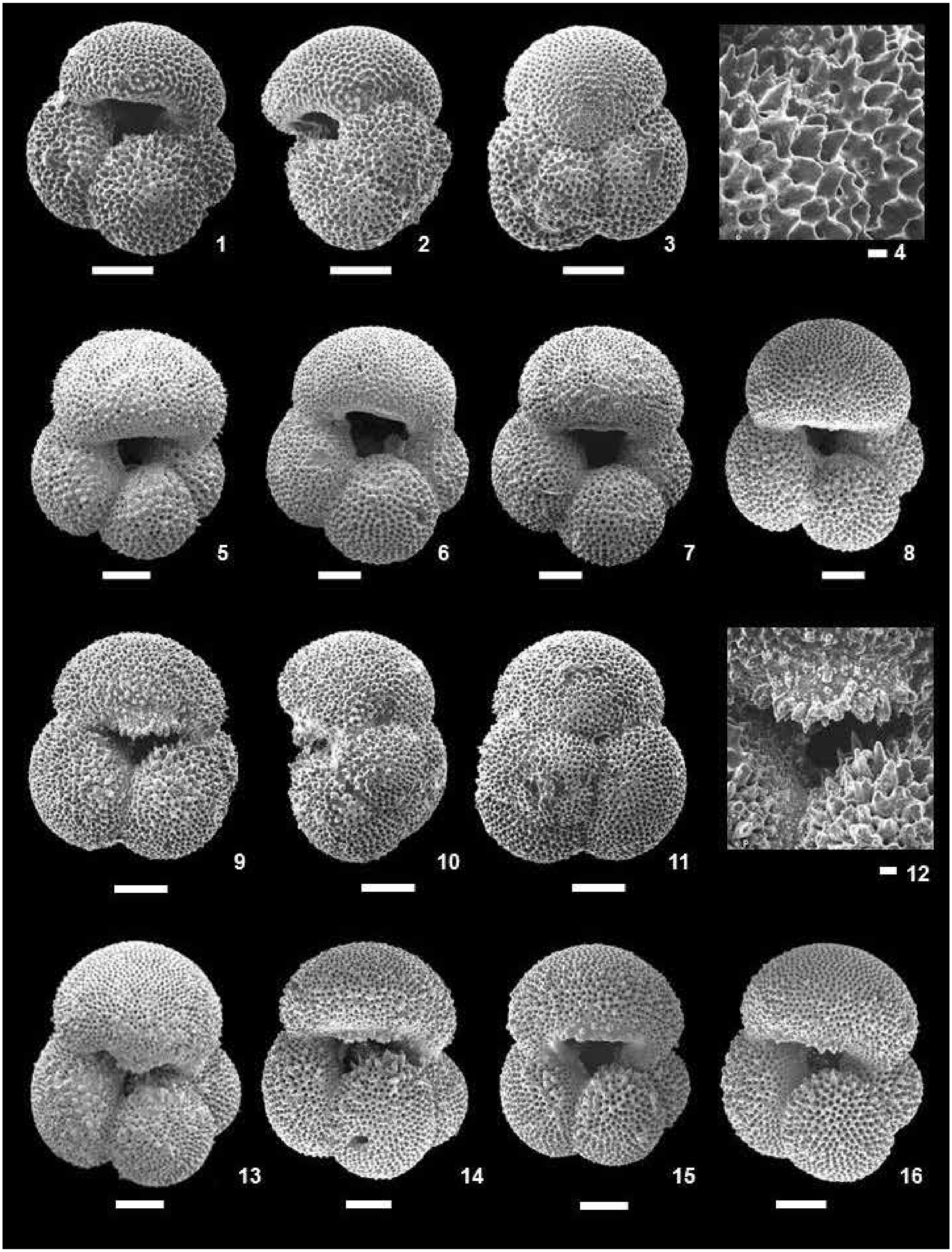

Plate 11.9 *Dentoglobigerina prasaepis* (Blow, 1969); *Dentoglobigerina pseudovenezuelana* (Blow and Banner, 1962)

REPOSITORY.— Holotype (USNM P4756) and paratypes (USNM P4757) deposited at the Smithsonian Museum of Natural History, Washington, D.C.

Dentoglobigerina prasaepis (Blow, 1969)

Plate 11.9, Figures 1-8

Globigerina ampliapertura euapertura Blow and Banner, 1962:84, pl. 11, figs. E-G (= holotype of *Globigerina prasaepis* as subsequently designated) [lower Oligocene *G. oligocaenica* Zone, Lindi area, Tanzania].

"*Turborotalia*" *euapertura* Jenkins.—Fleisher, 1975:pl. 3, fig. 8, 9 [lower Oligocene *"Turborotalia" ampliapertura* Zone, DSDP Site 305, Shatsky Rise, North Pacific Ocean]. [Not Jenkins, 1960.]

Globigerina euapertura Jenkins.—Poore, 1984:444, pl. 2, fig. 7 [lower Oligocene Zone OL2, DSDP Site 522, South Atlantic Ocean].—Leckie and others, 1993:123, pl. 4, fig. 10 [lower Oligocene Zone P18, ODP Hole 803D, Ontong Java Plateau, western equatorial Pacific Ocean], pl. 4, fig. 11 [upper Oligocene Subzone P21b, ODP Hole 803D, Ontong Java Plateau, western equatorial Pacific Ocean], pl. 4, fig. 12, 13 [lower Oligocene Subzone P21a, ODP Hole 628A, western North Atlantic Ocean]. [Not Jenkins, 1960.]

Turborotalia euapertura Jenkins.—Li and others, 2005:pl. 2 (partim), fig. 1 [lower Oligocene, ODP Hole 1148A, South China Sea]. [Not Jenkins, 1960.]

Globigerina prasaepis Blow, 1969:382 (partim), pl. 10, fig. 13 (holotype, reproduced from Blow and Banner, 1962:84, pl. 11, figs. E-G), pl. 18, figs. 5, 6 [paratypes, lower Oligocene Zone P19/20, Cipero Fm., Trinidad], pl. 18, fig. 7 [paratype, lower Oligocene Zone P19/20, Lindi area, Tanzania] (not pl. 18, figs. 3, 4 = *Dentoglobigerina venezuelana*).—Quilty, 1976:638, pl. 3, figs. 17, 18 [lower Oligocene Zone P19, DSDP Site 321, Nazca Plate, southeastern Pacific Ocean].—Blow, 1979:184-185 (partim), pl. 10, fig. 13 (holotype, reproduced from Blow and Banner, 1962:84, pl. 11, figs. E-G), pl. 18, figs. 5, 6 (paratypes, reproduced from Blow, 1969, pl. 18, figs. 5, 6), pl. 18, fig. 7 (paratype, reproduced from Blow, 1969, pl. 18, fig. 7) (not pl. 18, figs. 3, 4 = *Dentoglobigerina venezuelana*).

Turborotalia (*Turborotalia*) *prasaepis* Blow.—Fleisher, 1974:1036, pl. 20, fig. 7 [lower Oligocene Zone P18-P19, DSDP Site 219, Arabian Sea].

"Globigerina" prasaepis Blow.—Spezzaferri and Premoli Silva, 1991:246, pl. 7, fig. 1a-d [upper Oligocene Zone P22, DSDP Hole 538A, Gulf of Mexico], pl. 7, fig. 6a-c [lower Oligocene Zone P20, DSDP Hole 538A, Gulf of Mexico].—Spezzaferri, 1994:30, pl. 39, fig. 5a-c (reproduced from Spezzaferri and Premoli Silva, 1991, pl. 7, fig. 6a-c).

Dentoglobigerina prasaepis Blow.—Pearson and Wade, 2015:18, fig. 16.1a-d (SEMs of holotype of *Globigerina prasaepis* Blow, 1969), figs. 16.2-4, 16.6-16.8 [lower Oligocene Zone O1, TDP Site 17, Stakishari, Tanzania], fig. 16.5 [lower Oligocene Zone O1, TDP Site 12, Stakishari, Tanzania].

Not *Globigerina prasaepis* Blow.—Krasheninnikov and Pflaumann, 1978:591, pl. 2, figs. 4, 5 (= *Dentoglobigerina venezuelana*).

DESCRIPTION.

Type of wall: Cancellate, normal perforate, probably spinose in life.

Test morphology: Test large, medium trochospiral, globular, subcircular in outline, slightly lobate; in spiral view 3½ oval chambers in final whorl, increasing moderately rapidly in size, sutures depressed, straight; in umbilical view 3½-4 ovoid chambers increasing moderately in size, initially spherical but becoming more radially compressed as added, sutures deeply depressed, curved, umbilicus wide, aperture centered over the umbilicus, with a thin, even and smooth lip but no tooth; in edge view chambers ovoid in shape, embracing, ultimate chamber extends over the umbilicus, oval to subcircular in outline.

Size: Maximum diameter of holotype 0.41 mm, thickness 0.34 mm.

Plate 11.9, 1-8, *Dentoglobigerina prasaepis* (Blow, 1969); 9-16 *Dentoglobigerina pseudovenezuelana* (Blow and Banner, 1962)

Dentoglobigerina prasaepis **1-4** (holotype, BMNH P44522), (Pearson and Wade, 2015; fig. 16.1a-d) *Globigerina oligocaenica* Zone, lower Oligocene, Lindi area, Tanzania; **5**, (Pearson and Wade, 2015; fig. 16.4a) Zone O1, TDP Site 17, Stakishari, Tanzania; **6**, (Pearson and Wade, 2015; fig. 16.3) Zone O1, TDP Site 17, Stakishari, Tanzania; **7**, (Pearson and Wade, 2015; fig. 16.5) Zone O1, TDP Site 12, Stakishari, Tanzania; **8**, (Pearson and Wade, 2015; fig. 16.6a) Zone O1, TDP Site 17, Stakishari, Tanzania.

Dentoglobigerina pseudovenezuelana **9-12** (holotype, BMNH P44524), (Olsson and others, 2006, pl. 13.2, figs. 1-3, 5) *Globigerina oligocaenica* Zone, lower Oligocene, Lindi area, Tanzania; **13**, (Pearson and Wade, 2015; fig. 17.2a) Zone O1, TDP Site 17, Stakishari, Tanzania; **14**, (Pearson and Wade, 2015; fig. 17.5a) Zone O1, TDP Site 17, Stakishari, Tanzania; **15**, (Pearson and Wade, 2015; fig. 17.6a) Zone O1, TDP Site 12, Stakishari, Tanzania; **16**, (Pearson and Wade, 2015; fig. 17.4a) Zone O1, TDP Site 17, Stakishari, Tanzania. Scale bar: **1-3**, **5-11**, **13-16** = 100 µm; **4**, **12** = 10 µm.

DISTINGUISHING FEATURES.— *Dentoglobigerina prasaepis* is distinguished from *Globoturborotalita euapertura*, with which it has frequently been confused, by its pustulose wall and more rounded chambers, and less incised sutures. This species is broadly homeomorphic with some specimens of *Turborotalia ampliapertura*, but is distinguished primarily by its wall texture, and by having a broader, lower arched aperture in most specimens. It is distinguished from *D. venezuelana* by its looser coiling, less embracing chambers, and large, open umbilicus and from *D. taci* by its more compressed chambers and rectangular (rather than square) umbilicus (see Pearson and Wade, 2015: Table 3).

DISCUSSION.— According to Blow (1969) the species name refers to the "trough-like" aperture (Latin praesepe = trough), which according to Blow (1979:806) was unintentionally misspelled in the original description. *Dentoglobigerina prasaepis* has been a relatively under-utilized species. It is homeomorphic with both *Globoturborotalita euapertura* (Jenkins) and *Turborotalia ampliapertura* (Bolli). It was considered a junior synonym of *euapertura* by Jenkins and Orr (1972), Fleisher (1975) and Berggren and Miller (1988), whereas Blow and Banner (1962) and Blow (1969, 1979) thought it was closely related to *ampliapertura*. This species was discussed by Pearson and Wade (2015), who illustrated the holotype in SEM, showing that the wall texture is typical for *Dentoglobigerina* and hence *prasaepis* is unrelated to both *euapertura* and *ampliapertura*. It is close to *D. venezuelana* in general morphology, and was regarded as a likely ancestor of that species by Pearson and Wade (2015). Two of Blow's paratypes are herein regarded as closer to *venezuelana* than *prasaepis*.

PHYLOGENETIC RELATIONSHIPS.— We consider *D. prasaepis* to be morphologically transitional from *D. taci* to *D. venezuelana* (Pearson and Wade, 2015).

STRATIGRAPHIC RANGE.— The lowest confirmed occurrence is in lower Zone O1 (Fleisher, 1974; Pearson and Wade, 2015). Fleisher (1974) indicated a stratigraphic range confined to the lower Oligocene from Zone P18 to P21, and almost all confirmed occurrences are lower Oligocene. However, Blow (1979) suggested it extended as high as upper Oligocene Zone P22 (=Zone O6/O7) and Spezzaferri and Premoli Silva (1991) illustrated a specimen from that level.

TYPE LEVEL.— Lower Oligocene *G. oligocaenica* Zone of the Lindi area, Tanzania (referable to the upper part of Zone O1).

GEOGRAPHIC DISTRIBUTION.— So far this species has only been recorded from tropical / subtropical latitudes, worldwide.

STABLE ISOTOPE PALEOBIOLOGY.— Relatively positive $\delta^{18}O$ values suggest a thermocline dwelling habitat (Wade and Pearson, 2008; recorded as "*Globoquadrina*" *euapertura*).

REPOSITORY.— Holotype (P44522) deposited at the Natural History Museum, London.

Dentoglobigerina pseudovenezuelana (Blow and Banner, 1962)

Plate 11.9, Figures 9-16

Globigerina venezuelana Hedberg.—Bolli, 1957:110 (partim), pl. 35, fig. 16a-17 [upper Eocene *Porticulasphaera mexicana* Zone, Navet Fm., Trinidad]. [Not Hedberg, 1937.]

Globigerina yeguaensis pseudovenezuelana Blow and Banner, 1962:100, pl. 11, figs. J-L (holotype) [upper Eocene *Cribrohantkenina danvillensis* Zone, Lindi area, Tanzania], figs. N, O (paratype) [lower Oligocene *Globigerina oligocaenica* Zone, Lindi area, Tanzania].

Globigerina pseudovenezuelana Blow and Banner.—Blow, 1969:123, pl. 19, figs. 1, 2 [upper Eocene Zone P16, Lindi area, Tanzania].—Bolli and Saunders, 1985:180, fig. 13: 22a-c (reproduction of holotype image).

Globoquadrina pseudovenezuelana (Blow and Banner).—Fleisher, 1974, pl. 1, fig. 3 [lower Oligocene *Cassigerinella chipolensis – Pseudohastigerina barbadoensis* zone, DSDP Site 305, central North Pacific Ocean].

