SYSTEMATIC TAXONOMY OF EXCEPTIONALLY WELL-PRESERVED PLANKTONIC FORAMINIFERA FROM THE EOCENE/OLIGOCENE BOUNDARY OF TANZANIA

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ABSTRACT

Diverse and extremely well-preserved assemblages of planktonic foraminifera were recovered from three drill holes through the Eocene/Oligocene boundary in southern Tanzania (Tanzania Drilling Project Sites 11, 12, and 17). The excellent state of preservation of the tests permits detailed investigation of wall textures and surface ornamentation, helping us to elucidate details of functional morphology and clarify the species-level and higher taxonomy of the group. We illustrate and discuss the taxonomy and phylogenetic relationships of fourteen genera and thirty-five species including three new species: *Globoturborotalita barbula* n. sp., *Subbotina tecta* n. sp., and *Dentoglobigerina taci* n. sp. Observations / proposals include (i) that *Globigerinita unicava primitiva* Blow & Banner is assigned to *Catapsydrax unicavus*, (ii) that *Globorotalia* (*Turborotalia*) *permicra* Blow & Banner is a pre-adult *Globorotaloides*, (iii) a description of a peculiar new wall texture in *Globoturborotalita barbula* n. sp., (iv) a revised understanding of *Subbotina gortanii* based on a new appreciation of the holotypes of *Globigerina turritilina turritilina* Blow & Banner and *Globigerina turritilina praeturritilina* Blow & Banner, (v) a revision of the genus *Dentoglobigerina* Blow to include some species that lack umbilical teeth, (vi) evidence for spine holes in several species of *Dentoglobigerina*, (vii) assignment of *Globigerina prasaepis* Blow to *Dentoglobigerina* as a distinct species related to *D. venezuelana*, and (viii) a discussion of the wall texture, apertural system and symmetry of *Cribrohantkenina* and its evolutionary origins.

Keywords: Planktonic Foraminifera, Eocene, Oligocene, Tanzania, systematics, taxonomy

INTRODUCTION

The Eocene/Oligocene (E/O) boundary interval has been problematic for planktonic foraminiferal taxonomy because it is frequently affected by dissolution, diagenetic infilling, overgrowth and recrystallization in the deep sea and the classic Tethyan sections (including the stratotype at Massignano). By contrast, assemblages from the Kilwa Group sediments of Tanzania are exceptionally well-preserved (Pearson et al., 2001; Bown et al., 2008). Specimens appear 'glassy' (reflective and translucent) under the light microscope (Sexton et al., 2006; Wade & Pearson, 2008), typically showing all the signs of well-preserved and un-recrystallized material as described by Pearson & Burgess (2008), except for variable pyritisation in some samples and partial calcite cementation in samples close to micritic limestone beds. Here we take advantage of the superb microfossil preservation to investigate the taxonomy and microstructure so as to provide a reference for the study of similar assemblages in other areas.

1

Outcrops in southern coastal Tanzania have been important for Eocene and Oligocene planktonic foraminiferal taxonomy since the 1960s. In a classic monograph, Blow & Banner (1962) recorded a long list of species from the Lindi area (Table 1), many of which have subsequently been widely recognized by other workers and are important for global correlation, especially in the tropics and subtropics. Blow & Banner (1962) and Blow (1979) used outcrops in the Lindi area to typify several biozones, including the zones that span the Eocene/Oligocene boundary (although note that in modern practice, biozones do not have type areas or samples, just reference sections, with the definition of the zones depending entirely on the taxa that are used to define them; see Salvador, 1994). Blow & Banner's achievement is all the more remarkable for the fact that they were working from a limited number of samples sent to them by British Petroleum exploration geologists (A.P. Terris, R. Stonely and F.C.R. Martin; see Nicholas et al., 2006, for details), often with no knowledge of the stratigraphic order in which the samples occurred.

The taxonomy and stratigraphy of Paleogene planktonic foraminifera is currently being revised by a specialist Working Group of the International Subcommission on Paleogene Stratigraphy. The Working Group (as it will be referred to) has published taxonomic atlases of Paleocene (Olsson et al., 1999) and Eocene (Pearson et al., 2006a) species and is currently compiling an *Atlas of Oligocene Planktonic Foraminifera* (henceforth 'Oligocene Atlas'). As part of this effort

Table 1. List of species from Tanzania described by Blow & Banner (1962), including *Globigerina prasaepis* that was described by Blow (1969) from the same material. Those listed in bold occur in the Eocene/Oligocene transition interval and are discussed in this paper.

Globigerapsis tropicalis
Globigerina oligocaenica
Globigerina ouachitaensis gnaucki
Globigerina praebulloides leroyi
Globigerina praebulloides occlusa
Globigerina prasaepis
Globigerina pseudoampliapertura
Globigerina tripartita tapuriensis
Globigerina turritilina praeturritilina
Globigerina turritilina turritilina
Globigerina yeguaensis pseudovenezuelana
Globigerinita africana
Globigerinita globiformis
Globigerinita howei
Globigerinita martini martini
Globigerinita martini scandretti
Globigerinita unicava primitiva
Globorotalia (Turborotalia) permicra

it is important to revisit classic sections; in the case of Tanzania it is especially necessary because Blow and Banner's species were described before the age of Scanning Electron Microscopy (SEM) therefore details of wall structure and surface ornamentation need to be determined.

The latest phase of work on the Tanzanian sections began with exploratory fieldwork at which time most of the key outcrops studied by Blow & Banner (1962) were re-sampled. This work confirmed the extraordinarily well-preserved nature of the material and highlighted its importance for geochemical studies, especially oxygen isotope paleothermometry (Pearson et al., 2001) but it was also found that suitable outcrops are relatively rare because of the deep tropical weathering. To recover more of the stratigraphic record, a program of shallow drilling was conducted over several years (as reported by Pearson et al., 2004, 2006b; Nicholas et al., 2006; and Jiménez Berrocoso et al., 2010, 2012). About half of the total Paleogene stratigraphy has now been obtained in core and there is a further proposal to the International Continental Scientific Drilling Project (ICDP), currently under consideration, to core the entire Eocene in one deep borehole as a stratigraphic reference section (Pearson & Hudson, 2014). In addition, to recover Neogene and Paleogene sediments offshore an International Ocean Discovery Program proposal has been prepared.

During this research, previously unknown outcrops of the E/O boundary were located in the field (Nicholas et al., 2006). Three boreholes were drilled through the boundary in 2004 and 2005 (Tanzania Drilling Project Sites 11, 12 and 17; see Fig. 1). An age model for these cores was developed by Pearson et al. (2008) based on combined bio- and isotope stratigraphy. The evolutionary record of the planktonic foraminiferal turnover in these boreholes was studied by Wade & Pearson (2008), along with some stable isotope investigation of the assemblages. Detailed taxonomic work on the calcareous nannofossils (Dunkley Jones et al., 2008, 2009) and larger benthic foraminifera (Cotton & Pearson, 2011, 2012) from these cores has also been published.

Our taxonomic investigations of the planktonic foramnifera are supported by new SEM micrographs of some of Blow & Banner's (1962) holotypes taken for us by John Whittaker of the Natural History Museum in London, and in one case, some images of comparable material from Java. This allows us to clarify the status of the Blow & Banner (1962) species in relation to our newly studied assemblages. The detailed taxonomic and SEM work has also made it necessary to name some new species.

THE EOCENE/OLIGOCENE TRANSITION IN TANZANIA

The narrow continental shelf of Tanzania was formed from the rifting of Madagascar from mainland Africa starting in the Late Paleozoic (Nicholas et al., 2007). Shallow marine sediments of Jurassic and Early Cretaceous age are overlain by Albian marls which in turn are overlain by a thick clay-dominated succession of Late Cretaceous (Santonian) to Oligocene age named the Kilwa Group by Nicholas et al. (2006). The Kilwa Group consists of hemipelagic clays deposited in a bathyal outer shelf or slope environment. Tectonic movements since the Miocene have resulted in the uplift and emplacement of these sediments on the African margin. Exceptional preservation of organic biomarkers show that the clays have never been deeply buried (van Dongen et al., 2005) and it is thought that because of this and the relatively impermeable lithology, they contain exceptionally well-preserved foraminifera and nanno-fossils (Bown et al., 2008). The plankton assemblages appear to be typical of deep-sea sites, representing deep water, relatively oligotrophic conditions (Bown et al., 2008). The water depth at the time of deposition was initially estimated at 300–500 m (Nicholas et al., 2006) but following study of modern hemipelagic clays now accumulating offshore Tanzania, the deeper end of the estimate is now considered doubtful and may have exceeded 1000 m (John et al., 2013).

The Eocene/Oligocene boundary occurs in outcrop on a relatively poorly exposed slope cut by shallow gullies near the village of Stakishari in the Kilwa administrative district (Fig. 1). It occurs within the Pande Formation, which consists of greenish black to dark greenish grey clays with accessory beds of micritic limestone containing allochthonous shallow marine debris (Nicholas et al., 2006) including abundant larger benthic foraminifera. A lower Oligocene unconformity cuts out the boundary in two of the three boreholes but in one site (TDP Site 12) the boundary appears to be conformable in monotonous clay facies. The E/O transition interval is relatively expanded, with an average sedimentation rate of about 10 cm / kyr (Pearson et al., 2008). Note that the Eocene/Oligocene drill cores are from the same Formation but approximately 100 km north along strike from the Lindi area outcrops where the Blow & Banner (1962) samples were collected (see Fig. 1).