Dentoglobigerina pseudovenezuelana (Blow and Banner).—Blow, 1979:1307, pl. 244, figs. 5, 6 [upper Eocene Zone P16, Lindi area, Tanzania].—Olsson and others, 2006:404-408 (partim), pl. 13.2, figs. 1-5 (SEM of holotype of *Globigerina yeguaensis pseudovenezuelana* Blow and Banner), figs. 6-8, 10, 11, 13-16 [upper Eocene Zone E15/16, Shubuta Clay, Wayne County, Mississippi] (not pl. 13.2, figs. 9, 12 = *Dentoglobigerina eotripartita* n.sp.).—Pearson and Wade, 2015:18, figs. 17.1a-d (SEM of holotype of *Globigerina yeguaensis pseudovenezuelana* Blow and Banner reproduced from Olsson and others, 2006, pl. 13.2, figs. 1-3, 5), figs. 17.2, 17.4, 17.5 [upper Eocene Zone E15/16, TDP Site 17, Stakishari, Tanzania], fig. 17.3 [lower Oligocene Zone

O1, TDP Site 17, Stakishari, Tanzania].

Not *Dentoglobigerina pseudovenezuelana* (Blow and Banner).—Spezzaferri and Premoli Silva, 1991:243, pl. 3, figs. 5a, b (= indeterminate *Dentoglobigerina* sp.).

Not *Globigerina pseudovenezuelana* Blow and Banner.—Leckie and others, 1993:124, pl. 4, figs. 15-17 (= *Dentoglobigerina venezuelana*).

Not *Globoquadrina pseudovenezuelana* Blow and Banner.—Li and others, 2003:16, pl. 2, figs. 17, 18 (= *Dentoglobigerina venezuelana*).

DESCRIPTION.

Type of wall: Cancellate, normal perforate, probably spinose in life, pustulose in umbilical region.

Test morphology: Test large, trochospiral, compact, globular, subcircular in outline, chambers ovoid; in spiral view 3½ ovoid chambers in ultimate whorl, increasing moderately in size, sutures moderately depressed, straight; in umbilical view 3-3½ ovoid chambers increasing moderately in size, sutures deeply depressed, straight, umbilicus moderate in size, aperture centered over the umbilicus, bordered by an irregular pustulose lip or tooth; in edge view chambers ovoid in shape, embracing, ultimate chamber extends over the umbilicus, oval to subcircular in outline (modified from Olsson and others, 2006).

Size: Maximum diameter of holotype 0.51 mm, thickness 0.34 mm.

DISTINGUISHING FEATURES.— *Dentoglobigerina pseudovenezuelana* is distinguished from its ancestor *D. galavisi* by its more inflated chambers and in typically having 3½ rather than 3 chambers in the final whorl. Although it is called *pseudovenezuelana*, the resemblance is not especially close. *Dentoglobigerina venezuelana* tends to have a more spherical overall morphology, with large, appressed, pillow-like chambers, the last of which is very commonly reduced in size, and in generally lacking the very pustulose, ragged lip which is characteristic of *pseudovenezuelana*. In overall form, *D. pseudovenezuelana* is similar to *D. prasaepis* but tends to be much more pustulose around the umbilicus and tooth.

DISCUSSION.— Blow and Banner (1962) argued that specimens illustrated by Bolli (1957) as *venezuelana* belonged to two distinct species, and named *pseudovenezuelana* to accommodate one of them, selecting a holotype from Tanzania. This relatively uncommon species was discussed and figured by Olsson and others (2006) and Pearson and Wade (2015).

PHYLOGENETIC RELATIONSHIPS.— *Dentoglobigerina pseudovenezuelana* evolved from *D. galavisi* in the middle/late Eocene (Olsson and others, 2006). It is not considered the ancestor of *venezuelana*.

STRATIGRAPHIC RANGE.— According to Blow (1979), this species first appeared in Zone P13 (= E12) and persisted to Zone P19/20 (= upper Zone O1-O2). The highest occurrence recorded by us is from the lowermost part of Zone O2 of IODP Site U1334 (B.S. Wade, unpublished observation).

TYPE LEVEL.— The holotype is from the upper Eocene *Cribrohantkenina danvillensis* Zone, Lindi area, Tanzania (=Zone E16).

GEOGRAPHIC DISTRIBUTION.— Known only from a few low latitude locations.

STABLE ISOTOPE PALEOBIOLOGY.— Stable isotope data suggest calcification in a deep (thermocline) habitat (Poore and Matthews, 1984; Pearson and others, 2001; Wade and Pearson, 2008). Stable isotope data is supported by Mg/Ca thermometry (Wade and others, 2012).

REPOSITORY.— Holotype (P44524) and paratype (P44526) deposited at the Natural History Museum, London.

Dentoglobigerina sellii (Borsetti, 1959)

Plate 11.10, Figures 1-12; Plate 11.11, Figures 1-16
(Pl. 11.10, Figs. 1-3: new SEMs of holotype of *Globoquadrina sellii* Borsetti)
(Pl. 11.10, Figs. 4-6: new SEMs of holotype of *Globoquadrina obesa* Akers)
(Pl. 11.10, Figs. 7-9: new SEMs of holotype of *Globigerina clarae* Bermúdez)
(Pl. 11.10, Figs. 10-12: new SEMs of holotype of *Globigerina oligocaenica* Blow and Banner)

Globoquadrina obesa Akers, 1955:661, pl. 65, fig. 5a-c [lower Miocene *Miogypsina* Zone, Shell Godchaux Sugars No. 1 Well, Louisiana].

Globoquadrina sellii Borsetti, 1959:209, pl. 13, figs. 3a-c. [lower Oligocene “marne variegata”, Piacenza province, Northern Italy].—Blow, 1969:322, pl. 19, figs. 4, 5

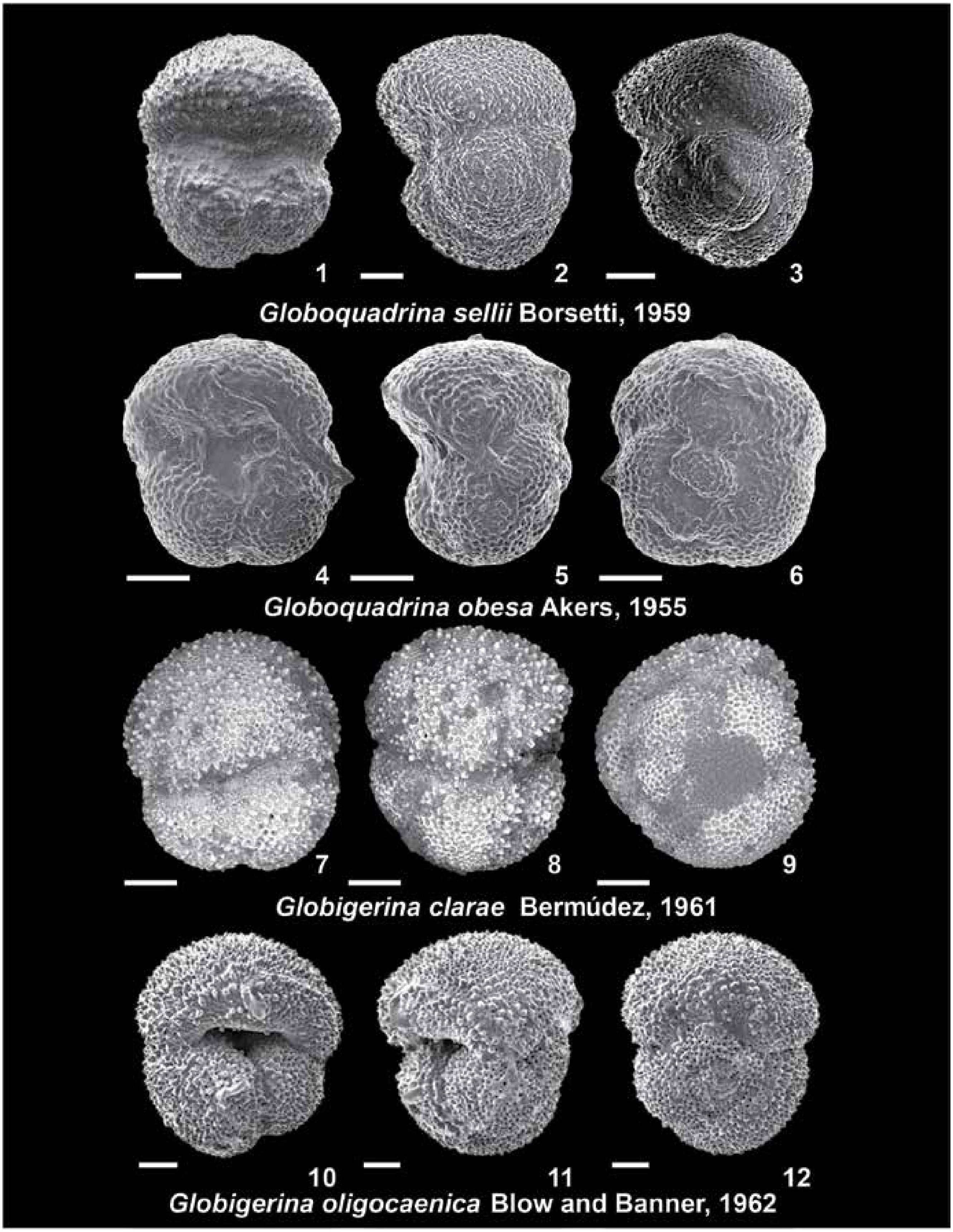

Plate 11.10 *Dentoglobigerina sellii* (Borsetti, 1959)

[lower Oligocene Zone P19, Lindi area, Tanzania], fig. 6 [lower Oligocene Zone P21, Alazan Fm. Mexico].—Fleisher, 1975, pl. 1, fig. 5 [upper Oligocene *Globigerina ciperoensis* Zone, DSDP Site 313, North Pacific Ocean], fig. 6 [lower Oligocene *"Turborotalia" ampliapertura* Zone, DSDP Site 313, North Pacific Ocean].—Bolli and Saunders, 1985:181, figs. 14.11a-c (reproduction of holotype image from Borsetti, 1959, pl. 13, figs. 3a-c).—Spezzaferri and Premoli Silva, 1991:248, pl. 9, figs. 7a-c [upper Oligocene Zone P22, DSDP Hole 538A, Gulf of Mexico].—Spezzaferri, 1994:42, pl. 42, figs. 5a-c (reproduction from Spezzaferri and Premoli Silva, 1991, pl. 9, figs. 7a-c).

Globigerina sellii (Borsetti).—Brönnimann and Resig, 1971:1302, pl. 8, fig. 9 [upper Oligocene to lower Miocene Zone N4, DSDP Hole 64.1, Ontong Java Plateau, western equatorial Pacific Ocean].—Stainforth and others, 1975:315-317, fig. 141, nos. 1-3 [Oligocene, Alazan Fm., Mexico], fig. 141, nos. 4a-c (reproduction of holotype of *Globoquadrina sellii* Borsetti from Borsetti, 1959, pl.13, figs. 3a-c), fig. 141, no. 5 (reproduction of paratype illustration of *Globigerina oligocaenica* Blow and Banner from Blow and Banner, 1962, pl. 10, fig. G), fig. 141, no. 6a-c (reproduction of holotype illustration of *Globigerina oligocaenica* Blow and Banner from Blow and Banner, 1962, pl. 10, figs. L-N).—Krasheninnikov and Pflaumann, 1978:592, pl. 3, figs. 6, 7 [Oligocene, DSDP Site 369, eastern North Atlantic Ocean].—Leckie and others, 1993, pl. 5, figs. 1, 4, 5 [upper Oligocene Zone P22, ODP Hole 628A, western North Atlantic Ocean], fig. 2 [lower Oligocene Zone P19, ODP Hole 628A, western North Atlantic Ocean], fig. 3 [upper Oligocene Zone P22, ODP Hole 803D, Ontong Java Plateau, western equatorial Pacific Ocean].

Dentoglobigerina tripartita sellii (Borsetti).—Chaproniere, 1981:117, fig. 8 (Fa-c) [upper Oligocene to lower Miocene Zone N3/4, Ashmore Reef No. 1 Well, northwest Australia].

Dentoglobigerina sellii (Borsetti).—Wade and others, 2016:pl. 6, fig. 6 [lower Oligocene Zone O3/O4, IODP Hole U1334A, equatorial Pacific Ocean].

Globigerina clarae Bermúdez, 1961:1166, pl. 2, figs. 4a-d [mid-Oligocene, Alazán Fm., Vera Cruz, Mexico].

Globigerina oligocaenica Blow and Banner, 1962:88-90, pl. 10, figs. G, L-N [lower Oligocene *Globigerina oligocaenica* Zone, Lindi Area, Tanzania].

Globoquadrina dehiscens praedehiscens Blow and Banner, 1962.—Spezzaferri and Premoli Silva, 1991:248, pl. 9, figs. 1a-c [upper Oligocene Zone P22, DSDP Hole 538A, Gulf of Mexico].—Spezzaferri, 1994:43, pl. 43, figs. 1a-c (reproduced from Spezzaferri and Premoli Silva, 1991, pl. 9, figs. 1a-c). [Not Blow and Banner, 1962.]

Not *Globigerina sellii* (Borsetti).—Postuma, 1971:272, pl. on p. 273, 7 images (= specimens intermediate between *Dentoglobigerina eotripartita* and *D. tripartita*).

Not *Globoquadrina sellii* Borsetti.—Li and others, 2005:19, pl. 2, figs. 8-10 (= *Dentoglobigerina tripartita*).

Not *Globoquadrina larmeui obesa* Akers.—Blow, 1969:342, pl. 28, figs. 7, 9 (? = *Dentoglobigerina larmeui*).—Quilty, 1976:644, pl. 11, figs. 3, 4 (= ? *Globorotaloides*).

DESCRIPTION.

Type of wall: Normal perforate, cancellate, probably spinose in life, densely pustulose with thin pustules well-distributed over the test.

Test morphology: Globular, subspherical, rounded outline; in spiral view 3 embracing, elliptical shaped chambers that rapidly increase in size, final chamber makes up to two-thirds of the test size when fully formed; in edge view globular, rounded in outline; in umbilical view 3 embracing chambers in final whorl that rapidly increase in size, final chamber exhibiting a broad, rather flattened but not planar umbilical face; umbilicus low and broad, open, aperture umbilical a low arch, sometimes with a broad, triangular tooth (as in the holotype) but commonly without.

Size: Maximum diameter of holotype 0.69 mm, minimum diameter 0.47 mm.

DISTINGUISHING FEATURES.— *Dentoglobigerina sellii* is distinguished from its probable ancestor, *D. tapuriensis*, by having more rapidly expanding chambers, a more flattened umbilical face to the final chamber, and a more spherical overall morphology. It forms an intermediate between *D. tapuriensis* and *D. binaiensis*. There is an evolutionary trend towards increasing the rate of chamber expansion and flattening of the final chamber face, eventually leading to the bizarre, cut-away appearance of the final chamber of *binaiensis* (see discussion under that taxon).

Plate 11.10 *Dentoglobigerina sellii* (Borsetti, 1959)

1-3 (holotype, IF-380), lower Oligocene "marne variegata", Piacenza province, Northern Italy; **4-6**, (holotype of *Globoquadrina obesa* Akers, 1955, USNM P4758), lower Miocene *Miogypsina* Zone, Shell Godchaux Sugars No. 1 Well, Louisiana; **7-9**, (holotype of *Globigerina clarae*, USMN 638924, Bermúdez, 1961) 'middle Oligocene', Alazán Fm., Mexico; **10-12**, (holotype of *Globigerina oligocaenica,* BMNM P44519*,* Blow and Banner, 1962), lower Oligocene *G. oligocaenica* Zone [= upper Zone O1], Lindi Area, Tanzania. Scale bar **1-12** = 100 μm.

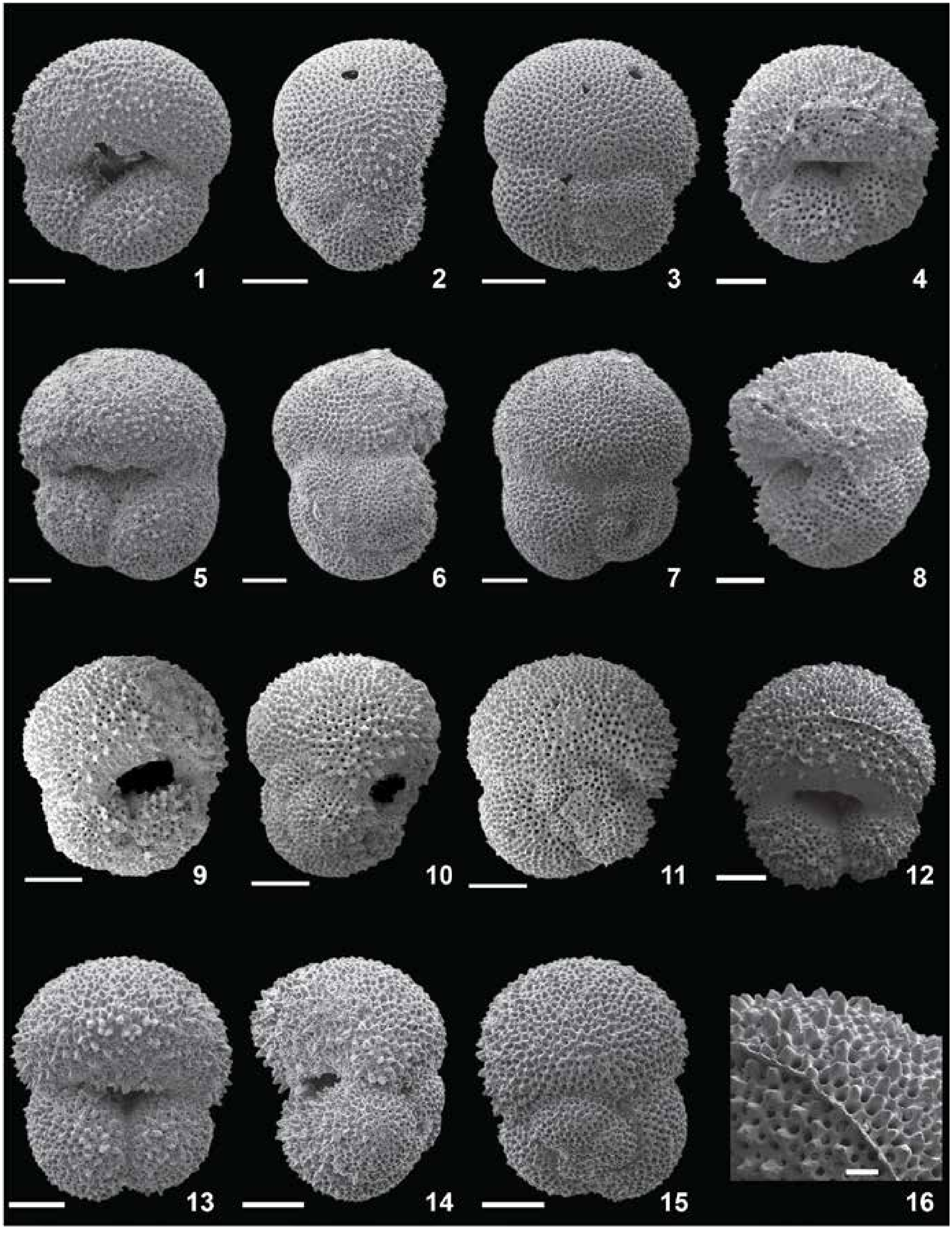

Plate 11.11 *Dentoglobigerina sellii* (Borsetti, 1959)

DISCUSSION.— We have investigated the holotype and paratypes of the almost entirely overlooked species *Globoquadrina obesa* Akers, 1955, described from the lower Miocene subsurface of Louisiana. Blow (1969, 1979) regarded it as a subspecies of *larmeui* and illustrated a form as *Globoquadrina larmeui obesa* Akers from the Pliocene. In our view Blow's (1969, 1979) *larmeui obesa* is not conspecific with *obesa* and we have not investigated it further. Quilty (1976) also illustrated a form as '*larmeui obesa*' that is not in our opinion related. Here we illustrate the holotype in SEM for the first time (Plate 11.10, Figs. 4-6) and assigned it to *Dentoglobigerina sellii*. The paratypes are assigned variously to *sellii* and *larmeui* and can be viewed at the Smithsonian Museum of Natural History website. It appears conspecific with *Globoquadrina sellii* Borsetti, and hence a potential senior synonym, but we recommend suppression of the name for the sake of nomenclatorial stability.

Globoquadrina sellii was described by Borsetti (1959) from Oligocene marls of Italy three years before the description by Blow and Banner (1962) of *Globigerina oligocaenica* from the lower Oligocene of Tanzania. Blow (1969) and all subsequent authors of which we are aware have regarded the two as synonyms. We illustrate both specimens in SEM for the first time (Plate 11.10, Figs. 1-3 and 10-12). The specimens are actually quite divergent in morphology: *sellii* has rather angular chamber shoulders and a distinct broad umbilical tooth, whereas *oligocaenica* is less angular and lacks a tooth. Most specimens illustrated in the literature have more in common with the *oligocaenica* morphotype than *sellii*. We considered whether the latter may in fact belong to the *tripartita* group, with which it shares several features. However, our study of *sellii* populations from the upper Oligocene and lower Miocene, close to the transition with *D. binaiensis*, has produced specimens similar to the holotype. Hence we regard *oligocaenica* and *sellii* as more phylogenetically primitive and advanced representatives, respectively, of the same evolving lineage.

Globigerina oligocaenica was described by Blow and Banner from the lower Oligocene of Tanzania. We have been unable to locate the type locality on the ground; it is from a higher stratigraphic level than the Eocene to lower Oligocene drill cores described by Pearson and Wade (2015), probably equivalent to uppermost Zone O1. We illustrate the holotype in SEM for the first time. It is a beautifully preserved specimen, showing clear affinity to *D. tapuriensis* from which the species has long been supposed to have evolved (Blow and Banner, 1962). *Globigerina clarae* was described by Bermúdez (1961) from Vera Cruz, Mexico. This species has long been considered a junior synoymn of *sellii* (e.g., Blow, 1979; Stainforth and Lamb, 1981).

Brönnimann and Resig (1971) described *Globigerinoides pseudosellii* from the lower Miocene of the southwest Pacific Ocean, for a *sellii*-like form with a supplementary aperture. This form was placed in synonymy with *Globigerinoides sicanus* by Fleisher (1974), with which we agree.

PHYLOGENETIC RELATIONSHIPS.— Evolved from *Dentoglobigerina tapuriensis* and is ancestral to *Dentoglobigerina binaiensis.*

STRATIGRAPHIC RANGE.— The first occurrence of this species is within Zone O1. Blow and Banner (1962) used the concurrent range of *oligocaenica* and *Pseudohastigerina barbadoensis* to define the lower Oligocene *G. oligocaenica* Zone, which was later emended to the *G. sellii* / *P. barbadoensis* concurrent range zone (Zone P19) by Blow (1969). The lowest occurrence of *sellii* has still not been calibrated to paleomagnetics, but was found within what is now recognized as Zone O1 by Premoli Silva and Spezzaferri (1991) and Leckie and others (1993). The uppermost occurrence has been recorded at the base of lower Miocene Zone M5 by Leckie and others (1993) from ODP Hole 806B and within Subzone M5a in the equatorial Pacific Ocean (IODP Site U1337) by Pälike and others (2010).

TYPE LEVEL.— Described from the lower Oligocene "marne variegata", Piacenza province, Northern Italy.

Plate 11.11 *Dentoglobigerina sellii* (Borsetti, 1959)

1-3, (same specimen) Zone O6, ODP Hole 628A, 17CC, Little Bahama Bank, western North Atlantic Ocean; **4**, **8** (same specimen) Zone O4, Alazon Fm., Tuxpan, Tampico, Mexico; **5-7**, (same specimen) Zone O6, ODP Hole 628A, 18/1, 100-102 cm, Little Bahama Bank, western North Atlantic Ocean; **9-11** (same specimen), **13-15** (same specimen), Zone O7, ODP Hole 628A, 17/3, 100-102 cm, Little Bahama Bank, western North Atlantic Ocean; **12**, **16** (same specimen), Zone O4, Alazon Fm., Tuxpan, Tampico, Mexico. Scale bar: **1-15** = 100 μm; **16** = 10 μm.

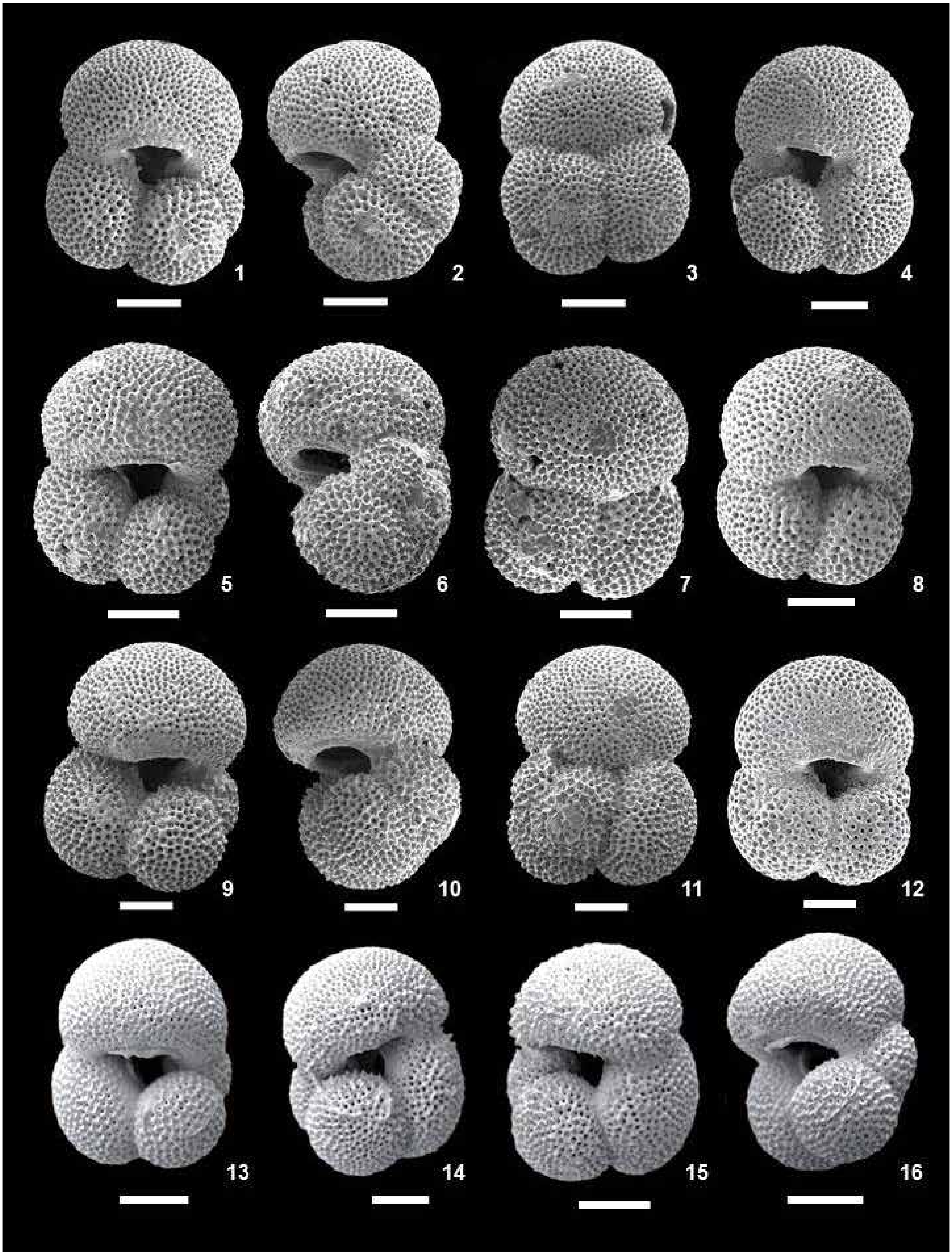

Plate 11.12 *Dentoglobigerina taci* Pearson and Wade, 2015

GEOGRAPHIC DISTRIBUTION.— Occurs in low to mid-latitudes.

STABLE ISOTOPE PALEOBIOLOGY.— Listed as a surface-dwelling form by Poore and Matthews (1984), although this may refer to a different species concept.

REPOSITORY.— Holotype (IF-380) deposited at the Micropaleontology-Stratigraphy Laboratory of the Institute of Geology and Paleontology, University of Bologna, Italy.

Dentoglobigerina taci **Pearson and Wade, 2015**

PLATE 11.12, FIGURES 1-16

Dentoglobigerina taci Pearson and Wade, 2015:18-19, figs. 18.1, 18.2, 18.4, 19.1-19.9 [lower Oligocene Zone O1, TDP Site 17, Tanzania], 18.3, 18.5 [upper Eocene Zone E15/16, TDP Site 12, Tanzania].

DESCRIPTION.