The entire study interval spans about 1.75 m. yr. of geological time from ∼ 34.65 Ma at the base of TDP Site 12 to ∼ 32.90 Ma at the top of TDP Site 17 (Pearson et al., 2008; timescale of Berggren et al., 1995). We have previously published (Wade & Pearson, 2008) a description of the pattern of turnover of planktonic foraminifera across the interval based on
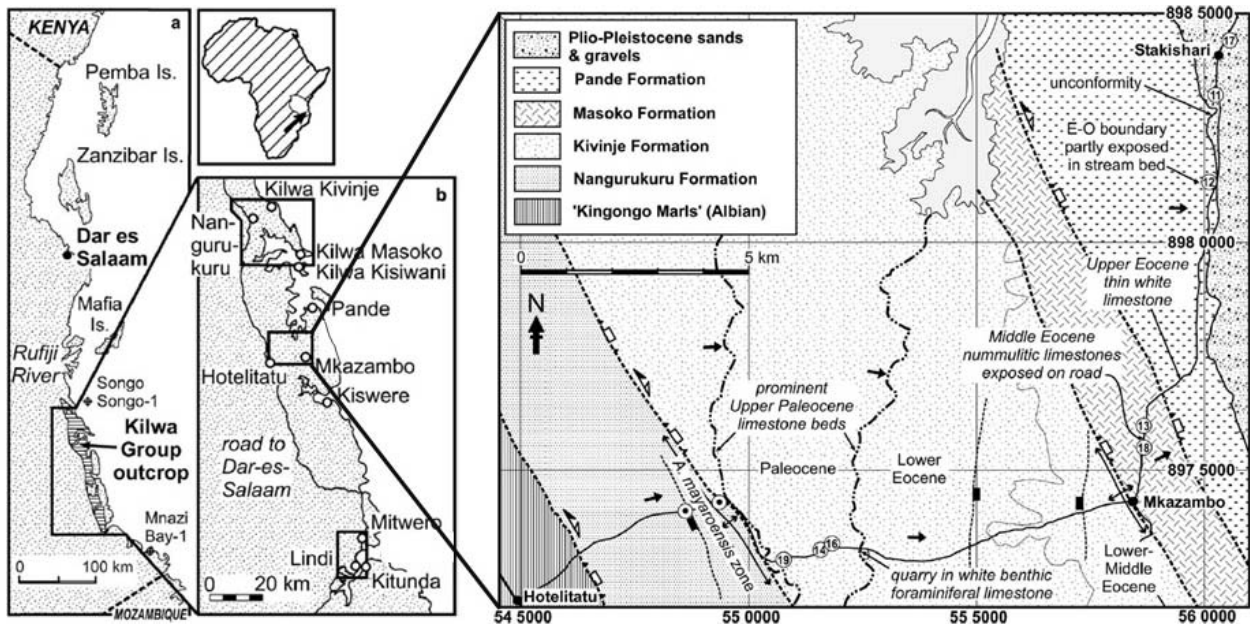

Figure 1. Location of the Tanzania Drilling Project drill sites considered in this study (Sites 11, 12, and 17, in the northeastern corner of the inset map) in relation to the local geology and other drill sites (modified from Nicholas et al., 2006). The Blow & Banner (1962) samples from the Eocene/Oligocene transition were from the Lindi and Kitunda area to the south of the main map.
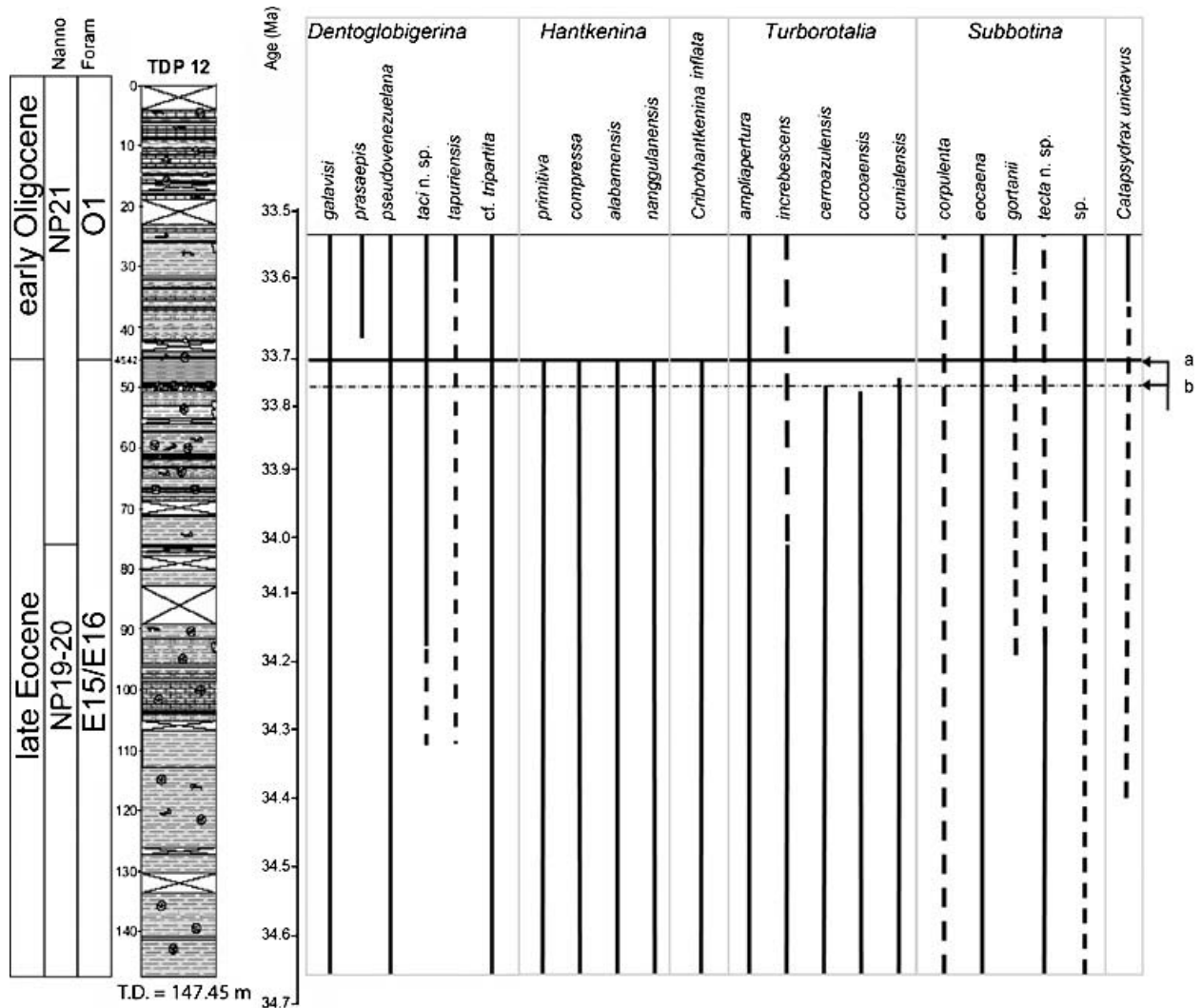
Figure 2. Summary stratigraphic range-chart of planktonic foraminifera from the > 250 μm size fraction in Tanzania Drilling Project Site 12 (modified from Wade & Pearson, 2008). Dashed lines = sporadic occurrences, (a) Highest occurrence (HO) Hantkeninidae marking the Eocene/Oligocene Boundary, (b) HO *Turborotalia cerroazulensis* group.

abundance counts from TDP Site 12, which is summarized and updated here and in Figure 2 to incorporate the taxonomic changes discussed in this contribution. In the Eocene part of the record, assemblages are moderately diverse and include various species of *Dentoglobigerina*, *Turborotalia*, *Subbotina*, *Hantkenina*, *Globoturborotalita* and others. Starting at about 34.0 Ma (the beginning of the Eocene/Oligocene Transition interval based on oxygen and carbon isotopes) there is a reduction in the Shannon diversity index (which reflects the number of species and their evenness) which culminates in the closely spaced extinction of the *Turborotalia cerroazulensis* group of species at ~33.76 Ma and the *Hantkenina / Cribro-*

hantkenina group at 33.70 Ma. The latter level is correlated with the Eocene/Oligocene boundary as defined at the Massignano Rupelian stratotype section in Italy, where the 'golden spike' is placed at the level of the *Hantkenina* extinction (Coccioni et al., 1988). This level also coincides precisely with a size reduction in *Pseudohastigerina micra* (Wade & Pearson, 2008). The short stratigraphic interval between the *Turborotalia* and *Hantkenina* extinctions is similar in timing to Massignano, although much thicker because of the higher sedimentation rate, and demonstrates the apparently complete nature of the section in TDP Site 12. Following these extinctions, Shannon diversity remains low, partly because of the high dominance of one

species, *Turborotalia ampliapertura*. Towards the top of the section there is a minor diversification of dentoglobigerinids, including the incoming of *D. prasaepis*. These first occurrences are at a distinctly higher level than the Eocene/Oligocene boundary proper, representing a time lag of a few hundred kyr, but they still occur before the main oxygen isotope step (sometimes referred to loosely as the 'Oi-1 event'; see Coxall & Pearson, 2007, for a discussion of this term) that corresponds to the rapid onset of the Early Oligocene Glacial Maximum.

Based on combined oxygen isotope and Mg/Ca data, sea surface temperatures are estimated at 33–35 °C in the Eocene, falling to about 31–33 °C in the Oligocene (Wade & Pearson, 2008; Lear et al., 2008), which is still several degrees warmer than modern. Investigation of stable isotope ratios of various species in the Eocene and Oligocene was used to infer aspects of the life habitat and depth of calification (Wade & Pearson, 2008; updated in Figure 3). The surface ocean habitats were dominated by small species of *Globoturborotalita* and *Pseudohastigerina*, while *Turborotalia ampliapertura* and some other species consistently register paleotemperatures 2–3 °C cooler than the surface. Deeper niches were occupied by the large dentoglobigerinids.

METHODS

Cores of NQ diameter (4.76 cm) were cleaned of external drilling mud and samples of 10 cm "half round" (cut vertically along the core) were soaked in water and washed through a 63 μm sieve. Picked specimens were treated to 10 s ultrasound in water to remove clays and other superficial particulates prior to mounting on SEM stubs and coating with gold / palladium. Multiple views were obtained by carefully removing, re-mounting and re-coating the specimens. Scanning electron microscopy was conducted at Cardiff University with a Philips XL30 ESEM with additional images from Rutgers University Amray 1830 I. Images were adjusted for brightness and contrast and cropped by using software to automatically identify the edge of the specimen by contrast thresholding. On occasions where the thresholding did not successfully find the edge of the foraminifer because of a lack of contrast, the periphery was manually traced at high magnification. The images illustrated here are a small proportion of the overall collection.

One of the main objectives of the SEM work was to image the wall surface ultrastructure and, for selected specimens, as dissected in wall cross-section, so as to apply the wall texture classification developed by
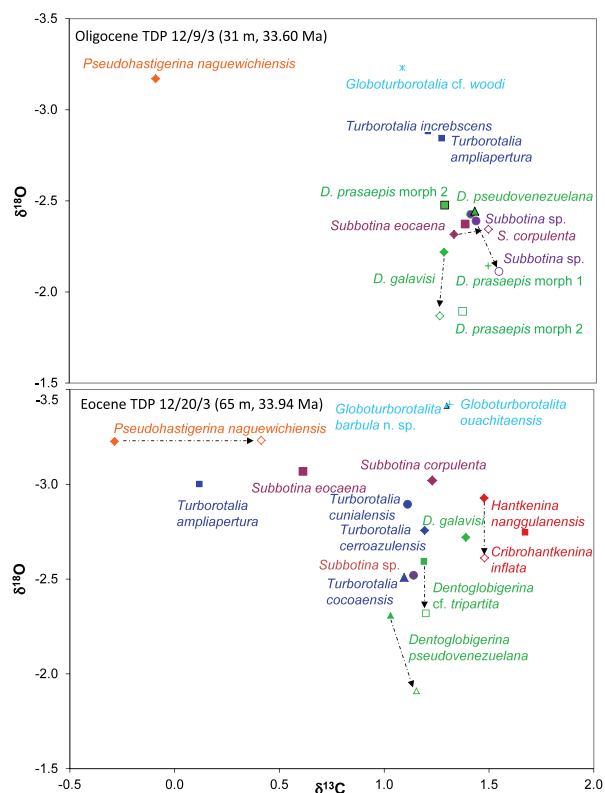

Figure 3. Multispecies stable isotope arrays from the upper Eocene and early Oligocene (modified from Wade & Pearson, 2008, to account for the taxonomic concepts discussed in this paper; note *D. prasaepis* morph 1 was previously included in "*Globoquadrina*" *venezuelana* and morph 2 was previously included in "*Globoquadrina*" *euapertura*), and were incorrectly labeled in Wade & Pearson, 2008.