Type of wall: Cancellate and probably spinose in life.

Test morphology: "Test large, globular, approximately 12-13 chambers arranged in a moderate trochospiral, outline oval and slightly lobate, chambers globular and radially compressed; in spiral view 3½ appressed and embracing chambers in final whorl, increasing moderately to rapidly in size, sutures slightly curved, depressed; in umbilical view 3½ globular and appressed chambers, increasing moderately rapidly in size, sutures depressed, straight or slightly curved, umbilicus moderately wide, rectangular, and deep; aperture umbilical, centrally placed usually with a lip of constant thickness; in edge view chambers globular in shape, embracing, the final chamber tending to lean slightly over the umbilicus. May be dextral or sinistral, with a slight bias in favor of sinistral coiling." (Pearson and Wade, 2015:18.)

Size: Maximum diameter of holotype 0.39 mm.

DISTINGUISHING FEATURES.— *Dentoglobigerina taci* is similar in gross morphology to *D. galavisi* but has a more open umbilicus and lacks the irregular triangular lip projecting over the umbilicus that is part of the diagnosis of *D. galavisi* sensu stricto (Blow, 1979; Olsson and others, 2006). Unlike *D. galavisi* it generally has a lip of relatively constant thickness rather than a tooth, and a rectangular umbilical depression rather than triangular in *D. galavisi*. This species differs from *D. prasaepis* by its less compressed chambers and square (rather than rectangular) umbilicus and from *D. pseudovenezuelana* principally by having a more open umbilicus than is normally seen in that species and by lacking the densely pustulose umbilical ornamentation characteristic of that species. It differs from *D. tapuriensis* principally by lacking the broad final chamber and broad, low aperture that is characteristic of that species (modified from Pearson and Wade, 2015). *Dentoglobigerina taci* is distinguished from *Subbotina eocaena* by its less globular chambers and more open, higher arched aperture.

Dentoglobigerina taci is morphologically similar to *Globoturborotalita cancellata* (Pessagno), but differs by having broader chambers, giving the test a squarer and less lobate outline, and the final chamber overhangs the umbilicus, as is typical in the genus. Its also has a less cancellate wall texture (see Chapter 8, this volume, for discussion and SEM images of *G. cancellata*).

DISCUSSION.— According to Pearson and Wade (2015), *taci* is morphologically and evolutionarily intermediate between *D. galavisi* and *D. tapuriensis*.

PHYLOGENETIC RELATIONSHIPS.— Evolved from *D. galavisi* in the upper Eocene (Pearson and Wade, 2015) and is ancestral to *D. tapuriensis*.

STRATIGRAPHIC RANGE.— Uppermost Eocene to lower Oligocene. The highest occurrence has yet to be determined.

TYPE LEVEL.— Lower Oligocene Zone O1, TDP Site 17, Stakishari, Tanzania.

GEOGRAPHIC DISTRIBUTION.— Low latitudes,

Plate 11.12 *Dentoglobigerina taci* Pearson and Wade, 2015

1-3 (holotype, NHMUK PM PF 71165), (Pearson and Wade, 2015; fig. 18.1a-c); **5-11**, Zone O1, TDP Site 17, Stakishari, Tanzania; **4** (Pearson and Wade, 2015; fig. 18.3a) Zone E15/16, TDP Site 12, Stakishari, Tanzania; **12**, Zone O1, DSDP Sample 242/13R/5, 38-40 cm, western Indian Ocean; **13-16**, Zone O1, Shubuta Fm., Alabama. Scale bar: **1-16** = 100 µm.

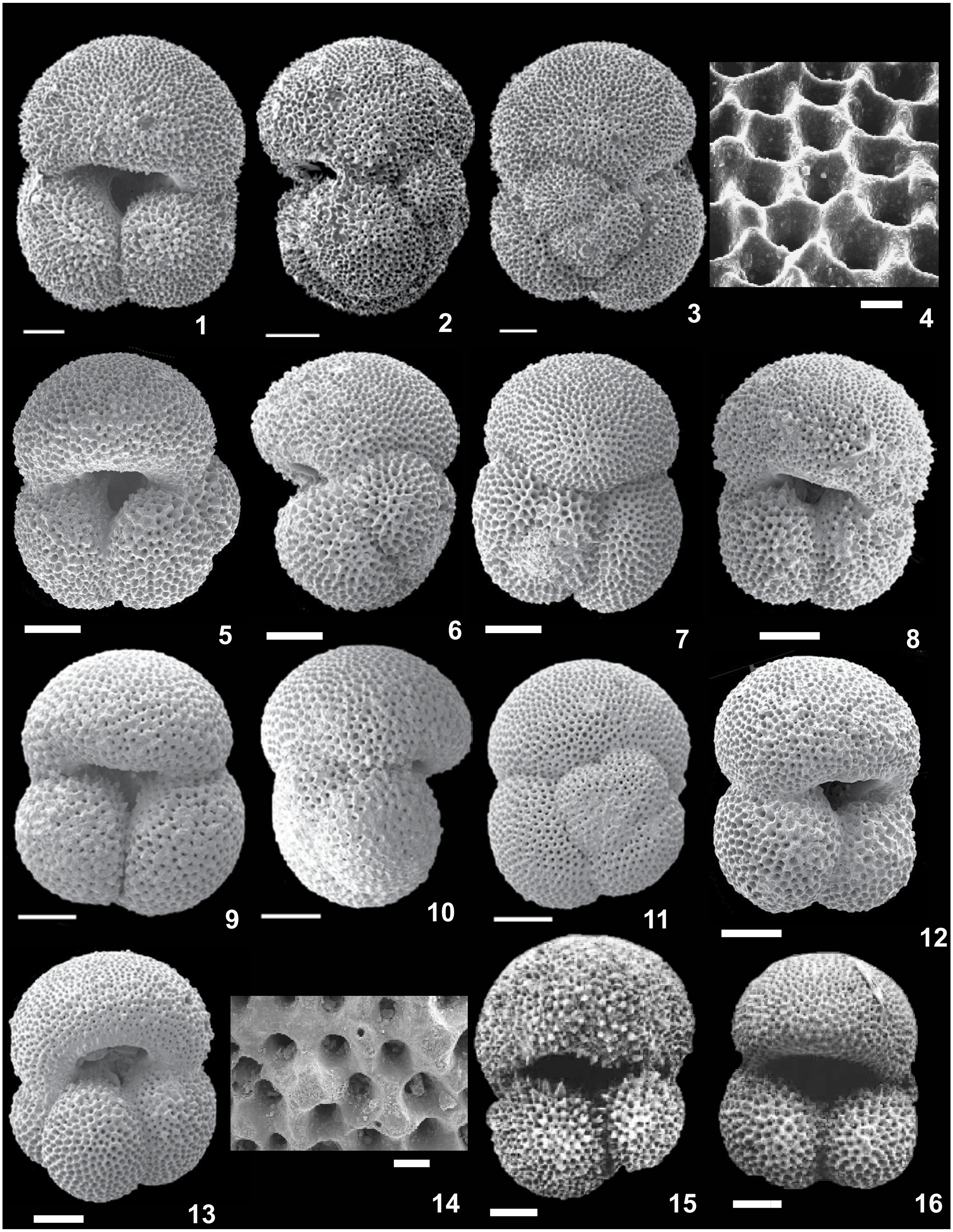

Plate 11.13 *Dentoglobigerina tapuriensis* (Blow and Banner, 1962)

currently confirmed only from the Indian Ocean (Tanzania), Gulf of Mexico (US Gulf Coast) and equatorial Pacific Ocean (IODP Site U1334).

STABLE ISOTOPE PALEOBIOLOGY.— Multispecies stable isotope data indicate negative $\delta^{18}O$ values in comparison to the rest of the assemblage, suggesting calcification in the mixed-layer (Moore and others, 2014, recorded as *Dentoglobigerina* sp. 1).

REPOSITORY.— Holotype (NHMUK PM PF 71165) and paratypes (NHMUK PM PF 71166-71174) deposited at the Natural History Museum, London.

Dentoglobigerina tapuriensis (Blow and Banner, 1962)

Plate 11.13, Figures 1-16

Globigerina tripartita tapuriensis Blow and Banner, 1962:97-98, pl. 10, figs. H-K [lower Oligocene *G. oligocaenica* Zone, Lindi area, Tanzania].

Globigerina tapuriensis Blow and Banner.—Blow 1969:322, pl. 16, figs. 7, 8 [lower Oligocene Zone P19, Lindi area, Tanzania].—Jenkins and Orr, 1972:1090, pl. 11, figs. 7-9 [lower Oligocene *P. barbadoensis* Zone, DSDP Hole 77B, eastern equatorial Pacific Ocean].—Blow, 1979:859-861, pl. 16, figs. 7, 8 (reproduced from Blow, 1969, pl. 16, figs. 7, 8), pl. 245, fig. 9 [lower Oligocene Zone P18, DSDP Site 14, central South Atlantic Ocean], pl. 247, fig. 2 [lower Oligocene Zone P19/20, DSDP Site 14, central South Atlantic Ocean].—Leckie and others, 1993:124, pl. 5, fig. 11 [lower Oligocene Zone P18, ODP Hole 803D, Ontong Java Plateau, western equatorial Pacific Ocean], pl. 5, fig. 12 [lower Oligocene Zone P20, ODP Hole 803D, Ontong Java Plateau, western equatorial Pacific Ocean], pl. 5, figs. 13, 15 [lower Oligocene Zone P19, ODP Hole 628A, Little Bahama Bank, western North Atlantic Ocean], pl. 5, fig. 14 [upper Oligocene Zone P22, ODP Hole 628A, Little Bahama Bank, western North Atlantic Ocean], pl. 5, fig. 16 [lower Oligocene Zone P18, ODP Hole 628A, Little Bahama Bank, western North Atlantic Ocean].

Globoquadrina tripartita tapuriensis (Blow and Banner).—Fleisher, 1974:1025, pl. 10, fig. 4 [lower Oligocene Zone P18/P19, DSDP Site 219, Arabian Sea].

"Globoquadrina" tapuriensis (Blow and Banner).—Spezzaferri and Premoli Silva, 1991:248, pl. 9, figs. 3a-c [lower Oligocene Subzone P21a, DSDP Hole 538A, Gulf of Mexico].

Dentoglobigerina tapuriensis (Blow and Banner).—Pearson and Wade, 2015:19, figs. 20.1a-d (SEMs of the holotype of *Globigerina tripartita tapuriensis* Blow and Banner), fig. 20.2 [lower Oligocene Zone O1, TDP Site 12, Stakishari, Tanzania], figs. 20.3, 20.5, 20.6, 20.8, 20.9 [lower Oligocene Zone O1, TDP Site 17, Stakishari, Tanzania], figs. 20.4a-b [upper Eocene Zone E15/16, TDP Site 12, Stakishari, Tanzania], fig. 20.7 [upper Eocene Zone E15/16, TDP Site 17, Stakishari, Tanzania].

Globoquadrina tripartita Koch.—Spezzaferri and Premoli Silva, 1991:248, pl. 3, figs. 2a-c.—Spezzaferri, 1994:42, pl. 42, figs. 2a-c (reproduced from Spezzaferri and Premoli Silva, 1991:248, pl. 3, fig. 2a-c). [Not Koch, 1926.]

Not *Globoquadrina tapuriensis* (Blow and Banner).—Li and others, 2005:19, pl. 2, fig. 7 (= *Dentoglobigerina tripartita*).

DESCRIPTION.

Type of wall: Cancellate and probably spinose in life.

Test morphology: Test large, chambers globular, arranged in a moderate trochospiral, outline oval, chambers moderately to strongly radially compressed; in spiral view 3, occasionally up to 3½ appressed and embracing chambers in final whorl, increasing rapidly in size, sutures straight to slightly curved, weakly depressed; in umbilical view 3, occasionally up to 3½ globular and appressed chambers in final whorl, increasing rapidly in size, sutures incised, straight or slightly curved, umbilicus wide, oval, and deep; aperture umbilical, a wide arch, centrally placed usually with a thin lip of constant thickness; in edge view chambers globular in shape, embracing, the final chamber leaning over the umbilicus.

Size: Maximum of holotype 0.73 mm.

Plate 11.13 *Dentoglobigerina tapuriensis* (Blow and Banner, 1962)

1-4 (holotype, BMNH P44518), *Globigerina oligocaenica* Zone, Lindi area, Tanzania; **5-7**, (Pearson and Wade, 2015; fig. 20.2) Zone O1, TDP Site 12, Tanzania; **8**, (Pearson and Wade, 2015; fig. 20.3) Zone O1, TDP Site 17, Stakishari, Tanzania; **9-11**, Zone O7, Atlantic Slope Project corehole 5B/190/29-35", western Atlantic Ocean; **12**, (Pearson and Wade, 2015; fig. 20.8) Zone O1, TDP Site 17, Stakishari, Tanzania, specimen transitional to *D. taci*; **13**, **14**, (Pearson and Wade, 2015; fig. 20.7) Zone E15/E16, TDP Site 17, Stakishari, Tanzania; **15**, (Leckie and others, 1993, pl. 5, fig. 14), Zone P22, ODP Hole 628A, Little Bahama Bank, western North Atlantic Ocean; **16**, (Leckie and others, 1993, pl. 5, fig. 13), Zone P19, ODP Hole 628A, Little Bahama Bank, western North Atlantic Ocean. Scale bar: **1-3**, **5-13**, **15-16** = 100 µm; **4**, **14** = 10 µm.

DISTINGUISHING FEATURES.— *Dentoglobigerina tapuriensis* is distinguished from its ancestor, *D. taci*, by its broader, more radially compressed final chamber, and by generally having fewer chambers in the final whorl and a narrower apertural lip. Like *D. taci*, it seems never to have an umbilical tooth. It is distinguished from its probable descendant, *D. sellii*, by having more lobate outline and less flattened umbilical face.

DISCUSSION.— This species was described by Blow and Banner (1962) from Tanzania. The holotype was illustrated in SEM by Pearson and Wade (2015) for the first time, along with a range of comparable specimens from drill sites in Tanzania. The species is generally quite rare, but has been reliably recorded from the lower Oligocene from all the major ocean basins.

PHYLOGENETIC RELATIONSHIPS.— Blow (1969) suggested an evolutionary lineage from *tripartita – tapuriensis – sellii – binaiensis*. While we agree with the *tapuriensis – sellii – binaiensis* evolutionary line, we now regard *D. galavisi* as the more likely ancestral form evolving through the intermediate *D. taci*.

STRATIGRAPHIC RANGE.— This species ranges through the entire Oligocene. Most authors have regarded it as originating in the basal Oligocene, but Wade and Pearson (2008) and Pearson and Wade (2015) recorded its lowest occurrence in the uppermost Eocene (Zone E15/E16). Spezzaferri and Premoli Silva (1991) recorded its highest occurrence in Subzone P21b. However, one of the specimens illustrated by Leckie and others (1993), on their pl. 5, fig. 14, is from upper Oligocene Zone P22, and we have observed and here illustrate specimens from Zone O7 of the western North Atlantic Ocean.

TYPE LEVEL.— The holotype is from Sample FCRM1964, from the *G. oligocaenica* Zone of the Lindi area, Tanzania (probably referable to lower Oligocene Zone O2).

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

STABLE ISOTOPE PALEOBIOLOGY.— No data available.

REPOSITORY.— Holotype (BMNH P44518) deposited at the Natural History Museum, London.

Dentoglobigerina tripartita (Koch, 1926)

Plate 11.14, Figures 1-9; Plate 11.15, Figures 1-16
(Pl. 11.14, Figs. 1-3: new SEMs of holotype of *Globigerina bulloides* (d'Orbigny) var. *tripartita* Koch)
(Pl. 11.14, Figs. 4-6: new SEMs of holotype of *Globoquadrina dehiscens praedehiscens* Blow and Banner)
(Pl. 11.14, Figs. 7-9: new SEMs of holotype of *Globigerina rohri* Bolli)

Globigerina bulloides var. *tripartita* Koch, 1926:742, fig. 21a, b [middle Tertiary, lower Globigerina marl, Sadjau-Njak, southeast Bulongan, East Borneo].

Globigerina tripartita Koch.—Blow and Banner, 1962:96 (partim), pl. 10, figs. A-C (re-illustration of holotype).—Brönnimann and Resig, 1971:1302, pl. 8, fig. 6 [upper Oligocene to lower Miocene Zone N4, DSDP Hole 64.1, Ontong Java Plateau, western equatorial Pacific Ocean].—Postuma, 1971:276, pl. on p. 277: 7 unnumbered figs. [Trinidad, unknown level].—Stainforth and others, 1975:325-328 (partim), fig. 148, nos. 2, 4 [lower to upper Oligocene *Globorotalia opima opima* Zone, Panama], fig. 148, no. 3 (reproduction of holotype illustration of *Globigerina tripartita* Koch from Koch, 1926, figs. 21a, b), fig. 148, nos. 7, 8 (reproduction of paratype and holotype illustrations of *Globigerina rohri* Bolli from Bolli, 1957, pl. 23, figs. 1a, 2b) (not fig. 148, nos. 1, 6 = *Dentoglobigerina eotripartita* n. sp.).—Quilty, 1976:639, pl. 4, figs. 9, 10 [upper Oligocene to lower Miocene Zone N4, DSDP Site 320, Nazca Plate, southeastern Pacific Ocean].—Bolli and Saunders, 1985:181, pl. 14, fig. 13 (reproduction of holotype from Blow and Banner, 1962, pl. 10, figs. A-C).—Leckie and others, 1993:124, pl. 5, figs. 6-8 [upper Oligocene Zone P22, ODP Hole 628A, western North Atlantic Ocean], pl. 5, fig. 9 [upper Oligocene Subzone P21b, ODP Hole 803D, Ontong Java Plateau, western equatorial Pacific Ocean], pl. 5, fig. 10 [lower Oligocene Zone P19, ODP

Plate 11.14 *Dentoglobigerina tripartita* (Koch, 1926)

1-3 (holotype Koch, 1926), Naturhistorisches Museum, Basel, middle Tertiary, Sadjau-Njak, East Borneo; **4-6** (holotype of *Globoquadrina dehiscens praedehiscens* Blow and Banner, 1962, BMNH P44562, upper Oligocene / lower Miocene *Globorotalia kugleri* Zone, Cipero Fm., Trinidad); **7-9** (holotype of *Globoquadrina rohri* Bolli, 1957, P5611), Oligocene *Globorotalia opima opima* Zone, Cipero Fm., Trinidad. Scale bar: **1-9** = 100 µm.

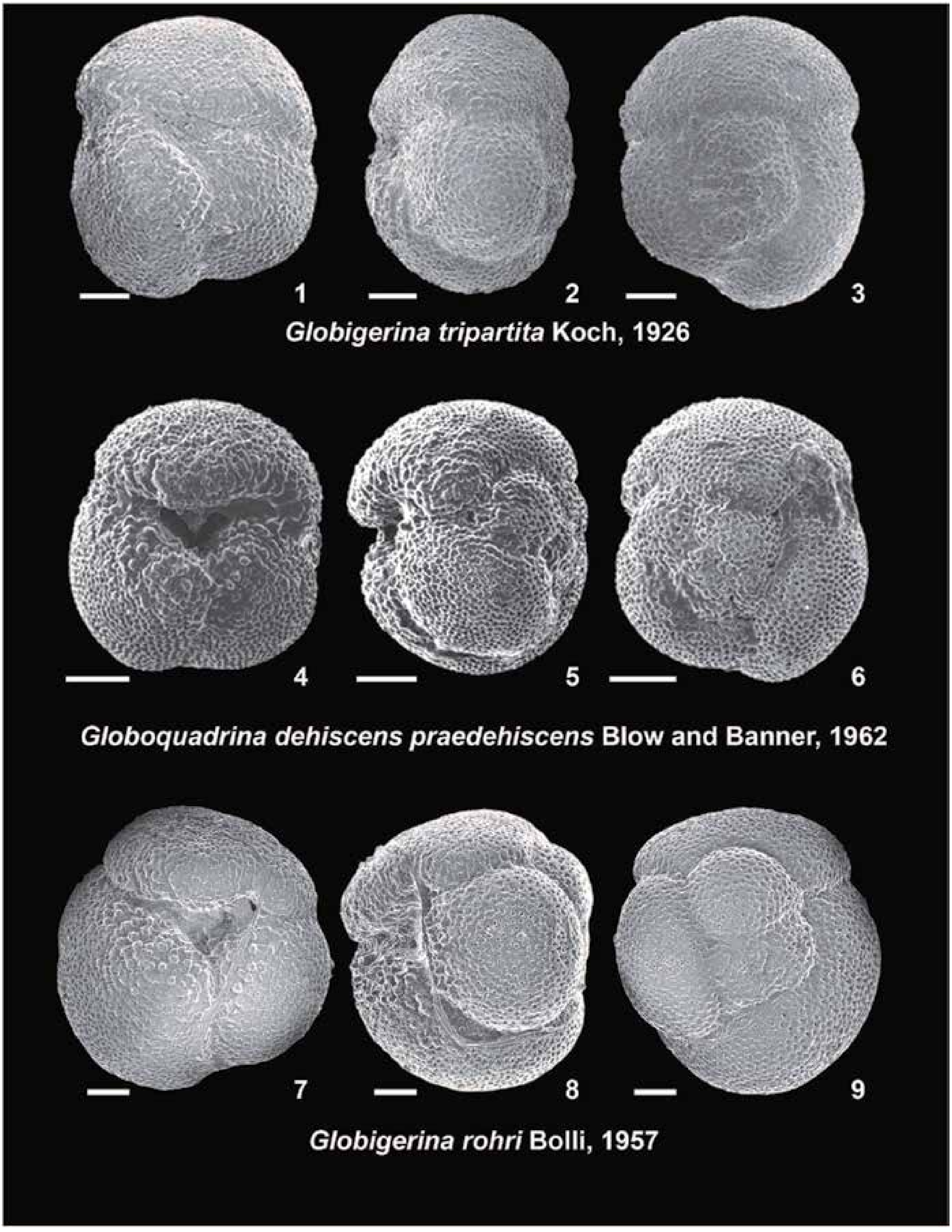

Plate 11.14 *Dentoglobigerina tripartita* (Koch, 1926)

Hole 803D, Ontong Java Plateau, western equatorial Pacific Ocean].

Globigerina tripartita tripartita Koch.—Raju, 1971:27, pl. 3, fig. 3 [lower Oligocene *Globigerina sastrii* Zone, Well No. KKL-4, Cauvery Basin, southern India].

Globoquadrina tripartita (Koch).—Fleisher, 1975, pl. 1, fig. 4 [lower Oligocene *"Turborotalia" ampliapertura* Zone, DSDP Site 313, central North Pacific Ocean].—Spezzaferri and Premoli Silva, 1991 (partim):248, pl. 9, fig. 2a-c [upper Oligocene Zone P22, DSDP Hole 528A, Gulf of Mexico].

Dentoglobigerina tripartita (Koch).—Fox and Wade, 2013:399, figs. 8.1-3 [middle Miocene Zone M7 (note this specimen is from Sample U1338B-38H-2, 40-42 cm, not Core 36H as it says in the caption), IODP Hole U1338B, equatorial Pacific Ocean].

Globigerina rohri Bolli, 1957:109, pl. 23, figs. 1a-4b [lower to upper Oligocene *Globorotalia opima opima* Zone, Cipero Fm., Trinidad].

Globoquadrina rohri (Bolli).—Blow, 1959:185, pl. 11, fig. 57a-c [lower Miocene *Catapsydrax stainforthi* Zone, San Lorenzo Fm., Venezuela].—Spezzaferri and Premoli Silva, 1991:248, pl. 9, figs. 5a-c [lower Oligocene Subzone P21a, DSDP Hole 528A, Gulf of Mexico].—Spezzaferri, 1994:43-44, pl. 42, figs. 1a-c (reproduced from Spezzaferri and Premoli Silva, 1991, pl. 9, figs. 5a-c).

Globigerina tripartita rohri Bolli.—Raju, 1971:27, pl. 3, figs. 2, 4a-b [lower Oligocene *Globigerina sastrii* Zone, Well No. KKL-4, Cauvery Basin, southern India].

"Dentoglobigerina" rohri (Bolli).—Pearson and Wade, 2009:203, pl. 3, figs. 1a-c [upper Oligocene Zone O6 (= O7 of this study), Cipero Fm., Trinidad].

Globoquadrina dehiscens praedehiscens Blow and Banner, 1962:116, pl. 15, figs. Q-S. [upper Oligocene *Globorotalia kugleri* Zone, Cipero Fm., Trinidad].—Blow, 1969:341, pl. 29, figs. 3-5 [upper Oligocene *Globorotalia kugleri* Zone, Cipero Fm., Trinidad].—Quilty, 1976:644, pl. 10, figs. 20-21 [lower Miocene Zone N8, DSDP Site 320, Nazca Plate, southeastern Pacific Ocean].—Iaccarino, 1985:304, fig. 5.11, no. 4 (reproduction of holotype from Blow and Banner, 1962, pl. 15, figs. Q-S).

Globoquadrina praedehiscens Blow and Banner.—Poore, 1979:470, pl. 18, figs. 4-6 [lower Miocene Zone N5, DSDP Site 407, North Atlantic Ocean], fig. 7 [upper Oligocene Zone P22, DSDP Site 407, North Atlantic Ocean].—Kennett and Srinivasan, 1983:182, pl. 45, figs. 4-6 [lower Miocene *Catapsydrax dissimilis* Zone, DSDP Site 208, Lord Howe Rose, Tasman Sea].—Berggren and others, 1983, pl. 1, fig. 1 [lower Miocene Zone N5, DSDP Site 516, Rio Grande Rise, South Atlantic Ocean].

Globigerina sakitoensis Asano, 1962:60, pl. 22, fig. 1a-c [Oligocene, 126 m in drill hole, Nakado, Kyushu, Japan].

Globigerina sastrii Raju, 1971:26, pl. 4, figs. 1a-c (holotype) [lower Oligocene *Globigerina sastrii* Zone, Well No. KKL-4, Cauvery Basin, southern India], figs. 2a-c (paratype) [lower Oligocene *Globigerina sastrii* Zone, Well No. TPD-1, Cauvery Basin, southern India].

Globigerina sellii (Borsetti).—Postuma, 1971:272, pl. on p. 273, 7 images (= form intermediate between *Dentoglobigerina eotripartita* and *D. tripartita*) [lower Oligocene *Globigerina oligocaenica* Zone, Lindi area, Tanzania]. [Not Borsetti, 1959.]

Globoquadrina sellii Borsetti.—Li and others, 2005:19, pl. 2, figs. 8-10 [upper Oligocene Zone P22, ODP Hole 1148A, South China Sea]. [Not Borsetti, 1959.]

Globoquadrina tapuriensis (Blow and Banner).—Li and others, 2005:19, pl. 2, fig. 7 [lower Oligocene Subzone P21a, ODP Hole 1148A, South China Sea]. [Not Blow and Banner, 1962.]

Globoquadrina dehiscens (Chapman, Parr, and Collins) sensu lato.—Li and others, 2005:19, pl. 2, figs. 11, 12 [upper Oligocene Zone P22, ODP Hole 1148A, South China Sea]. [Not Chapman, Parr, and Collins, 1934.]

Not *Globigerina tripartita* Koch.—Blow and Banner, 1962:96, pl. 10, figs. D-F.—Blow, 1969:322, pl. 16, fig. 6 (= *Dentoglobigerina eotripartita* n. sp.).

Not *Dentoglobigerina tripartita* (Koch).—Blow, 1979:1310, pl. 244, figs. 3, 4.—Olsson and others, 2006:408-410 (partim), pl. 13.3, figs. 4-11, 13-15 (= *Dentoglobigerina eotripartita* n. sp.).—Li and others, 2005:19, pl. 2, fig. 6 (= *Dentoglobigerina venezuelana*).—Olsson and others, 2006:408-410 (partim), pl. 13.3, figs. 12, 16 (= *Dentoglobigerina galavisi*).

Not *Globoquadrina tripartita* (Koch).—Spezzaferri and Premoli Silva, 1991:248, pl. 3, figs. 2a-c.—Spezzaferri, 1994:42, pl. 42, figs. 2a-c (reproduced from Spezzaferri and Premoli Silva, 1991:248, pl. 3, fig. 2a-c) (= *Dentoglobigerina tapuriensis*).

Not *Globoquadrina dehiscens praedehiscens* Spezzaferri and Premoli Silva, 1991:248, pl. 9, figs. 1a-c.—Spezzaferri, 1994:43, pl. 43, figs. 1a-c (reproduced from Spezzaferri and Premoli Silva, 1991, pl. 9, figs. 1a-c) (= *Dentoglobigerina sellii*).