Fleisher (1974, 1975), Steineck and Fleisher (1978), Hemleben and others (1999) and Hemleben and Olsson (2006). A critical but sometimes difficult distinction is that between cancellate spinose and cancellate non-spinose wall textures because spines are generally shed by the foraminifer at the end of the life cycle or, if retained, broken off in the sediment and during sample processing. Good fortune and excellent preservation is required, hence only a few Paleogene taxa have been imaged with true spines, notably *Orbulinoides beckmanni* (Bolli et al., 1957a, pl. 6, figs. 8-9; Premoli Silva et al., 2006, pl. 7.11, fig. 4; same specimen as Bolli et al., 1957a, illustrated by SEM), *Turborotalita praequinqueloba* (Hemleben and Olsson, 2006, pl. 4.5, figs. 5, 8; Olsson et al., 2006b, pl. 6.20, figs. 12, 16), *Globoturborotalita ouachitaensis* (Olsson et al. 2006b, pl. 6.5, figs. 6, 16), *Subbotina senni* (Olsson et al., 2006b, pl. 6.17, fig. 10; Premoli Silva et al., 2006, pl. 7.1, fig. 2), *Globigerinatheka barri* (Premoli Silva et al., 2006, pl.

7.6, fig. 14), and *Globigerinatheka index* (Premoli Silva et al., 2006, pl. 7.5, figs. 7-8). Equally compelling as when they are seen projecting from the test surface, true spines can sometimes be seen in the cross section of the dissected wall, as in *Guembelitrioides nuttalli* (Premoli Silva et al., 2006, pl. 7.1, fig. 12) and, in this work, *Globoturborotalita barbula* n. sp. (Fig. 7.5). Sometimes the tips of possible / probable spines broken off at the surface can be seen inhabiting spine holes (e.g., Hemleben and Olsson, 2006, pl. 4.1, fig. 6; this work, Fig. 21.4e) but in such cases the evidence is less certain. In the absence of spines, the small circular holes left behind after shedding can often be seen on the surface, and examples have been illustrated for many taxa. When they are abundant and systematically distributed on a very well-preserved test surface they can be completely convincing; but when sparse on a test that has suffered from some corrosion they can be difficult to be confident of, and potentially can be confused with small corrosion pits. Hence in this work, possible spine holes are illustrated on various specimens and taxa so as to form part of the cumulative evidence by which certain species or genera may be regarded as having been spinose in life. It should be kept in mind that even in known modern spinose species, many specimens do not show any spine holes because of gametogenic calcification of the wall, hence 'absence of evidence' of spines is not 'evidence of absence' except after the study of very many well-preserved specimens.

TAXONOMIC PRINCIPLES

Taxa are discussed below alphabetically by Super-family, then Family, genus and species following the higher taxonomic scheme of Pearson et al. (2006a). We have not attempted exhaustive synonymy lists; many of the Eocene species were revised in various contributions to Pearson et al. (2006a) while others will be discussed in the forthcoming Oligocene Atlas. Our synonymy lists focus on key references necessary for the interpretation of our observations. Our taxonomic approach follows that taken in the *Atlas of Eocene Planktonic Foraminifera* (Pearson et al., 2006a, p. 16–19). Higher taxa are restricted to natural groups according to our current understanding of their evolutionary relationships; that is they must be either monophyletic or paraphyletic (it being impossible to partition a branching tree into just monophyletic groups). Families are based as far as possible on their distinctive wall textures. We do not allow polyphyletic form-genera as were used by many previous workers (including Blow & Banner, 1962, and

Blow, 1979). We regard generic names merely as useful tags and we try to respect traditional usage where possible. Mostly, genera are based on some key aspect of test architecture (e.g., planispiral / trochospiral, keels or tubulospines, umbilical / extraumbilical apertures, etc.) but in reality the distinctions can be quite subtle (e.g., *Subbotina* vs. *Dentoglobigerina* as discussed in this contribution). Genera can be monospecific (e.g., *Cribrohantkenina*). Species are strictly morphospecies, based on similarity to the type specimen. This means that a given specimen is assigned to a particular species because it is more similar to the holotype of that species than it is to the type of any other species. In this way species can be considered as sectors of morphospace centred on the type specimens (Pearson, 1998). We use the twin tools of subjective synonymy and the raising of new species to aim for as fine a subdivision of the observed morphological variation as we think is communicable between workers and merited for biostratigraphic and other purposes. We do not use subspecies or subgenera as they are superfluous.

The diagnosis of some species and even some genera is partly or wholly based on test features that only appear late in the growth of the organism. For example, *Cribrohantkenina* requires the presence of areal apertures which may only become evident on the final one or two chambers. While this is standard practice in foraminiferal studies, it does underline the fact that species must be considered morphotaxa and do not necessarily equate to biological populations. The discovery that most modern morphospecies encompass multiple genetic variants that may be reproductively isolated from one another underlines this problem. Despite much debate among specialists over the years, there is no fixed rule as to whether features such as bullae (small umbilical chamberlets that seem to be related to reproduction) or umbilical teeth (which may be related to feeding strategies) form part of the diagnosis of a given species or genus. For some taxa these features seem obligate, that is, possessed by every individual, and so form part of the diagnosis (e.g., bullae in *Catapsydrax* when adult; teeth in *Subbotina tecta* n. sp.) whereas for other taxa they are seemingly optional (e.g., bullae in most species; teeth in some dentoglobigerinids and subbotinids), hence each case must be taken on its merits.

In a thoughtful article, Scott (2011) has recently questioned the emphasis placed on holotypes in foraminiferal classification (many of his comments apply, more generally, to all biological classification). Scott (2011) acknowledged that holotypes must be name-bearing types, but argued that they may be

inappropriate as exemplars of their species and should not have primacy in that respect. Only the study of large populations and geographic variability can properly characterise a given species. We agree with this insofar as the 'species' which one is attempting to recognize is considered a biological entity, that is having been a reproductively isolated population, but we emphasize that the Linnean species rank is not used here (nor in Pearson et al., 2006a) in that sense. We think that a population-based species concept is unworkable in the fossil record for most routine applications and likely to lead to endless vagueness and inconsistency in the way taxonomic names are applied, with a deleterious impact on biostratigraphy, which is the main applied use of the group. A given worker does not have the luxury of being able to conduct large scale population-based analyses on every sample he/she is confronted with, and then compare the data with other geographic areas and stratigraphic levels. Even if they did, the statistical tools for delimiting 'natural' populations may not be reliable. This is particularly the case when gradual anagenetic evolution is encountered.

Consider one of the groups discussed in this contribution, and used as a practical exemplar of this point by Pearson et al. (2006a, p. 16–17): the *Turborotalia cerroazulensis* group of (morpho)species. As originally proposed by Toumarkine and Bolli (1970), we see an intergradation through time between the species (i.e., morphospecies) *frontosa*, *pomeroli*, *cerroazulensis*, *cocoaensis*, and *cunialensis* (the final three of which are later discussed and illustrated in this contribution; see Figs. 28–29). Pearson & Ezard (2014) have recently subjected this group to a large scale morphometric study including multiple measurements on over 10,000 specimens, confirming this intergradation through time. Hence this illustrates that the co-existence of morphospecies in the geologic record, even for millions of years, does not of itself imply that biological speciation (cladogenesis) has occurred, as was recently argued by Strotz and Allen (2013; see Aze et al., 2013). One response would be to lump all these 'species' as a single evolving population, but that would destroy their considerable practical biostratigraphic utility. To take that approach to its absurd extreme, if we had perfect knowledge of evolving populations and full intergradation up and down the tree of life, we would have to lump all species into one. The dilemma is fundamental: how can we apply a classification with fixed points of reference when the reality is continual evolutionary flux over millions of years which is very incompletely sampled?

Our solution to this basic problem (which is derived from the approach taken by Fordham, 1986) is to produce a dual system of classification based on the one hand on practical Linnean morphospecies, which are artificial taxonomic entities that stake out morphospace, with the stratigraphic ranges representing how long those sectors of morphospace were occupied; and on the other on the evolving lineages that in principle start at the point where morphological separation of populations can be identified (implying cladogenesis has occurred) and ending in final extinction. Such a lineage is not restricted within any morphological bounds and hence it may traverse a range of morphospecies. An attempt at constructing a lineage phylogeny for all macroperfortae planktonic foraminifera of the Cenozoic was made by Aze et al. (2011). This concept of a lineage is in effect an attempt to identify a natural evolving population of the sort envisaged by Scott (2011). Hence the various *Turborotalia* species listed above are considered arbitrary morphological groupings based on their respective holotypes belonging to one lineage which, as it happens, can be shown statistically to have branched into two before the final extinction (Pearson & Ezard, 2014). The endpoints of these two branches correspond approximately to the morphospecies of *Turborotalia cunialensis* and *T. cocoaensis*, but the correspondence is not perfect and in fact it never could be unless some extreme form of punctuated equilibrium was operating.

Finally it is worth stressing that although the avowedly artificial nature of Linnean species as employed by us may be disconcerting to some, it is in practice what has always been done by biostratigraphers. Just because a specialist can parcel a set of skulls into *Homo habilis*, *H. erectus*, etc., based on morphologic similarity to the type specimens, and even use these units succesfully for biostratigraphic purposes, it does not mean that what has been classified necessarily correspond to separately evolving populations (e.g., Lordkipanidze et al., 2013): the reality may have been intergradation through time and / or any amount of unknown branching and local extinction which can only be revealed as more evidence is amassed.