Plate 11.15 *Dentoglobigerina tripartita* (Koch, 1926)

1-3 (same specimen), Zone O6 Sample ODP 628A/24X/1, 100-102 cm, Little Bahama Bank, western North Atlantic Ocean; **4**, **8** (same specimen), Zone M1, ODP Site 904A/35/5, 101-106 cm, western North Atlantic Ocean (same specimen); **5-7** (same specimen), Zone O7, Sample ODP 628A/17H/CC, Little Bahama Bank, western North Atlantic Ocean; **9-11** (same specimen), Zone O7, Sample ODP 628A/17H/3, 100-102 cm, Little Bahama Bank, western North Atlantic Ocean; **12**, Zone O6, Cipero Fm., RDL sample 1017, Trinidad; **13-16** (same specimen), Subzone M1a, Atlantic Slope Project corehole 5, 16B/29-35", western Atlantic Ocean. Scale bar: **1-15** = 100 µm; **16** = 10 µm.

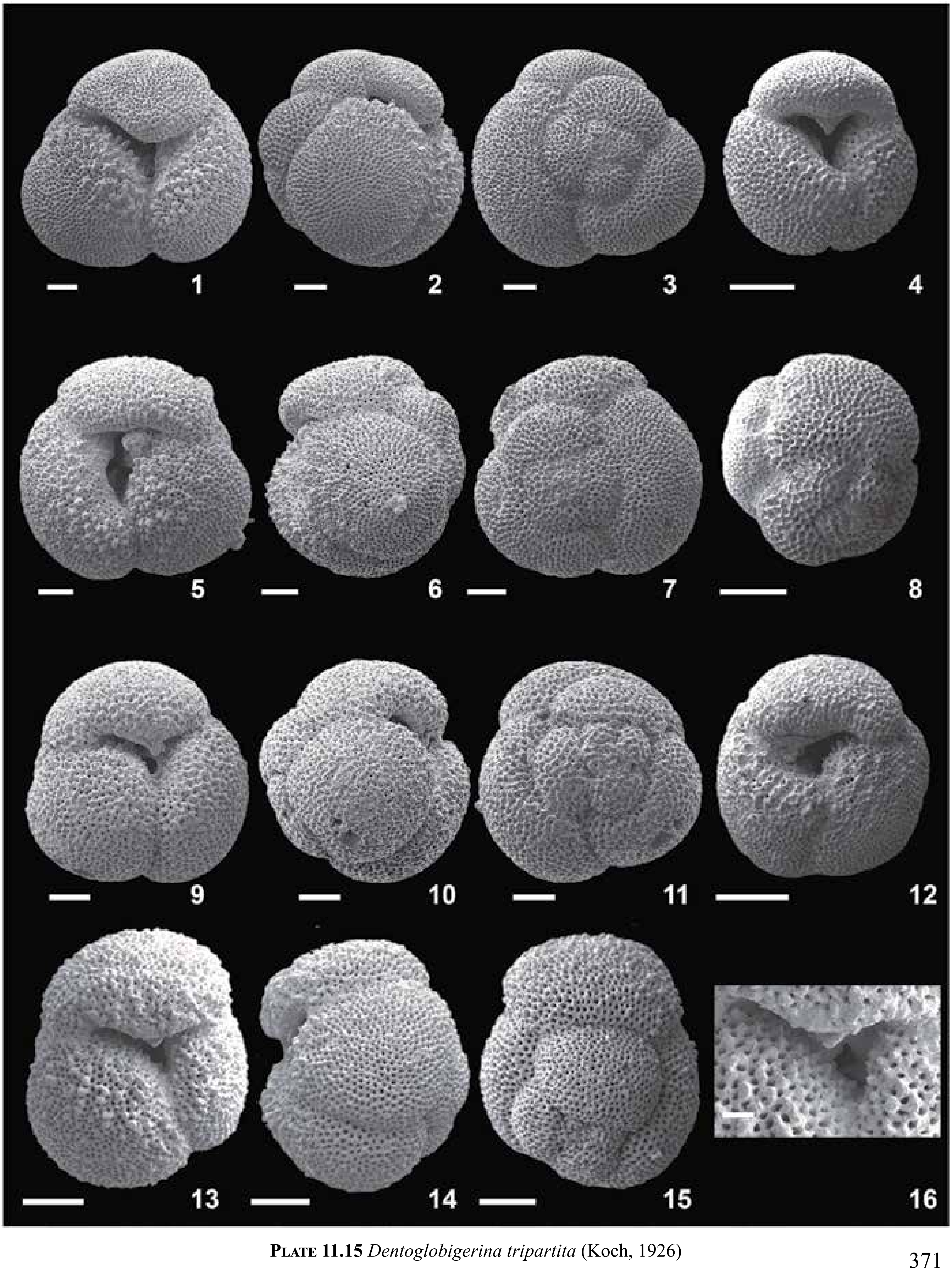

Plate 11.15 *Dentoglobigerina tripartita* (Koch, 1926)

DESCRIPTION.

Type of wall: Cancellate, probably spinose in life, pustulose, with concentrations of pustules on the umbilical shoulders.

Test morphology: Large, robust, globular, sub-spherical, outline sub-circular; in spiral view 3 embracing, elliptical shaped chambers, arranged in a moderate trochospire, that rapidly increase in size in final whorl, ultimate chamber may be reduced in size; in edge view globular, sub-circular in outline; in umbilical view 3 embracing chambers in final whorl that rapidly increase in size, final chamber commonly reduced in size, somewhat reniform, umbilicus small, triangular, open, aperture umbilical bordered by an irregular triangular shaped tooth covered in small pustules.

Size: Maximum diameter of holotype 0.52 mm, minimum diameter 0.50 mm.

DISTINGUISHING FEATURES.— *Dentoglobigerina tripartita* is distinguished from *D. eotripartita* by its larger and more robust, sub-spherical morphology. It is distinguished from *D. sellii* by the more compressed and reniform final chambers, and in lacking the large inflated final chamber typical of the *sellii* species.

DISCUSSION.— This is a very common species that can dominate assemblages, especially in the upper Oligocene, and it also persists well into the Miocene. Its evolution seems to have involved gradual development of more compact spherical forms, at times having even fewer than three whole chambers in the final whorl, and there is also an increasingly frequent occurrence of a small, cap-like final chamber.

When the *Atlas of Eocene Planktonic Foraminifera* was published, we had been unable to obtain SEMs of the holotype of *Globigerina tripartita* Koch, and we based our concept on the re-illustration provided by Blow and Banner (1962) and the concept developed by Blow and Banner (1962), Blow (1969) and Blow (1979) from their studies of material from the upper Eocene of Tanzania. Here we provide new SEMs of the holotype for the first time which reveal a robust, sub-spherical form, as is typical in particular of upper Oligocene assemblages, which contrasts with the smaller, more gracile forms described by Blow and Banner (1962) and various other authors up to Olsson and others (2006) from the Eocene. In this study we follow Pearson and Wade (2015) in regarding those forms as distinct, and we name a new species, *D. eotripartita*, to accommodate them (see discussion under that species). Our revised concept of the true *tripartita* is exemplified by specimens previously illustrated by Brönnimann and Resig (1971), Quilty (1976), and Leckie and others (1993) from a variety of deep sea drill sites.

Bolli (1957) named *Globigerina rohri* from the *opima* Zone of Trinidad, but seems to have been unaware of the previously described *Globigerina tripartita* Koch. Blow and Banner (1962) re-studied and re-illustrated the holotype of *tripartita* and proposed that it was a senior synonym of *rohri* (see also Blow, 1969, 1979), which was followed by Stainforth and others (1975) and most other authors and seems also to have been accepted by Bolli (see Bolli and Saunders, 1985, in which *rohri* is not mentioned). However, Spezzaferri and Premoli Silva (1991:248) and Spezzaferri (1994) recognized *tripartita* and *rohri* as distinct taxa.

Blow and Banner (1962) described *Globoquadrina dehiscens praedehiscens* from the upper Oligocene of Trinidad, arguing that the morphology was the direct ancestor of *Globoquadrina dehiscens*. Blow (1969) illustrated another adult specimen and the internal morphology of two dissected specimens, revealing what he called the "*Globigerina tripartita* early stage" (Blow, 1969, caption to pl. 29). We would now regard this as a "*Dentoglobigerina eotripartita*" early stage. In our view, this interesting observation supports the evolutionary relationship between *eotripartita* and *tripartita*, and indicates that the *eotripartita* morphology likely persists as a juvenile into the uppermost Oligocene. Whereas most authors to date have accepted the notion of an evolutionary lineage from *praedehiscens* to *dehiscens*, others (e.g., Fleisher, 1974, and Stainforth and others, 1975) have disagreed, regarding *praedehiscens* as a variant of *tripartita* (see also discussion in Iaccarino, 1985). Pearson and Wade (2009) examined new specimens from very close to the type locality of *praedehiscens* and placed it in questionable synonymy with *tripartita*.

As part of our study we have examined the type specimens of all three of these historically important species and obtained new SEMs (compared on Plate 11.14). Although one can recognize minor differences between the specimens (e.g., *rohri* is somewhat more spherical, and *praedehiscens* has a more obvious umbilical tooth) such variability is within the normal bounds of populations. Moreover, there is little difference in the reported stratigraphic ranges of the three taxa. Hence we here regard them as synonyms, with *tripartita* having seniority. In our investigations we have found no evidence that *tripartita* (=*praedehiscens*) is ancestral to *dehiscens*. Instead, we describe morphological intermediates between *Dentoglobigerina larmeui* and *Globoquadrina dehiscens* (see discussion under those taxa), the latter taxa forming a separate but morphologically similar subclade in the dentoglobigerinid tree (Figure 11.1).

Globigerina sakitoensis Asano was described from the Oligocene of Japan. Blow (1969) and (1979) considered this form to be synonymous with *Dentoglobigerina sellii* and *Dentoglobigerina tapuriensis*, respectively. Although we have not obtained new holotype images of this species, based on the original drawings and description, we considered this form to be a junior synonym of *Dentoglobigerina tripartita*. *Globigerina sastrii* Raju is a rather extreme, almost bilobate form that we also include here in synonymy.

PHYLOGENETIC RELATIONSHIPS.— *Dentoglobigerina tripartita* evolved from *D. eotripartita* n. sp. in the early Oligocene.

STRATIGRAPHIC RANGE.— This species has a distinct acme in the upper Oligocene. The oldest figured specimen we assign to this species is from lower Oligocene Zone O2 of DSDP Site 313, where the range is reported to extend intermittently down into the upper part of Zone O1 (Fleisher, 1975). We have observed *tripartita* sensu stricto appearing in the middle part of Zone O1 at IODP Site U1334 (B.S. Wade, unpublished data). The reported highest occurrence is variable, possibly because of varying species concepts. At IODP Sites U1337 and U1338 in the equatorial Pacific Ocean it is common to the top of Subzone M5b, and then infrequent until middle Miocene Zone M10/M11 (Pälike and others, 2010). The youngest figured specimen is from Zone M7 (Fox and Wade, 2013).

TYPE LEVEL.— Described from the 'middle Tertiary' (probably Oligocene) of Borneo.

GEOGRAPHIC DISTRIBUTION.— Cosmopolitan; it is common in the tropics and Miocene examples have been found up to 63°N at DSDP Site 407 (Poore, 1979).

STABLE ISOTOPE PALEOBIOLOGY.— Oligocene specimens from ODP Hole 758A registered among the most positive $\delta^{18}O$ of planktonic assemblages indicating a deep habitat, although earliest Oligocene specimens may have had a shallower water preference (van Eijden and Ganssen, 1995).

REPOSITORY.— Deposited at the Natural History Museum, Basel, Switzerland.

Dentoglobigerina venezuelana (Hedberg, 1937)

Plate 11.16, Figures 1-16
(Pl. 11.16, Figs. 1-3: new SEMs of holotype of *Globigerina venezuelana* Hedberg)

(Note: This synonymy list focuses on taxonomically important works and Oligocene to lower Miocene occurrences)

?*Globigerina conglomerata* Schwager, 1866:255-256, pl. 7, fig. 113 [upper Tertiary 'lower and upper clays' (probably lower Pliocene Zone PL1-2), Kar Nicobar, Bay of Bengal].

?*Globigerina conglomerata* Banner and Blow, 1960 (neotype of *Globigerina conglomerata* Schwager, ?Pliocene, Kar Nicobar, Bay of Bengal].

?*Globigerina bulloides* d'Orbigny var. *quadripartita* Koch, 1926:737, fig. 20a-c ['Middle Tertiary', Southwest Bulongan, Borneo].

Globigerina venezuelana Hedberg, 1937:681, pl. 92, fig. 7a, b [lower Miocene, Carapita Fm., northeastern Venezuela].—Postuma, 1971:278, pl. on p. 279, seven un-numbered figs. [unknown level, Trinidad].—Stainforth and others, 1975:331 (partim), fig. 1.51, nos. 3-6 [lower Miocene *Catapsydrax stainforthi* Zone, Cipero Fm., Trinidad] (not fig. 1.51, nos. 1, 2 = *Subbotina jacksonensis*).—Bolli and Saunders, 1985:180-181, fig. 13.20a, b (reproduction of the holotype illustration from Hedberg, 1937, pl. 92, fig. 7a, b).

Globoquadrina venezuelana (Hedberg).—Blow, 1959:186, pl. 11, figs. 58a-c [lower Miocene *Globigerinatella insueta* Zone, San Lorenzo Fm., Venezuela], pl. 11, fig. 59 [middle Miocene *Globorotalia mayeri* Zone, Pozón Fm., Venezuela].—Kennett and Srinivasan, 1983:180, pl. 44, figs. 2, 5-7 [middle Miocene Zone N10, DSDP Site 289, Ontong Java Plateau, western equatorial Pacific Ocean].—Pearson and Chaisson, 1997:60, pl. 2, fig. 14 [lower Miocene Zone N4, ODP Hole 929A, Ceara Rise, western North Atlantic Ocean].—Wade and Pälike, 2004, fig. 1c [upper Oligocene Zone O5, ODP Site 1218, equatorial Pacific Ocean], fig. 1d [upper Oligocene Zone O6, ODP Site 1218, equatorial Pacific Ocean].