SYSTEMATIC TAXONOMY

Note: We have followed the latest Cushman Foundation style in constructing the synonymy lists. Instances where we attribute an illustrated specimen to a species which was originally put in another taxon, but we do not attribute that taxon to the species, are recorded with a

short 'not' statement. For example, under *Globoturborotalita barbula* is the following record:

? *Subbotina gortanii* (Borsetti) *in* Hemleben and Olsson, 2006, pl. 4.1, figs. 4-6 (upper Eocene, Atlantic City borehole, ODP 150X, New Jersey). (Not Borsetti, 1959.)

This means we (questionably) attribute the illustrated specimen to *Globoturborotalita barbula*, but not Borsetti's taxon *gortanii*.

Order Foraminiferida d'Orbigny, 1826

Suborder Globigerinina Delage & Hérouard, 1896

Superfamily Globigerinoidea Carpenter et al., 1862

Family Globigerinidae Carpenter et al., 1862

Genus *Catapsydrax* Bolli et al., 1957

Type species: *Globigerina dissimilis* Cushman & Bermúdez, 1937, p. 56

Remarks. This genus was revised by Olsson et al. (2006a). It has an obligate bulla in the adult stage.

Catapsydrax unicavus Bolli et al., 1957

Figs. 4.1a-5c

(Figs. 4.1a-d: new SEMs of holotype of *Globigerinita unicava primitiva* Blow & Banner)

Catapsydrax unicavus Bolli, Loeblich, & Tappan *in* Bolli et al., 1957, p. 37, pl. 7, fig. 9a-c (upper Oligocene, Cipero Fm., Trinidad), pl. 37, fig. 7a, b (middle Eocene Navet Fm., Trinidad).
Globigerinita unicava primitiva Blow & Banner *in* Blow & Banner, 1962, p. 114–115, pl. XIV, figs. J-L (upper Eocene *Globigerapsis semi-involuta* Zone, Lindi area, Tanzania).
Catapsydrax unicavus Bolli, Loeblich, & Tappan *in* Olsson et al., 2006a, p. 75–79, pl. 5.3, figs. 1-17 (various localities including SEMs of the holotype).
Catapsydrax unicavus Bolli, Loeblich, & Tappan *in* Pearson and Wade, 2009, p. 200–202, pl. 2, fig. 2a-g (upper Oligocene 'Biozone O6' [now O7], Cipero Fm., Trinidad).

Remarks. The species is distinguished from bullate species of *Subbotina* (e.g., *S. corpulenta*; see Figure 10.3-4c) by the compact test, thick calcite crust and relatively incised sutures, together with the somewhat flatter early whorl. Additionally the bullae in *Subbotina*

tend to be more inflated and detached from the earlier chambers. Specimens that lack pronounced crust development may be difficult to distinguish from *Subbotina*. The bulla varies in size from specimen to specimen (see Figs. 4.1a-5a) and has just one opening on the umbilical side, which distinguishes the species *unicavus* from others in the genus such as *C. dissimilis* which has multiple openings around the bulla. The opening in *C. unicavus* is always directed to the posterior, that is, towards or beyond the umbilicus, depending on the size of the bulla. The calcite crust is generally well-developed in adult forms, as we previously described and illustrated in specimens from Trinidad (Pearson and Wade, 2009). As in the Trinidad material, the calcite crust is most strongly developed on the earlier chambers of the final whorl and the bulla (compare Fig. 4.5b and 4.5c). This crust may be related to gametogenesis in the relatively deep mesopelagic environment inhabited by this species, as has been determined from isotopic data (e.g., Poore & Matthews, 1984; Boersma et al., 1987; Wade & Pearson 2008; Pearson & Wade, 2009).

Blow & Banner (1962) named the subspecies *Globigerapsis unicava primitiva* from the upper Eocene *semi-involuta* Zone of Tanzania, which is from slightly below the stratigraphic interval covered by this study. The specimen is illustrated in SEM for the first time as Figure 4.1a-d beside a range of similar forms from our new material. According to Blow & Banner (1962, p. 114), the subspecies differs from *unicavus* by "possessing more strongly vaulted ventral surfaces to the primary chambers, a more inflated bulla (which protrudes above the umbilicus) and in possessing more depressed later chambers". The holotype of *Catapsydrax unicavus* Bolli et al. 1957 from the upper Oligocene of Trinidad was illustrated in SEM by Olsson and others (2006a). Comparison of the types of *primitiva* and *unicavus* bears out the distinction drawn by Blow & Banner (1962), although Blow (1969, pl. 25, figs. 1-2) later illustrated a specimen he assigned to *primitiva* which does not show the supposed distinctive features of *primitiva*, and in fact is very similar to the holotype of *unicavus* (see also Blow, 1979). Olsson et al. (2006a) assigned a wide variety of forms to *unicavus*, including relatively inflated specimens that are similar to the type of *primitiva*. By an oversight, Olsson et al. (2006a) did not illustrate or discuss *Globigerinita unicava primitiva* Blow & Banner (although they did discuss and illustrate another of Blow & Banner's (1962) species from Tanzania, *Catpsydrax globiformis*, which is a distinct form). In our view there is a case for recognizing both *primitiva* and *unicavus* as distinct

8

species but we have chosen not to do this to promote stability of usage, pending the utility of the split being demonstrated biostratigraphically or in some other way. We note that the *primitiva* and *unicavus* morpholgies are linked by intermediates.

Genus *Globigerina* d'Orbigny, 1826

Type species: *Globigerina bulloides* d'Orbigny, 1826, p. 250

Remarks. This genus was revised by Olsson et al. (2006b). Critical to the concept is the *bulloides*-like spinose wall texture with raised spine bases, although the pores may not be as densely distributed as in most modern *bulloides*.

Globigerina officinalis Subbotina, 1953

Figs. 5.1–5.2

Globigerina officinalis Subbotina *in* Subbotina, 1953, p. 105, pl. 11, figs. 1-7 (upper Eocene *Bolivina* Zone, Khieu (or Kheu) River, Northern Caucasus, Russia).

Globigerina officinalis Subbotina *in* Olsson et al., 2006b, p. 114, pl. 6.1, figs. 1-3 (paratype, upper Eocene *Bolivina* Zone, Khieu River, Northern Caucasus), figs. 4, 12 (upper Eocene Zone E15/16, Shubuta Clay, Yazoo Fm., Mississippi), figs. 5-10 (upper Eocene, ODP Site 150X, Island Beach borehole, New Jersey), figs. 11, 16 (Oligocene Zone NP23, Ottenthal, Austria), figs. 13-15 (holotype of *Globigerina praebulloides leroyi* Blow & Banner 1962, lower Oligocene *Globigerina oligocaenica* Zone, Lindi area, Tanzania).

Globigerina praebulloides leroyi Blow & Banner *in* Blow & Banner, 1962, p. 93, pl. 9, figs. R-T (lower Oligocene *Globigerina oligocaenica* Zone, Lindi area, Tanzania).

Remarks. The holotype of *Globigerina praebulloides leroyi* Blow & Banner was illustrated in three views by Olsson et al. (2006b) and included within their concept of *officinalis*. Here we compare it (reproduced in umbilical view in Fig. 5.1) with another specimen from Tanzania (Fig. 5.2) both of which illustrate its distinctive *bulloides*-type wall texture which is, nevertheless, not as densely porous as is typical of modern *G. bulloides*. We defer to the forthcoming Oligocene Atlas for discussion of the synonymy of *officinalis* and *leroyi* and criteria for distinguishing these forms from *Globigerina praebul-*

loides and *Globigerina bulloides*. See also discussion under *Globoturborotalita ouachitaensis* for means of distinguishing it from that form.

Genus *Globorotaloides* Bolli, 1957b

Type species: *Globorotaloides variabilis* Bolli, 1957b, p. 117

Remarks. This genus was discussed by Olsson et al. (2006a).

Globorotaloides forma *permicrus* (Blow & Banner, 1962)

Figs. 5.3–5.5d

(Figs. 5.5a-d: new SEMs of holotype of *Globorotalia* (*Turborotalia*) *permicra* Blow & Banner)

Globorotalia (*Turborotalia*) *permicra* Blow & Banner *in* Blow & Banner, 1962, p. 120, pl. XII, figs. N-P (lower Oligocene *Globigerina oligocaenica* Zone, Lindi area, Tanzania).

Globorotalia (*Turborotalia*) *permicra* Blow & Banner *in* Blow, 1979, p. 1089–1091 (partim), pl. 35, fig. 9 (Oligocene Zone P19, Lindi area, Tanzania). Not Pl. 245, fig. 4 (lower Oligocene Zone P18, DSDP Site 14, South Atlantic Ocean) (=*Tenuitella munda*).

Not *Globorotaloides permicrus* (Blow & Banner) *in* Spezzaferri & Premoli Silva, 1991, p. 248, pl. X, fig. 1a-c (lower Oligocene Zone P21a, DSDP Hole 538A, Gulf of Mexico) (?=*Globorotaloides variabilis*).

Not *Globorotaloides permicrus* (Blow & Banner) *in* Spezzaferri, 1994, p. 46, pl. 35, figs. 2a-c (re-illustration from Spezzaferri & Premoli Silva, 1991) (?=*Globorotaloides variabilis*).

Remarks. This taxon has been used by several workers but with variable species concepts. New SEM images of the holotype (Fig. 5.5a-d) show that it is a very small specimen, lacking a well-developed wall structure but is certainly macroperforate. We have found similar specimens in our material (e.g., Figs. 5.3–4). The inner whorl is relatively flat, as is typical of the genus *Globorotaloides*. The species was first assigned to this genus by Premoli Silva & Boersma (1988) although without illustration. The specimen illustrated by Spezzaferri & Premoli Silva (1991) and Spezzaferri (1994) is much larger and has a well-developed cancellate wall texture. In our view the *permicrus* holotype is a juvenile morphology in which the full development of the adult

is not easy to determine, hence we refer to it informally as 'forma' *permicrus* (see International Code of Zoological Nomenclature, 1999, p. 104 for guidance on the term 'forma'). Although there is a case for regarding it as it as a senior synonym of *Globorotaloides quadrocameratus* Olsson, Pearson, and Huber, 2006 (especially in that the number of chambers per whorl typically reduces during ontogeny in this genus so that a five-chambered juvenile will likely have 4 to 4½ in the adult phase), we do not recommend using the name because it is a juvenile morphology and we cannot be confident of the adult form and wall texture. Some specimens (e.g., Fig. 5.6) show the beginnings of a cancellate wall texture on earlier chambers and are hence intermediate between forma *permicrus* and *quadrocameratus* in morphology. Several authors have reported *Globorotaloides permicrus* from the upper Eocene (Premoli Silva & Boersma, 1988; Nishi & Chaproniere, 1994, Petrizzo et al., 2005) but it is difficult to evaluate these records without illustrations.