"Globigerina" venezuelana (Hedberg).—Spezzaferri and

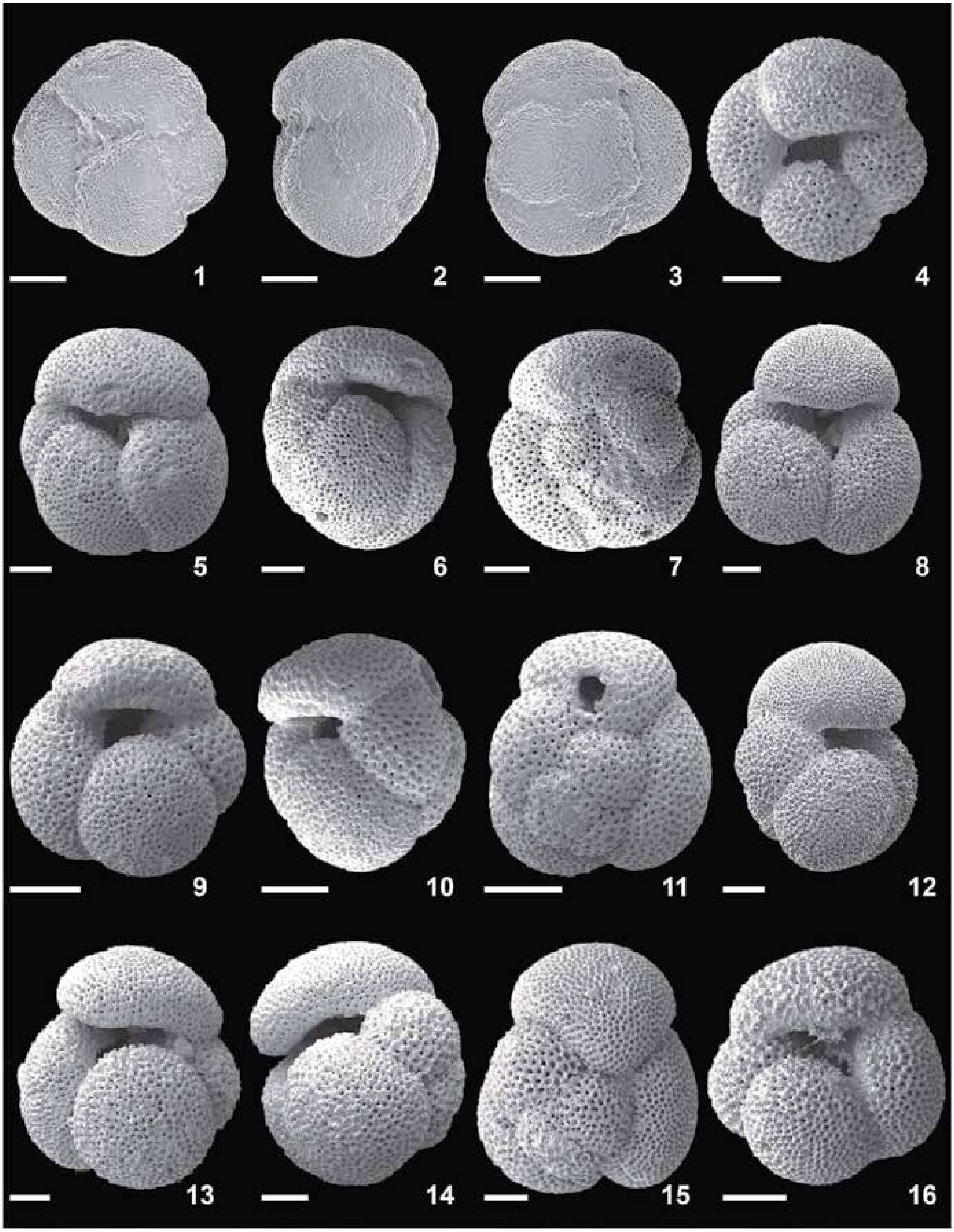

Plate 11.16 *Dentoglobigerina venezuelana* (Hedberg, 1937)

Premoli Silva, 1991:246, pl. 7, fig. 2a-c [upper Oligocene Zone P22, DSDP Hole 538A, Gulf of Mexico], fig. 5a, b [DSDP Site 522, Angola Basin].—Spezzaferri, 1994:30, pl. 37, figs. 2a-3d [lower Miocene Subzone N4a, ODP Hole 667A, equatorial Atlantic Ocean], pl. 38, figs. 2a-3c [lower Miocene Subzone N4b, ODP Hole 667A, equatorial Atlantic Ocean].

"Dentoglobigerina" venezuelana (Hedberg).—Pearson and Wade, 2009:203, pl. 3, fig. 3a-c [upper Oligocene Zone O6 (now considered O7), Cipero Fm., Trinidad].—Fox and Wade, 2013:400, figs. 8.4-8.6, 13.4 [lower Miocene Subzone M5a, IODP Site U1338, eastern equatorial Pacific Ocean].

?*"Dentoglobigerina" venezuelana* (Hedberg).—Stewart and others, 2012:85, pl. 1, figs. 1a-3f [upper Oligocene – lower Miocene Zones P22-N4, ODP Hole 925A, Ceara Rise, western North Atlantic Ocean].

Dentoglobigerina venezuelana (Hedberg).—Wade and others, 2016:pl. 6, fig. 7 [upper Oligocene Zone O6, IODP Hole U1334A, equatorial Pacific Ocean].

Globigerina prasaepis Blow, 1969:382 (partim, not holotype), pl. 18, figs. 3, 4 [lower Oligocene Zone P19/20, Cipero Fm., Trinidad].—Blow, 1979:184-185 (partim), pl. 18, figs. 5, 6 (reproduced from Blow, 1969, pl. 18, fig. 7).—Krasheninnikov and Pflaumann, 1978:591, pl. 2, figs. 4, 5 [Oligocene, DSDP Site 369, eastern North Atlantic Ocean]. [Not Blow, 1969.]

Globigerina euapertura / Globigerina pseudovenezuelana transition.—Leckie and others, 1993, pl. 4, fig. 14 [lower Oligocene Zone P18, ODP Hole 628A, Little Bahama Bank, western North Atlantic Ocean].

Globigerina pseudovenezuelana Blow and Banner.—Leckie and others, 1993:124, pl. 4, fig. 15 [lower Oligocene Zone P18, ODP Hole 628A, Little Bahama Bank, western North Atlantic Ocean], fig. 16 [upper Oligocene Zone P22, ODP Hole 628A, Little Bahama Bank, western North Atlantic Ocean], fig. 17 [lower Oligocene Zone P18, ODP Hole 803D, Ontong Java Plateau, western equatorial Pacific Ocean]. [Not Blow and Banner, 1962.]

Globoquadrina pseudovenezuelana Blow and Banner.—Li and others, 2003:16, pl. 2, figs. 17, 18 [level above the upper Eocene, ODP Hole 1134A, Great Australian Bight.] [Not Blow and Banner, 1962.]

DESCRIPTION.

Type of wall: Cancellate, probably spinose in life, pustulose, sometimes with concentrations of pustules on the umbilical shoulders.

Test morphology: Large to very large, robust, globular, spherical, outline circular; in spiral view 3½-4 embracing, reniform chambers that slowly increase in size in the final whorl, final chamber commonly reduced in size and flattened, sutures weakly depressed; in edge view globular, oval in outline; in umbilical view 3½-4 appressed and embracing chambers in final whorl that slowly increase in size, final chamber commonly reduced in size, partially closing the umbilicus, sutures depressed; umbilicus small, commonly triangular in shape, aperture umbilical, often concealed, may be bordered by an irregular triangular tooth or a lip with no tooth.

Size: Maximum diameter of holotype 0.52 mm, minimum diameter 0.50 mm.

DISTINGUISHING FEATURES.— Our taxonomic concept of *D. venezuelana* is quite broad, and includes specimens that may contain a lip or a tooth. The holotype of *D. venezuelana* is a large specimen, these large sized forms are quite rare in the Oligocene. *Dentoglobigerina venezuelana* is distinguished from the ancestral form, *D. prasaepis*, by its larger size, more embracing chambers, and tight umbilicus. It is somewhat homeomorphic with *Globoturborotalita euapertura*, but is distinguished by its wall texture, less incised sutures, and by having globular rather than wedge-shaped chambers in the early part of the final whorl. See under *D. pseudovenezuelana* for criteria for separating that species. It bears a close similarity with *Subbotina jacksonensis* (Bandy) described from the upper Eocene of Alabama, but *S. jacksonensis* has a higher trochospire and a final chamber that projects over the umbilicus.

DISCUSSION.— So-called '*Globoquadrina conglomerata* (Schwager)' is a commonly recognized component of modern living Indo-Pacific populations (Parker, 1962, 1967; Saito and others, 1981; Hemleben and others, 1989; and many subsequent studies), but here we point out that the specific name is, unfortunately, probably not valid for the living form, and that *conglomerata* is likely a prior synonym for the fossil species *Dentoglobigerina venezuelana* (Hedberg); however, to avoid further confusion, we do not advocate

Plate 11.16 *Dentoglobigerina venezuelana* (Hedberg, 1937)

1-3 (holotype, USNM 23614), lower Miocene, Carapita Fm., northeastern Venezuela; **4-7**, **9-11**, **16**, Zone O5, Atlantic Slope Project corehole 5, 5A/0-6", western Atlantic Ocean; **8**, **12**, Zone O7, Sample ODP 628A/17H, 100-102 cm, Little Bahama Bank, western North Atlantic Ocean; **13-15**, Zone O5, Atlantic Slope Project corehole 5B, 19D/29-35", western Atlantic Ocean. Scale bar: **1-16** = 100 µm.

using the name in that sense.

Schwager (1866) described *Globigerina conglomerata* from 'upper Tertiary' samples collected from Car (= 'Kar') Nicobar in the Bay of Bengal. Banner and Blow (1960) noted that Schwager's illustrated specimen was lost and selected a neotype from a collection of 40 specimens that had been sent by Schwager to H.B. Brady in London and discussed briefly by Brady (1884). Banner and Blow (1960) regarded all 40 specimens as conspecific with the type illustration, although Brady (1884) had expressed doubts on this. The neotype is deposited at the British Museum (Natural History) number P44031 and the rest of the collection is also there. The neotype (a large specimen, diameter 0.75 mm) was illustrated (line drawing) in three views and was accompanied by a detailed description by Banner and Blow (1960). Srinivasan and Sharma (1974) re-studied the type locality of *conglomerata* and showed that it is lower Pliocene (assigned to their Zone N19 and the lower part of Zone N20 = Zones PL1-2). We have viewed the lectotype and the rest of Schwager's collection at the Natural History Museum, London. In our view the collection is a typical lower Pliocene mixture of *Dentoglobigerina venezuelana* and *D. altispira*. The presence of *D. altispira* shows it must be older than Pliocene (~3.5 Ma). We note that the holotype comes from the same 'lower and upper clays' as *Sphaeroidinellopsis seminulina* Schwager, another reminder that it must be lower Pliocene at youngest. In our view the neotype is conspecific with *venezuelana*. We defer to workers on modern planktonic foraminifera to determine the correct name for the living form; here we refer to it as '*Dentoglobigerina* cf. *conglomerata* Schwager'.

Dentoglobigerina venezuelana may also have been described as *Globigerina bulloides* d'Orbigny var. *quadripartita* Koch, 1926, but that species was regarded as a *nomen dubium* by Blow and Banner (1962) who observed that the holotype was broken (see also Postuma, 1971).

Dentoglobigerina venezuelana has sometimes been confused with *Globoturborotalita euapertura*, *Dentoglobigerina prasaepis* and *D. pseudovenezuelana*. It is likely ancestral to the modern species, *D*. cf. *conglomerata*, which appears to have evolved from it over the Pliocene epoch, possibly via an intermediate form *Globoquadrina pseudofoliata* Parker (Parker, 1967; Chaisson and Leckie, 1993).

PHYLOGENETIC RELATIONSHIPS.— *Dentoglobigerina venezuelana* evolved from *D. prasaepis* in the early Oligocene (Pearson and Wade, 2015) and probably gave rise to the extant species *D.* cf. *conglomerata*.

STRATIGRAPHIC RANGE.— The lowest occurrence is not well constrained. Observations from DSDP Site 612 (H.K. Coxall, pers. comm.) and from Armenia suggest evolution in the late Eocene with confirmed occurrences from the lower Oligocene Zone O1 (Leckie and others, 1993). It persists to the Pliocene (e.g., Chaisson and Leckie, 1993).

TYPE LEVEL.— From Sample E4032 (topmost sample of the 'middle zone') of the 'middle Tertiary' Carapita Formation of Venezuela (Hedberg, 1937). Also occurring in this zone is '*G. triloba*'. The Carapita Fm. is now considered to be mostly lower Miocene (see Figure 20 of Ostos and others, 2005), with the type level likely mid-lower Miocene.

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

STABLE ISOTOPE PALEOBIOLOGY.— A variety of authors have analyzed this species for stable isotopes, and large specimens commonly register values indicative of a deep-dwelling habitat (e.g., Gasperi and Kennett, 1993; Pearson and Shackleton, 1995; Pearson and others, 1997; Pearson and Wade, 2009; Nathan and Leckie, 2009) but some studies have indicated a shallower calcification depth (e.g., Poore and Matthews, 1984; Wade and others, 2007; Beltran and others, 2014; Moore and others, 2014). The discrepancy may be partially resolved if the species lived near the surface when pre-adult, but with late-stage calcification at depth. Stewart and others (2012) published stable isotope data from a number of morphotypes of "*venezuelana*", suggesting a shallow habitat for pre-adult forms, deepening in the adult stage. However, we have found their images difficult to evaluate because of unorthodox umbilical orientations and lack of multiple views.

REPOSITORY.— Holotype (USNM 23614) deposited at Smithsonian Museum of Natural History, Washington, D.C.

Genus *Globoquadrina* Finlay, 1947

TYPE SPECIES.—*Globorotalia dehiscens* Chapman, Parr, and Collins, 1934.

DESCRIPTION.

Type of wall: cancellate, honeycomb wall, sometimes with pustulose chamber shoulders, becoming smooth and reflective in some specimens.

Test morphology: Trochospiral, quadrate, ultimate chamber with an angular apertural face; primary aperture umbilical with an asymmetrical triangular tooth.

DISTINGUISHING FEATURES.— The genus was erected by Finlay (1947) for forms with a subquadrate outline and umbilical aperture.