Globorotaloides quadrocameratus Olsson, Pearson & Huber, 2006

Figs. 5.6-5.8

Globorotaloides quadrocameratus Olsson, Pearson & Huber *in* Olsson, Pearson & Huber, 2006, p. 83–84, pl. 5.5, figs. 1-16 (various localities).

Remarks. Olsson et al. (2006a) distinguished this species from others in the genus by its small lobulate test, coarsely cancellate wall and 4–4½ chambers in the final whorl. Our observations extend the known stratigraphic range into the lower Oligocene.

Genus *Globoturborotalita* Hofker, 1976

Type species: *Globigerina rubescens* Hofker, 1956

Zeaglobigerina Kennett & Srinivasan, 1983, p. 42.

Remarks. This genus consists of small cancellate-spinose planktonic foraminifera with an umbilical aperture. It was revised by Olsson et al. (2006b) who determined its first occurrence at the Paleocene / Eocene thermal maximum event and assigned several Eocene and Oligocene species to this group. The genus survives today in *G. rubescens*. Two species included by Olsson et al. (2006b) were originally described from Tanzania (*G. gnaucki* and *G. martini*), hence it is useful to illustrate more well-preserved individuals for compar-

ison. We also describe a new species with a very distinctive wall texture, as follows.

Globoturborotalita barbula Pearson & Wade, new species

Figs. 6.1a-5b, 7.1a-5, 8.1a-8

Etymology. The name refers to the distinctive 'barbules' (see below) concentrated in the sutures.

Description. Wall cancellate, normal perforate, spinose, wall structure with concentrations of minute spikes (herein termed 'barbules') in the sutural areas. Test moderate to very high trochospiral, usually increasing in spire height through ontogeny, globular, petaloid in outline, chambers globular and inflated; in spiral view usually 3½ (occasionally 4) globular, slightly embracing chambers in the final whorl, increasing moderately in size, sutures depressed, straight or gently cuving; in umbilical view 3½ (occasionally 4) globular, slightly embracing chambers, increasing moderately in size, last chamber usually kummerform, sutures incised, straight or gently curving, umbilicus large and open, aperture umbilical, a rounded arch, bordered by an imperforate, thickened rim; in edge view chambers globular in shape, slightly embracing. Maximum diameter of holotype 230 μm. The species is typically small (150–200 μm) in the adult form, but may be as large as 350 μm. There is no marked preference in coiling direction.

Remarks. Globoturborotalita barbula n. sp. is a common component of the Tanzanian assemblages both before and after the Eocene/Oligocene boundary and we have also confirmed that it is equally common in the Eocene/Oligocene transition of Java (unpublished data). It fluctuates in size from level to level, such that in some samples it is common in the > 250 μm size fraction while at other levels, all specimens fall through that sieve. That the species possessed true spines is demonstrated by the presence of spines embedded in the wall (Fig. 7.5) and abundant circular spine holes in some specimens (Fig. 7.4b). A remarkable feature of this species is the high density of minute, highly conical, spikes that are concentrated in the sutural regions of the test on both the umbilical and spiral sides – every specimen we have examined in SEM (about 50 from Tanzania and 20 from Java) exhibit this characteristic to a marked degree. Where present on the test, these spikes, which we refer to as 'barbules', cover the cancellate wall texture and are often densely clustered and interfingering in the incised sutures, particularly on the umbilical side. The barbules are typically 1 micron

in diameter at their base and may be up to 5 microns in length, tapering to a fine, rounded point typically only 100 nm across (Fig. 7.1d). The barbules appear rooted in a superficial layer of calcite that may be thickened into a rough encrustation (Fig. 7.3). That the structures are biogeneic, and not diagenetic, is demonstrated by the fact that circular spine holes frequently penetrate the layer in which the barbules are rooted (Fig. 7.4b). The density of barbules declines away from the sutures (Figs. 7.1c, 7.2) and much of the rest of the test has a typical *sacculifer*-type cancellate wall.

Small spikes similar to barbules are relatively common in planktonic foraminifera, especially in sutural areas, including in other species of *Globoturborotalita*, but they are usually sparse and variably expressed in different specimens. This species has a very high concentration of well-developed barbules, making a uniquely distinctive wall texture. We speculate that the barbules were used in some way for anchoring or straining food particles, like the apertural teeth in other species of planktonic and benthic foraminifera. Another possibility (M.-P. Aubry, personal communication, 2008) is that they are related to the management (habitat maintenance) of small symbionts such as dinoflagellates.

The barbules are fundamental to our concept of the new species. It is also distinguished from most other *Globoturborotalita* by its moderate to high trochospire (very high in some large specimens) and its slightly lower rate of chamber enlargement. In other respects it is similar to *G. ouachitaensis* from which we suggest that it evolved. We note that Olsson et al. (2006b) illustrated three specimens as *Subbotina gortanii* that are very similar in gross morphology to *G. barbula* n. sp., but apparently (insofar as is possible to see in the low magnification images) do not show the barbules, and hence we tentatively assign them to *G. ouachitaensis* (see further discussion under *S. gortanii* and *G. ouachitaensis*). *Globoturborotalita barbula* has probably been overlooked on account of its small size. We initially assigned such specimens to *Subbotina gortanii* (see Wade & Pearson, 2008) following the concept of Olsson et al. (2006b) because of the globular chambers and high spire, but we now appreciate that *S. gortanii* is typically much larger with more closely appressed and embracing chambers (see discussion under that species below). The oxygen and carbon stable isotope data reported as '*Subbotina gortanii* (125–250 μm)' in Pearson et al. (2007) and Wade & Pearson (2008) were actually from *Globoturborotalita barbula* n. sp. These isotope data are virtually identical to *Globoturborotalita ouachitaensis* from the same sample (Fig. 3) indicating a warm surface water habitat distinct from species of *Subbotina* which apparently calcified in deeper, cooler, water.

Stratigraphic range. The full stratigraphic and geographic range has yet to be determined, but so far we have identified it in Zones E15/16 and O1.

Repository. Holotype (NHMUK PM PF 71143) and paratypes (NHMUK PM PF 71144 – 71157) deposited in the Natural History Museum, London. The type series includes three unfigured paratypes from Sample NKK1-52, 70–78 cm, upper Eocene Zone 16 of Kali Kunir, Java, Indonesia (NHMUK PM PF 71148 – 71150). Note that some of the figured paratypes (Figs. 7.1a-d, 7.2, 7.3, 7.4a-b, 7.5, and 8.4a-b) are formally part of the type series but were destroyed in the study of wall ultrastructure and so are not curated.

Globoturborotalita gnaucki (Blow and Banner, 1962)

Fig. 9.1–9.2

Globigerina ouachitaensis gnaucki Blow & Banner *in* Blow & Banner, 1962, p. 91, pl. IX, figs. L-N, (lower Oligocene *Globigerina oligocaenica* Zone, Lindi area, Tanzania).
Globoturborotalita gnaucki (Blow & Banner) *in* Olsson et al., 2006b, p. 118–121, pl. 6.4, figs.1–15 (various localities including new SEMs of the holotype).

Remarks. This species was originally described from the lower Oligocene of Tanzania. It was revised by Olsson et al. (2006b) who illustrated the holotype in three views along with several other specimens. It is distinguished from other *Globoturborotalita* by the lobulate test, broad umbilicus and anterio-umbilical aperture. It is scarce in the Tanzania material in comparison to other species of the genus. Here we compare the holotype (Fig. 9.1) with a slightly smaller specimen (Fig. 9.2). Occasional specimens of *Globoturborotalita barbula* n. sp. (e.g., Fig. 8.6) have a similar morphology but are distinguished by possessing the distinctive wall texture of that species

Globoturborotalita martini (Blow & Banner, 1962)

Figs. 9.3–9.12

(Figs. 9.5a-d: new SEMs of the holotype of *Globigerinita martini scandretti* Blow & Banner)

Globigerinita martini martini Blow & Banner *in* Blow & Banner, 1962, p. 110, pl. 14, fig. O (upper Eocene *Cribrohantkenina danvillensis* Zone, Lindi area, Tanzania).

11

Globigerinita martini scandretti Blow & Banner *in* Blow & Banner, 1962, p. 111, pl. 14, figs. V-X (lower Oligocene *Globigerina oligocaenica* Zone, Lindi area, Tanzania).

Globoturborotalita martini (Blow & Banner) *in* Olsson et al., 2006b, p. 121–122, pl. 6.2, figs. 8-18 (various localities including new SEMs of the holotype).

Remarks. This species was originally described from the upper Eocene of Tanzania, with a subspecies (*scandretti*) from the Oligocene of Tanzania. It was revised by Olsson et al. (2006b) who illustrated the holotype in three views. Like the holotype (Fig. 9.3), many specimens in our material possess a small inflated bulla. Here we illustrate a range of specimens, including one that lacks a bulla revealing the small umbilical aperture (Fig. 9.6a-b). It is interesting that even very small specimens (diameter $\sim$ 70 μm) with a poorly developed wall texture, may show a reduced final chamber or bulla (Fig. 9.9). This suggests that the species was an opportunistic, fast-developing form. Blow & Banner (1962) distinguished *scandretti* (Fig. 9.5a-d) by its more rapidly enlarging and embracing chambers, but we find that such features are very variable in populations and no consistent subdivision could be made.

Globoturborotalita ouachitaensis (Howe and Wallace, 1932)

Fig. 10.1a-2

Globigerina ouachitaensis Howe & Wallace *in* Howe & Wallace, 1932, p. 74, pl. 10, fig. 5a-b, partim (upper Eocene, Jackson Fm., Danville Landing, Louisiana).

Globoturborotalita ouachitaensis (Howe & Wallace) *in* Olsson et al. 2006b, p. 122–125, pl. 6.5, figs. 1-16 (various localities).

? *Subbotina gortanii* (Borsetti) *in* Hemleben and Olsson, 2006, pl. 4.1, figs. 4-6 (upper Eocene, Atlantic City borehole, ODP 150X, New Jersey). (Not Borsetti, 1959.)

? *Subbotina gortanii* (Borsetti) *in* Olsson et al. 2006b (partim), p. 138–142, pl. 6.10, figs. 13-17 (upper Eocene, Atlantic City borehole, ODP 150X, New Jersey). (Not Borsetti, 1959.)

Remarks. This small globigeriniform species was revised by Olsson et al. (2006b). It is very similar in size and morphology to *Globigerina officinalis* in the same material (compare with Figs. 5.1–5.2) but is distin-

guished by the cancellate *sacculifer*-type wall; the two species would be very difficult to distinguish in less well preserved material. Olsson et al. (2006b) and Hemleben and Olsson (2006) illustrated several specimens of *ouachitaensis* from a sample at 1338 ft. in the Atlantic City borehole, New Jersey (ODP Hole 150X). From the same sample, those authors also illustrated several similar but higher-spired specimens as '*Subbotina gortanii*'. However those specimens are much smaller than is normal for adult *S. gortanii* (see discussion under that species). They are very similar in gross morphology to *Globoturborotalita barbula* n. sp. but apparently lack the dense concentrations of barbules along the sutures which is so distinctive of that species, hence they are here regarded as a questionable high-spired variant of *G. ouachitaensis*.

Globoturborotalita sp. cf. *G. woodi* (Jenkins, 1960)

Figs. 5.9-5.10c

cf. *Globigerina woodi* Jenkins *in* Jenkins, 1960, p. 352, pl. 2, fig. 2a-c (lower Miocene, Lakes Entrance Oil Shaft, Victoria, Australia).

Remarks. Small cancellate globigeriniforms with four globular chambers and an arched umbilical aperture occur in the Tanzanian material. They are comparable in some respects to Jenkins's taxon but tend to be much smaller in size and with a smaller aperture. However the aperture is larger than in *Globoturborotalita ouachitaensis* and the coiling is less compact, with a more open umbilicus than in that species. Further investigations are required to determine if the "cf. *woodi*" form in our material is related to true *woodi*, the holotype of which is from the lower Miocene of Australia. If so it would be a very low stratigraphic occurrence for the species. An alternative possibility is that such morphologies represent pre-adult dentoglobigerinids although the wall texture tends to be more regularly cancellate than is typical of *Dentoglobigerina*. Stable isotope data indicate a surface mixed-layer habitat (Wade & Pearson, 2008; see Fig. 3).

Genus *Subbotina* Brotzen & Pozaryska, 1961

Type species: *Globigerina triloculinoides* Plummer, 1926, p. 134

Remarks. This genus was revised by Olsson et al. (2006b). See discussion under *Dentoglobigerina* for means of distinguishing it from that genus. Characteristic features of the various species of *Subbotina*

discussed in this paper are presented in Table 2. The genus has generally been regarded as universally spinose (Olsson et al., 2006b), although the only species for which we have evidence of spine holes in our study is the form recorded as *Subbotina* sp. Lack of evidence for spine holes does not necessarily imply that the species were non-spinose in life.

Subbotina corpulenta (Subbotina, 1953)

Fig. 10.3-4c

Globigerina corpulenta Subbotina *in* Subbotina, 1953, p. 101, pl. 9, figs. 5a-7c, pl. 10, figs. 1a-4c (various localities).

Subbotina corpulenta (Subbotina) *in* Olsson et al., 2006b, p.129–134, pl. 6.7, figs. 1-14 (various localities including new SEMs of the holotype).

Remarks. This relatively large and inflated species was revised by Olsson et al. (2006b). Although not shown by the holotype, it commonly possesses an inflated bulla as in the illustrated specimens. We include within this species rather quadrate forms with an umbilical-extraumbilical aperture which we previously (Wade & Pearson, 2008) referred to as *Subbotina hagni* Gohrbandt based on the concept of that taxon in Olsson et al. (2006b). However re-investigation of *hagni* at its type locality by Rögl & Egger (2012) has convinced us that *hagni* it is better referred to the genus *Parasubbotina* and is not closely related to the large subbotinids. Stable isotope data indicate a mixed-layer to thermocline habitat (Wade & Pearson, 2008; see Fig. 3).

Subbotina eocaena (Gümbel, 1868)

Figs. 10.5a-8b

Globigerina eocaena Gümbel *in* Gümbel, 1868, p. 662, pl. 2, fig. 109a, b (upper Eocene, precise locality uncertain, Bavarian Alps, Austria).

Globigerina (*Subbotina*) *eocaena* Gümbel *in* Hagn & Lindenberg, 1966, p. 349–350, pl. 1, fig. 1a-c (neotype), pl. 1, figs. 2-4 (upper Eocene Gerhartsreiter Graben, Siegsdorf, Austria).

Globigerina (*Subbotina*) *eocaena* Gümbel *in* Hagn & Lindenberg, 1969, p. 3a-c (reproduction of neotype illustration) (upper Eocene Gerhartsreiter Graben, Siegsdorf, Austria).

Subbotina eocaena (Gümbel) *in* Olsson et al., 2006b, p. 134–138, pl. 6.9, figs. 1-16 (various localities).

Remarks. This species has been something of a 'wastebasket' taxon due to its generalized morphology, the fact that it was described early in the history of foraminiferal research, and with a name (the '*Globigerina* from the Eocene') which could apply to a wide range of taxa. A neotype was selected by Hagn & Lindenberg (1969) which helped fix the taxonomic concept. It was recently revised by Olsson et al. (2006a) who describe it as having a thin irregular lip. It is morphologically very close to *Subbotina tecta* n. sp., except that it has more radially compressed chambers and lacks the prominent polygonal tooth (see description of that species). Some specimens appear transitional between the two species (e.g., Fig. 10.7a-b). Stable isotope data indicate a mixed-layer to upper thermocline habitat (Wade & Pearson, 2008; see Fig. 3).

Subbotina gortanii (Borsetti, 1959)

Figs. 11.1a-8

Catapsydrax gortanii Borsetti *in* Borsetti, 1959, p. 205, pl. 1, fig. 1a-d (lower Oligocene, Piacenza province, northern Italy).

Globigerina turritilina turritilina Blow & Banner *in* Blow & Banner, 1962, p. 98, pl. XIII, figs. D-G (lower Oligocene *Globigerina oligocaenica* Zone, Lindi area, Tanzania).

Globigerina turritilina praeturritilina Blow & Banner *in* Blow & Banner, 1962, p. 99, pl. XIII, figs. A-C (upper Eocene *Globigerapsis semi-involuta* Zone, Lindi area, Tanzania).

Subbotina gortanii (Borsetti) *in* Olsson et al., 2006b (partim), p. 138–142, pl. 6.10, figs. 1-17 (various localities). Not pl. 6.10, figs.13–17 (upper Eocene, Atlantic City borehole, ODP 150X, New Jersey) (?=*Globoturborotalita ouachitaensis*).

Remarks. Subbotina gortanii is characterised by its high spire and globular embracing chambers. It may or may not show a tooth-like projection on the apertural lip. Olsson et al. (2006b) included in synonymy *Globigerina turritilina turritilina* and *Globigerina turritilina praeturritilina* of Blow & Banner (1962), which were described from the lower Oligocene and upper Eocene respectively of Tanzania. Blow & Banner's type specimens were illustrated in SEM by Olsson et al. (2006b), but unfortunately the scale bars were wrongly labelled as 100 μm instead of 200 μm, giving the impression that the specimens are much smaller than they actually are. Here we re-illustrate these forms to the correct scale (Figs. 11.1a-2d). In our

Table 2. Distinguishing features of *Subbotina* discussed in this paper. Note that lack of evidence of spine holes in our material does not necessarily indicate that the species were non-spinose.

Subbotina	Test shape	Chambers in final whorl	Chamber shape	Umbilical shape	Umbilical features	Evidence of spine holes?
corpulenta	Large, rounded (with bulla)	3½-4	Globular, slightly compressed	Square, deep, open	Thin lip, frequent inflated bulla	No
eocaena	Globigeriniform	3½	Globular, slightly compressed	Rectangular	Thin lip, arched umbilical aperture	No
gortanii	Conical, high spired	3½-4	Rounded, becoming radially compressed	Square, deep, open	Thin lip or projecting tooth	No
tecta n. sp.	Globigeriniform	3½	Spherical	Rectangular	Square to triangular shield-like tooth	No
sp.	Globigeriniform	3½	Spherical to slightly compressed	Square, deep, open	Large projecting tooth	Yes

study we have found specimens of *S. gortanii* that are large and comparable to the types of *turritilina* and *praeturritilina* (Figs. 11.3–8). Small high-spired forms in the upper Eocene of Tanzania which we initially assigned to *S. gortanii* (Wade & Pearson, 2008) were all found to have a distinctive wall texture with barbules and so are here assigned to *Globoturborotalita barbula* n. sp. (see discussion under that species). As discussed above, three small specimens from the upper Eocene of New Jersey illustrated by Olsson et al. (2006b) as *S. gortanii* are referable to either *G. barbula* n. sp. or, more probably, *G. ouachitaensis*. According to our new understanding of these taxa, *S. gortanii* is distinguished from *Globoturbototalita barbula* n.sp. by its much larger adult size, more compressed and embracing chambers and in lacking the distinctive barbules of that species. Further discussion of this species, with reference to new SEMs of the holotype, is deferred to the Oligocene Atlas.

Subbotina tecta Pearson & Wade, new species

Fig. 12.1a-3d, Fig. 13.1a-7b

? *Globigerina yeguanesis* Weinzierl and Applin *in* Postuma, 1971, p. 162, pl. on p. 163 (Sample E 227, Alabama). (Not Weinzierl and Applin, 1929.)

? *Globigerina galavisi* Bermúdez *in* Raju, 1971, p. 24, pl. 5, figs. 2a–3 (*G. mexicana* zone, borehole NGT-1, Cauvery Basin, south-east India). (Not Bermúdez, 1961.)

? *Dentoglobigerina galavisi* Bermúdez *in* Blow, 1979 (partim), p. 1301–1305, pl. 177, figs. 8-9 (middle Eocene, Kilwa area, Tanzania). (Not Bermúdez, 1961.)

Subbotina yeguaensis (Weinzierl and Applin) *in* Olsson et al., 2006b (partim), p. 162–163, pl. 6.18, fig. 12, 16 (Zone E15/16, Shubuta Clay, Wayne County, Mississippi). (Not Weinzierl and Applin, 1929.)

Etymology. Named for *tecta*, Latin, a shield, with reference to the prominent tooth that shields the umbilicus.

Description. Wall symmetrically cancellate, *sacculifer*-type, probably spinose in life. Test composed of 10 to 13 near spherical chambers arranged in a low trochospiral, oval and strongly lobate in outline; in spiral view 3½ to occasionally 4 globular, embracing chambers in final whorl, increasing rapidly in size, sutures straight and depressed, becoming moderately incised between later chambers; in umbilical view 3½ globular chambers, increasing rapidly in size, sutures depressed to incised, straight, umbilicus small, aperture umbilical to slightly extraumbilical in position, obscured by a distinctive trapezoidal to triangular, non-porous, often pustulose tooth, with relict teeth of earlier chambers sometimes visible, the adjacent chamber shoulders sometimes distinctly pustulose; in edge view chambers globular in shape, embracing, tooth convex and arching over the umbilicus. Maximum diameter of holotype 610 μm. Coiling direction is approximately random.