DISCUSSION.— Although safely restricted to a single species by us, this genus has not always been a caged beast, but rather has rampaged up and down the stratigraphical column and across unrelated groups, devouring a wide variety of forms. Finlay's (1947) original concept was for species which combine "the open umbilicus, terminal face, and apertural flaps of *Globotruncana*, the angular ventrally pointed chambers of *Globorotalia*, and the general compact shape of *Globigerina*" and he included in his genus not only *Globorotalia dehiscens* Chapman, Parr and Collins, but also *Globorotalia centralis* Cushman and Bermúdez (an Eocene form now considered *Turborotalia*), and two important Miocene species that are now placed in *Dentoglobigerina* (*Globigerina altispira* Cushman and Jarvis and *Globigerina venezuelana* Hedberg). Bolli, Loeblich and Tappan (1957:31) used it for forms that have an umbilical aperture and "apertural flaps covering each aperture" but Blow (1969:338 and 339) complained that this definition could also lead to inclusion of a wide variety of other forms. Even so, he used the genus for both the *dehiscens* and the *altispira* groups while recognizing that "this is probably an error". By subsequently introducing the genus *Dentoglobigerina* for globigeriniform species with umbilical teeth, Blow (1979) arguably compounded the problem, because it left unresolved the status of related forms that lack umbilical teeth (e.g., *tapuriensis*) or those in which umbilical teeth are not obligatory. Because of this dilemma, subsequent workers have varied greatly in their method of delimiting *Globoquadrina* and *Dentoglobigerina*, perhaps unsure of the phylogenetic link between the types of the two genera and how, where, and when the boundary between them should be drawn (e.g., Kennett and Srinivasan, 1983; Bolli and Saunders, 1985; Spezzaferri, 1994). Both genera have frequently been used in inverted commas, expressing this uncertainty. Our solution is to broaden the concept of *Dentoglobigerina* so that it does not require possession of an umbilical tooth (see discussion under that genus), and because we recognize the type species of that genus (*galavisi*) as the progenitor of the entire clade, we apply the genus to almost all its descendants; all that is except *dehiscens*, type species of the now monospecific genus *Globoquadrina*. Partly this is because treating the genera as synonyms would make *Globoquadrina* the senior name, upsetting the established usage of *Dentoglobigerina*; partly also it recognizes the distinctive quadrate nature of *dehiscens*, a highly specialized and morphologically derived branch of the *Dentoglobigerina* clade. Our solution is similar to that first proposed by Parker (1967) who complained that using *Globoquadrina* as a form-genus would result in widespread polyphyly and hence it was best restricted to *dehiscens* and just one closely related variant. If this relationship between *Dentoglobigerina* and *Globoquadrina* is correct, it implies that *Globoquadrina* belongs in the spinose Family Globigerinidae. Despite this, we have not so far found evidence of spines or spine holes in *G. dehiscens* and it may have secondarily lost its spines (see discussion above under Family Globigerinidae).

PHYLOGENETIC RELATIONSHIPS.— *Globoquadrina* evolved from *Dentoglobigerina* in the latest Oligocene or earliest Miocene (see discussion under *G. dehiscens*).

STRATIGRAPHIC RANGE.— Subzone M1b to mid Zone M14 (see discussion under *G. dehiscens*).

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

Globoquadrina dehiscens (Chapman, Parr, and Collins, 1934)

Plate 11.17, Figures 1-16

(Note: This is a common, distinctive and biostratigraphically important species in the Miocene. Here we present an abbreviated synonymy list)

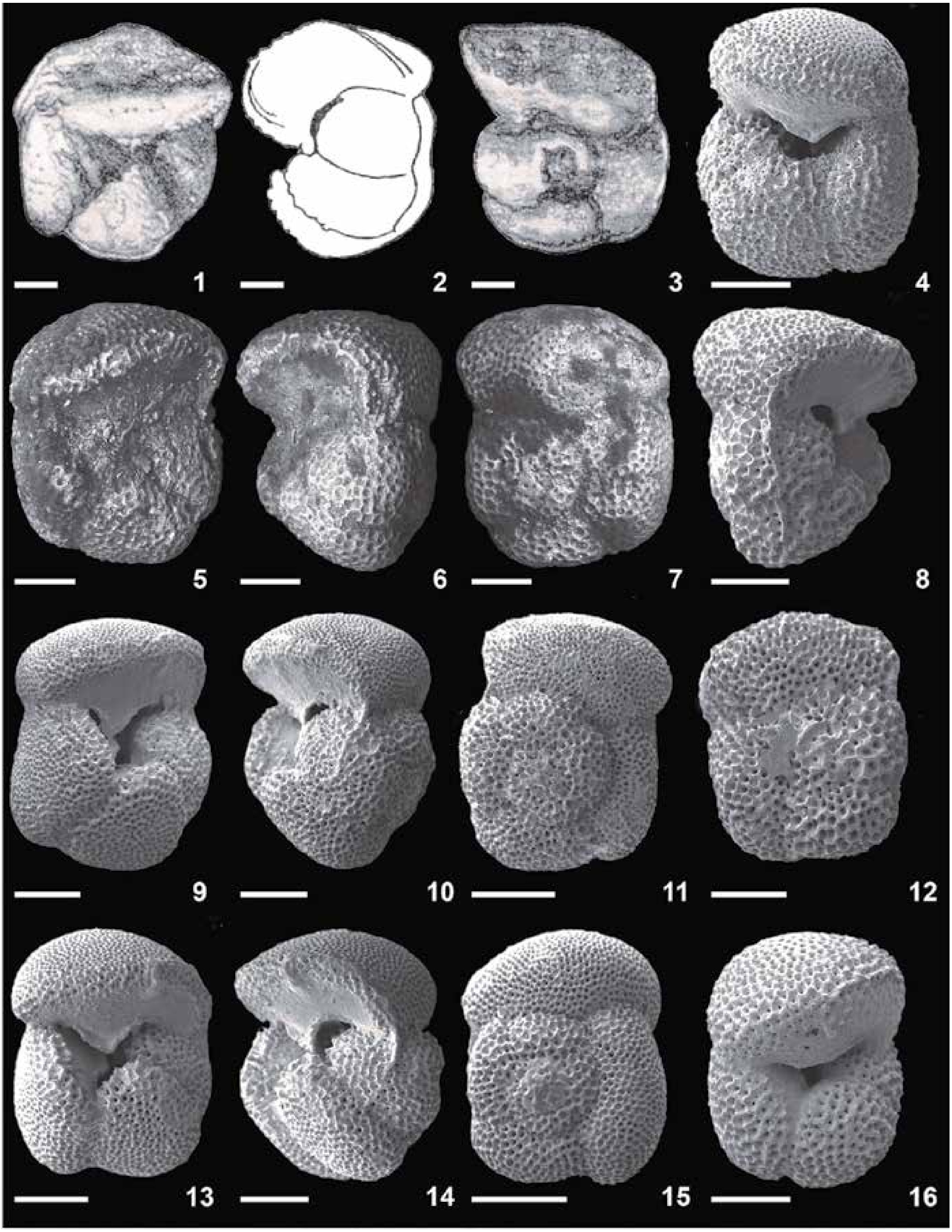

Plate 11.17 *Globoquadrina dehiscens* (Chapman, Parr, and Collins, 1934)

Globorotalia dehiscens Chapman, Parr, and Collins, 1934:569, pl. 11, figs. 36a-c. [Balcombian stage (= middle Miocene), Kackeraboite Creek, Victoria, Australia].

Globoquadrina dehiscens (Chapman, Parr, and Collins).—Bolli, Loeblich, and Tappan, 1957:31, pl. 5, figs. 5a-c [hypotype, Balcombian stage (= middle Miocene), Victoria, Australia].—Bolli, 1957:111, pl. 24, figs. 3a-4c [middle Miocene *Globorotalia fohsi lobata* Zone, Cipero Fm., Trinidad].—Postuma, 1971:312, seven un-numbered figures on p. 313 [level not specified, Trinidad].—Stainforth and others, 1975:266, 268, fig. 113, nos. 1-3 [middle Miocene, Cipero Fm., Trinidad], nos. 4a-c (reproduction from Bolli, Loeblich, and Tappan, 1957, pl. 5, figs. 5a-c), nos. 5, 6 (topotypes of *G. langhiana*, middle Miocene Langhian stage, Italy).—Kennett and Srinivasan, 1983:184, pl. 45, figs. 7-9 [upper Miocene Zone N8, DSDP Site 289 western equatorial Pacific Ocean].—Bolli and Saunders, 1985:183, figs. 15.4a, b (reproduction of holotype illustration of *Globoquadrina subdehiscens* Finlay), figs. 15.5a-c (reproduction from Bolli, Loeblich, and Tappan, 1957, pl. 5, figs. 5a-c), figs. 15.6a-c (reproduction from Bolli, 1957, pl. 24, fig. 3a-c), figs. 15.7a-c (reproduction of holotype illustration of *G. quadraria* Cushman and Ellisor).—Chaisson and Leckie, 1993:159 (partim), pl. 9, fig. 15 [middle Miocene Zone N8/9, ODP Hole 806B, Ontong Java Plateau, western equatorial Pacific Ocean], fig. 16 [middle Miocene Zone N13, ODP Hole 806B, Ontong Java Plateau, western equatorial Pacific Ocean] (not pl. 9, fig. 14 = *Dentoglobigerina juxtabinaiensis* Fox and Wade).—Spezzaferri, 1994:43, pl. 43, figs. 2a-c [lower Miocene Zone N8, DSDP Site 151, Gulf of Mexico].—Pearson, 1995:48, pl. 4, figs. 21, 24 [middle Miocene Zone N9, ODP Hole 871A, western tropical Pacific Ocean].

Globoquadrina dehiscens dehiscens (Chapman, Parr, and Collins).—Blow, 1959:182, pl. 8, figs. 49a-c [Miocene, eastern Falcón, Venezuela].—Blow, 1979:1353, pl. 29, fig. 1 [middle Miocene Zone N14, Buff Bay Fm., Jamaica].—Chaproniere, 1981:118, fig. 8: Ha-c) [lower Miocene Zone N3/4, Ashmore Reef No. 1 Well, northwest Australia].

Globorotalia quadraria Cushman and Ellisor, 1939:11, pl. 2, figs. 5a-c [Miocene, Terrebone Parish, Louisiana].

?*Globorotalia subdehiscens* Finlay, 1947:291 (unfigured) [Miocene Pakaurangi Point, New Zealand].

Globoquadrina sp. Bolli, Loeblich, and Tappan, 1957:31, pl. 5, fig. 6 [Miocene, Lengua Fm., Trinidad].

Not *Globoquadrina dehiscens* (Chapman, Parr, and Collins).—Chaisson and Leckie, 1993:159, pl. 9, fig. 13 (= *D. juxtabinaiensis*).

Not *Globoquadrina dehiscens* sensu lato (Chapman, Parr, and Collins).—Li and others, 2005:19, pl. 2, figs. 11, 12 (= *D. tripartita*).

DESCRIPTION.

Type of wall: Normal perforate, weakly cancellate.

Test morphology: Low trochospiral, peripheral margin quadrate; in spiral view 4 chambers rapidly increasing in size (although the final chamber can be kummerform), elongate oval in shape, sutures flush, slightly curved; in umbilical view 4 chambers rapidly increasing in size, triangular in outline, becoming progressively flattened and angular; umbilicus open, surrounded by steep walls of chambers, diagonally flattened umbilical face of final chamber, umbilical shoulder sometimes pustulose, umbilical face wholly or partially non-perforate with an elongate pointed triangular apertural tooth; in edge view chambers triangular and projecting over the umbilicus, spiral side flat.

Size: Maximum diameter 0.30 mm, minimum diameter 0.25 mm.

DISTINGUISHING FEATURES.— *Globoquadrina dehiscens* is distinguished from closely related species of *Dentoglobigerina* (*D. larmeui* and *D. baroemoenensis*) by its quadrate outline, steeply and diagonally flattened, imperforate umbilical face, and elongate pointed triangular apertural tooth. This species is distinguished from *D. tripartita* by having 4 chambers in the final whorl, the flattened umbilical face and by the typically more prominent umbilical tooth/teeth.

DISCUSSION.— We were not able to obtain new images of the holotype so we use the type illustration as our guide (Pl. 11.17, Figs. 1-3). This is a common, distinctive and biostratigraphically important form. When the diagnostic characteristics are well developed it is virtually unmistakable but populations can be variable and some individuals can show morphological

Plate 11.17 *Globoquadrina dehiscens* (Chapman, Parr, and Collins, 1934)

1-3, (holotype, re-illustration from Chapman, Parr, and Collins, 1934, pl. 11, figs. 36a-c); **4**, Zone M1, ODP Site 904/33/1 - 44", western North Atlantic Ocean; **5-7**, *Globorotalia quadraria* Cushman and Ellisor (holotype, USNM 25231), Miocene, Humble Oil and Refining Co. No. 1 Ellender Well, Terrebonne Parish, Louisiana; **8**, **12**, **9-11** (same specimen), **13-15** (same specimen), Subzone M1b, RDL sample 814, Cipero Fm., Trinidad; **16**, Zone M1, ODP Site 904/33/1 - 44", western North Atlantic Ocean. Scale bar: **1-16** = 100 µm.

overlap with species such as *D. tripartita, D. larmeui*, *D. binaiensis*, and *D. baroemoenensis*. The latter species, in particular, can show sharply angular chambers with pustulose umbilical shoulders, including the holotype itself (see discussion under *D. baroemoenensis*). Many authors since Grimsdale (1951) and Blow (1959) have considered *Globorotalia quadraria* Cushman and Ellisor to be a junior synonym of *Globoquadrina dehiscens*, which we have confirmed with new SEM images of the holotype of *Globorotalia quadraria*. According to Jenkins (1960), who examined topotype specimens, *Globorotalia subdehiscens* Finlay is a probable synonym of *dehiscens*. We have not investigated all possible synonymies in the Miocene, which we defer to future work. *Globoquadrina dehiscens* has long been considered nonspinose since Steineck and Fleisher (1975), although Cifelli (1982) argued that it was spinose. We have not observed spines or spine holes in this species but include it in the spinose group because of its apparently close evolutionary relationship with spinose *Dentoglobigerina*.

PHYLOGENETIC RELATIONSHIPS.— *Globigerina dehiscens praedehiscens* Blow and Banner has long been cited as the ancestor of *G. dehiscens*. However, *G. praedehiscens* is now considered a junior synonym of *D. tripartita*. We concluded that this taxon evolved from *Dentoglobigerina larmeui* as originally suggested by Jenkins (1960).

STRATIGRAPHIC RANGE.— The lowest occurrence of *G. dehiscens* is used to mark the base of Subzone M1b (Kennett and Srinivasan, 1983; Berggren and others, 1995; Wade and others, 2011). This appears to be reliable in the subtropics (e.g. Keller, 1980; Kennett and Srinivasan, 1983; Poore, 1984, Chaisson and Leckie, 1993; Leckie and others, 1993; Pearson, 1995) but a lower occurrence has been recorded in the southern latitudes of the Atlantic and Pacific Oceans (Premoli Silva and Spezzaferri, 1990; Spezzaferri, 1994). The highest occurrence in the uppermost Miocene has not been investigated in this study.

TYPE LEVEL.— Collected by Chapman, Parr and Collins from Kackeraboite Creek, Port Phillip area, Victoria, Australia, originally described as being from the “Tertiary, Oligocene, Balcombian”. The Australian Balcombian Stage is now recognized as middle Miocene (approximately 15.5-15.0 Ma).

GEOGRAPHIC DISTRIBUTION.— Widespread, cosmopolitan.

STABLE ISOTOPE PALEOBIOLOGY.— Classified as an intermediate-dweller by Keller (1985). Recorded as erratic and variable by Pearson and Shackleton (1995).

REPOSITORY.— Chapman collection, Australia.

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