Remarks. This species was referred to as '*Subbotina* sp. 1' in Wade & Pearson (2008). *Subbotina tecta* n.sp. is closely related to *S. eocaena* (Guembel) from which it probably evolved in the uppermost Eocene. It is distinguished from *S. eocaena* in our study by its more spherical chambers (although note that the neotype drawing of *S. eocaena* has very spherical chambers) and by possessing a large and prominent tooth, which is evidently a modification of the slightly pustulose lip of

S. eocaena. When well developed, the tooth is positioned high over the umbilicus and forms a distinct platform above the primary aperture (Fig. 13.6b, Fig. 13.7b). The two species are linked by intermediate forms (Fig. 10.7a-b) and their distinction may be subjective; however, a distinct tooth rather than an irregular lip is critical for our diagnosis of *S. tecta* and in such specimens the chambers are almost always more spherical. The distinctive apertural system and tooth in *S. tecta* may have been related to feeding, for example for securing prey in the umbilical region, and if this is correct it could indicate that *S. tecta* was a separate biospecies with a particular dietary specialization. The new species is distinguished from *S. yeguaensis* by having a lower trochospire and less embracing, more spherical chambers. It is distinguished from *Subbotina* sp. of this work (see below) by having a lower trochospiral and narrower umbilicus, and generally, a less slender, blunter tooth.

A specimen of *S. tecta* was illustrated by Olsson et al. (2006b, plate 6.18, fig. 12) as *S. yeguaensis*. In the past, other specimens may have been assigned to either *D. galavisi* or *S. yeguaensis* (possibly including the specimen illustrated as *Globigerina yeguaensis* by Postuma, 1971); however, *S. tecta* is a very distinctive morphotype which may be confined to the uppermost Eocene and lowermost Oligocene. We have found comparable specimens in DSDP Site 242 (Indian Ocean), ODP Site 647 (North Atlantic Ocean), IODP Site U1334 (equatorial Pacific Ocean), Armenia, and the US Gulf Coast, some of which we intend to illustrate in the forthcoming Oligocene Atlas. No stable isotope data are available.

Stratigraphic range. In Tanzania this species is known from Zones E15/16 and O1. Specimens we have found from other localities (see above) are all from this same interval. Questionable specimens illustrated by Raju (1971) are from the *G. mexicana* zone of India, equivalent to Zone E14, hence likely from a lower stratigraphic level than we have been able to confirm and he recorded the highest occurrence in *G. sastrii* zone, equivalent to Zone O1. We did not find this species in any middle Eocene cores from Tanzania. Blow (1979) illustrated a specimen from the middle Eocene of Tanzania (Zone P11 = Zone E9) that is quite convincingly *S. tecta*, but we have studied the type locality including many outcrop and borehole samples and never found this morphology, so we suspect contamination with an upper Eocene sample.

Repository. Holotype (NHMUK PM PF 71158) and six figured paratypes (NHMUK PM PF 71159 – 71164) deposited in the Natural History Museum, London.

Note that three of the paratypes (Fig. 13.4a-c, 13.5, and 13.6a-b) are part of the type series but were destroyed in the study of wall ultrastructure.

Subbotina sp.

Fig. 14.1-9b

Globigerina sp. aff. *yeguaensis* Weinzierl & Applin *in* Blow & Banner, 1962, pl. XI, figs. P, Q (lower Oligocene *G. oligocaenica* Zone, Lindi area, Tanzania). (Not Weinzierl & Applin, 1929.)

Globigerina eocaena Guembel *in* Stainforth et al., 1975 (partim), p. 268–270, fig. 115, no. 5–7 (upper Eocene Pachuta member, Yazoo Fm., Alabama). (Not Guembel, 1868.)

Dentoglobigerina cf. *globularis* Bermúdez *in* Wade et al., 2007, pl. II, figs. a-d (upper Oligocene, ODP Hole 1218B, equatorial Pacific Ocean). (Not Bermúdez, 1961.)

Description. Wall cancellate, *sacculifer*-type, spinose in life. Test large, globular, 10 to 13 chambers arranged in three whorls, in a moderately high trochospiral, lobate, oval in outline, chambers spherical to subspherical; in spiral view 3½- 4 globular, embracing chambers in final whorl, increasing gradually in size, sutures straight or gently curved, moderately incised; in umbilical view 3½ globular chambers, increasing moderately rapidly in size, sutures depressed to incised, straight, umbilicus wide, square, deep, aperture umbilical, usually with teeth projecting into umbilicus from one or more chambers. Teeth vary from small and triangular to narrow elongate projections, often with a distinct rim or lip around the edges of the tooth that connect with the apertural lip; in edge view chambers globular in shape, embracing, teeth leaning into the umbilicus.

Remarks. This species was referred to as 'Subbotina sp. 2' in Wade & Pearson (2008). It is closely related to *S. tecta* n. sp. but is distinguished by its higher trochospiral coiling, wider, deeper, and generally more square umbilicus and detailed morphology of the teeth, which, although highly variable, can be quite elongate and are generally rimmed by a thin lip of constant thickness. It is distinguished from *S. yeguaensis* by its smaller size, more globular chambers, more incised umbilical sutures and by possessing true teeth rather than a broad, tapering lip. Although forms we attribute to this morphotype have previously been attributed to *Dentoglobigerina globularis* Bermúdez, the latter has more radially compressed and appressed chambers (see

also discussion under the generic diagnosis of *Dentoglobigerina*, below). Our specimens show clear spine holes indicating a spinose condition in life. The relatively free, loosely attached spherical chambers establish the relationship with other *Subbotina* species. The species probably developed from *S. tecta* n. sp. in the uppermost Eocene.

Family Globoquadrinidae Blow, 1979

Genus *Dentoglobigerina* Blow, 1979

Type species: *Globigerina galavisi* Bermúdez, 1961

Remarks. Table 3 presents the distinguishing features of *Dentoglobigerina* species discussed in this paper. The genus was originally erected by Blow (1979) with *galavisi* as the type species. Blow's generic concept was a form-genus; that is, it encompassed all globigeriniform species that possessed a tooth. This led him to include some species that in our understanding are not closely related, while at the same time excluding forms like *tapuriensis* that Blow himself considered to be closely related to the type species *galavisi*, but lack a tooth. Our generic concept is based on supposed evolutionary relationships, hence our inclusion of taxa is very different.

There has been considerable confusion in the literature regarding the status of the genera *Dentoglobigerina* and *Globoquadrina* (erected by Finlay, 1947, with the Miocene species *dehiscens* as the type species), with various authors assigning key species to one or other genus (see for example, discussion in Bolli and Saunders, 1985, p. 183). Here we follow our earlier suggestion (Pearson & Wade, 2009, p. 201–203) that *Globoquadrina* should be restricted to distinctly quadrate Miocene forms (i.e., just *dehiscens* and perhaps one or two closely related forms) while most other species in the group, including the living species *conglomerata* Schwager, should be assigned to *Dentoglobigerina*.

Dentoglobigerina was amended by Olsson et al. (2006c) who stressed two features; first the cancellate and supposedly non-spinose wall, and second the apertural tooth (which gives the genus its name). As the genus was thought to be non-spinose, Olsson et al. (2006c) were forced to hypothesize a non-spinose ancestor and suggested *Acarinina*, which has a different (muricate) wall texture and general morphology, although evidence for the evolutionary transition was not presented.

In the course of our study we have found evidence for spine holes in several species that appear to be closely related to the type species *galavisi* (including in *galavisi*

itself) which is evidence that the group did in fact possess true spines (see Table 3 and Figs. 15.7b, 17.6d, 18.2c, 18.5d, 20.7b, and 21.4e) although they may have been sparsely distributed. This in turn implies that the true ancestry of the group could lie in the *Subbotina* clade as was traditionally thought (e.g., Blow, 1979; Bolli and Saunders, 1985). That conclusion would leave us with a conundrum, however, because the one living species (*conglomerata*) is reportedly non-spinose (e.g., Hemleben et al., 1989) hence either there are two clades with convergent morphology, one spinose and one non-spinose, or spines were lost somewhere in the ancestry of *conglomerata*, or the living species is in fact spinose. The issue has been extensively debated by the Working Group and will be more fully treated in the forthcoming Oligocene Atlas. Here we focus on the evidence from Tanzania of the radiation of species around the Eocene/Oligocene boundary and we defer formal re-description of the genus to the Atlas.

There is one further issue relating to the generic diagnosis that should be emphasized and will be treated in the re-description: the lack of umbilical teeth on some specimens and even some species as a whole (as in *tapuriensis*). In the modern species *conglomerata*, a tooth is present on some specimens but not on others. We have confirmed this by our own examination of *conglomerata* from many different modern localities, including an excellent reference set (the Buckley Collection) in the micropaleontological collections at the Natural History Museum, London. This is problematic because the tooth is an obvious feature of the test and has often been used in identification to species level, as well as in the generic diagnosis. Like the spinose / non-spinose issue, full resolution of this and formal re-description of the genus is best left for the forthcoming Oligocene Atlas where all the evidence can be presented, not just that from Tanzania.

If the criteria of umbilical teeth and the spinose versus non-spinose nature of the wall texture cannot be used to distinguish the genus from *Subbotina*, it begs the question what are in fact the distinguishing features. In our view the chief difference is that the chambers are generally more compressed and more closely appressed than in *Subbotina*, which result in a test that is more tightly coiled. Characteristically, in edge view, the final chamber frequently appears flattened and leans over the umbilicus. There is also a greater tendency toward pustulose wall texture, especially in the umbilical region. These features seem to unite a natural group of globigeriniform morphospecies that are very well represented in the Tanzanian material.

Table 3. Distinguishing features of *Dentoglobigerina* discussed in this paper. Note that lack of evidence of spine holes in our material does not necessarily indicate that the species was non-spinose.

Dentoglobigerina	Chambers in final whorl	Chamber shape	Umbilical shape	Umbilical features	Evidence of spine holes?
galavisi	3	Moderately compressed	Broad triangular	Asymmetrical narrow tooth, pointing down the suture	Yes
prasaepis	3½	Globular, slightly compressed	Rectangular, broad, open	Thin lip	No
pseudovenezuelana	3-3½	Globular, slightly compressed	Narrow triangular	Irregular, pustulose tooth	Yes
taci n. sp.	3½	Globular	Open, square	Thin lip	Yes
tapuriensis	3	Compressed	Elliptical, deep	Thin lip	Yes
cf. *tripartita*	3	Radially flattened	Narrow triangular	Symmetrical narrow tooth, pointing down the suture	Yes

Dentoglobigerina galavisi (Bermúdez, 1961)

Fig. 15.1a-8b

Globigerina galavisi Bermúdez *in* Bermúdez, 1961, p.1183, pl. 4, fig. 3 (upper Eocene Jackson Fm., Mississippi).

Dentoglobigerina galavisi (Bermúdez) *in* Blow, 1979 (pars), p. 1301–1305, pl. 5, figs.1–3 (holotype redrawn), pl. 16, fig. 4 (metatype from upper Eocene Jackson Fm., Mississippi), pl. 6, fig. 5 (upper Eocene Zone P15, Lindi, Tanzania).

Dentoglobigerina galavisi (Bermúdez) *in* Olsson et al., 2006c, p. 403–404, pl. 13.1, figs. 1-16 (various localities including SEMs of the holotype).

Remarks. We follow the concept of *D. galavisi* as described by Olsson et al. (2006c). This species apparently gave rise to several other species of *Dentoglobigerina*, and intermediate morphologies between the various species are common. As this species is the central form from which all other species of the genus are derived, we re-illustrate the holotype (Fig. 14.1a-c) as a reference starting point for consideration of the *Dentoglobigerina* group. We also show a possible spine hole in one specimen (Fig. 14.7b). Stable isotope data indicate a thermocline habitat, becoming deeper with increasing test size (Wade & Pearson, 2008; see Fig. 3).

Dentoglobigerina prasaepis (Blow, 1969)

Fig. 16.1a-8

(Fig. 16.1a-d: new SEM illustration of the holotype of *Globigerina prasaepis* Blow, 1969)

Globigerina ampliapertura euapertura (Jenkins) *in* Blow & Banner, 1962, p. 84, pl. XI, figs. E-G (holotype by subsequent designation; Oligocene *G. oligocaenica* Zone, Lindi area, Tanzania). (Not Jenkins, 1960.)

Globigerina prasaepis Blow *in* Blow, 1969, p. 184-5, pl. 10, fig. 13 (holotype), pl. 18, fig. 3-6 (Oligocene, lower part of the Cipero Fm., San Fernando, Trinidad), pl. 18, fig. 7 (Zone P19/20, Lindi area, Tanzania).

Remarks. The holotype of this taxon is illustrated here for the first time in SEM, including detail of the wall texture. On the basis of alleged similarity of wall texture, Blow & Banner (1962) and Blow (1969, 1979) considered this form to be closely related to the species *ampliapertura*, which is now placed in the genus *Turborotalia* (see below). We, however, place it in the *Dentoglobigerina* group because the wall is cancellate and acicular-pustulose as opposed to smooth and cylindrical-pustulose as in *T. ampliapertura* and related species. There is, however, strong morphological convergence between this morphology and some specimens of *T. ampliapertura* (compare with Fig. 27) hence the distinction would be difficult to make in less well-preserved material. In Wade & Pearson (2008) we included these forms in either cf. *praedehiscens*, *euapertura* or *venezuelana*, but here we choose to lump these forms based on our study of the holotype of the little known species *Globigerina prasaepis* Blow (see fig. 16.1a-d) and further study of their extensive intergradation and variability in our new material. We divide the *prasaepis* group from *venezuelana* sensu stricto on the basis of the somewhat less inflated and appressed chambers and less globular overall morphology. Nevertheless the resemblance between *prasaepis* and *venezuelana* is close, and we propose that the *D. prasaepis* morphotype is transitional to *D. venezuelana* sensu stricto. The *D. prasaepis* morphospecies also intergrades across a spectrum with *D. taci* and *D. tapuriensis*, and can be distinguished by its broad and

17

rectangular umbilicus. It differs from "*Globoquadrina*" *euapertura* by its more pustulose and less cancellate wall texture and rounded chamber shape. Stable isotope data indicate a thermocline habitat, becoming deeper with increasing test size (Wade & Pearson, 2008; taxonomy updates in Fig. 3).

Dentoglobigerina pseudovenezuelana (Blow & Banner, 1962)

Fig. 17.1a-6d

Globigerina yeguaensis pseudovenezuelana Blow & Banner *in* Blow & Banner, 1962, p. 100, pl. XI, figs. J-L (upper Eocene *Cribrohantkenina danvillensis* Zone, Lindi area, Tanzania), figs. N, O (lower Oligocene *Globigerina oligocaenica* Zone, Lindi area, Tanzania).

Dentoglobigerina pseudovenezuelana (Blow & Banner, 1962) *in* Blow, 1979, p. 1307–1310, pl. 19, figs. 1, 2 (lower Oligocene *Globigerina oligocaenica* Zone, Lindi area, Tanzania), pl. 244, figs. 5, 6 (upper Eocene Zone P16, Lindi area, Tanzania).

Dentoglobigerina pseudovenezuelana (Blow & Banner, 1962) *in* Olsson et al., 2006c, p. 404–408, pl. 13.2, figs. 1-16 (various localities including SEMs of holotype).

Remarks. This species was originally described from Tanzania, the holotype being from the upper Eocene and a paratype from the lower Oligocene. Some specimens from the Tanzanian drill cores are very similar to the holotype (Figs. 17.2, 17.5) while others show morphological gradation with *D. galavisi* (Fig. 17.3). Others display a larger, more open umbilicus than the type specimen (Fig. 17.6a-c). The apertural apparatus varies from being a distinct tooth, as in the holotype, to an irregular lip. It, and the umbilical shoulders of the chambers are typically very pustulose in this species, often more so than is typical of closely related forms (Fig. 17. 1d). This may indicate some dietary specialization. The wall texture is cancellate, like other *Dentoglobigerina*, and we have found evidence of spine holes in some specimens (Fig. 17.6d). The species can attain a very large size, approaching 1 mm in diameter. Despite this and the name, the resemblance to *Dentoglobigerina venezuelana* (a species that becomes very common in the Miocene) is not very close, the latter species generally having more inflated and appressed chambers and a more spherical overall morphology. The name *pseudovenezuelana* should not be used for foraminifera that look a bit like *venezuelana* but somehow are not quite right!

Dentoglobigerina taci Pearson & Wade, new species

Fig. 18.1a-5d, Fig. 19.1a-9d

Etymology. Contraction from the Latin *tacitum* (secret or quiet) referring to the fact that this common morphology has long been overlooked.

Description. Wall cancellate and probably spinose in life. 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. Maximum diameter of holotype 390 μm. May be dextral or sinistral, with a slight bias in favor of sinistral coiling.

Remarks. Taxonomic assignment of the abundant well-preserved dentoglobigerinids of Tanzania to previously established and relatively distinctive species such as *galavisi*, *tapuriensis*, 'cf. *tripartita*' and *pseudovenezuelana,* leaves frequent specimens that lack the distinguishing features of those species but which nonetheless are obviously closely related. These forms, which we include in the new species *taci*, first appear in the upper Eocene, that is, at a similar level to the first true *tapuriensis*, and they persist into the Oligocene. Previous workers (e.g., Coccioni et al., 1988) may have recorded similar specimens using open nomenclature by referring them to "cf. *tapuriensis*", as did we initially (as '*Dentoglobigerina* sp. 1'; Wade & Pearson, 2008, p. 253). The new species 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 diagnosis of *D. galavisi* sensu stricto (Blow, 1979; Olsson et al., 2006c). Unlike *galavisi* it generally has a lip of relatively constant thickness rather than a tooth, and a rectangular umbilical depression rather than triangular in *galavisi*. It differs 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

18

species. It differs from *D. tapuriensis* principally by lacking the broad final chamber and broad, low aperture that is characteristic of that species. We regard the new species as being morphologically and evolutionarily intermediate between *D. galavisi* and *D. tapuriensis*. The *taci* n. sp. / *tapuriensis* group also intergrades with *D. prasaepis* which is distinguished from *taci* n. sp. by its larger test and more spherical morphology. It differs from *Subbotina eocaena* by its more pustulose wall texture and squarer umbilical aperture.

Stratigraphic range. Uppermost Eocene to lower Oligocene (becoming rare up section). The highest occurrence has yet to be determined.

Repository. Holotype (NHMUK PM PF 71165) and nine figured paratypes (NHMUK PM PF 71166 – 71174) deposited in the Natural History Museum, London. Note that four of the paratypes (Fig. 18.3a-b, 18.5a-d, 19.5, and 19.6) are part of the type series but were destroyed in the study of wall ultrastructure.

Dentoglobigerina tapuriensis (Blow & Banner, 1962)

Fig. 20.1a-9

(Figs. 20.1a-d: new SEMs of the holotype of *Globigerina tripartita tapuriensis* Blow & Banner)

Globigerina tripartita tapuriensis Blow & Banner *in* Blow & Banner, 1962, p. 97, pl.X, figs. H-K (lower Oligocene *G. oligocaenica* Zone, Lindi area, Tanzania).
Globigerina tapuriensis Blow & Banner *in* Blow, 1969, p. 322, pl. 16, figs. 7, 8 (lower Oligocene Zone P19, Lindi area, Tanzania).
Globigerina tapuriensis Blow & Banner *in* Blow, 1979, p. 859–861, pl. 16, figs. 7, 8 (reproduced from Blow, 1969), 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).

Remarks. Dentoglobigerina tapuriensis was described from the lower Oligocene of Lindi, Tanzania by Blow & Banner (1962). Despite the name, the type sample is not from Ras Tipuli (= 'Ras Tapuri' of Blow & Banner, 1962) but rather from the other side of Lindi Bay. Blow & Banner (1962) distinguished it from *tripartita* by the more convex dorsal surface and more convex apertural face of the chambers, more open umbilicus, and wider aperture. Another feature is the lack of a distinct umbilical tooth and the presence of a 'rim-like' lip (which is especially evident on the penultimate chamber of the well-preserved holotype

specimen, shown here in SEM for the first time). Very similar morphotypes are common in our material, showing the characteristic three chambers in the final whorl, strong radial compression of the final and penultimate chamber and broad, low arched aperture. Like the holotype, our specimens have a relatively narrow and sometimes pustulose lip, but no triangular tooth development. Blow (1979) excluded this species from his genus *Dentoglobigerina* because it lacks a tooth, despite regarding it as closely related to *tripartita*. Whereas previous authors (e.g., Spezzaferri, 1994) have tentatively referred this species to '*Globoquadrina*' because of the lack of a tooth, we include it in *Dentoglobigerina* because of its close resemblance to and integradation with other species in that genus according to our concept. The most similar morphology in our material is represented by *Dentoglobigerina taci* n.sp., particularly with respect with the absence of an apertural tooth and broad umbilicus in that form. We speculate that *D. taci* n. sp. forms an evolutionary link between *D. galavisi* and *D. tapuriensis*. The latter evolved by reduction and loss of the umbilical tooth, increased compression of the chambers and reduction in the number of chambers per whorl from 3½ to 3 and by developing an overall more globular, spherical morphology, while at the same time the tests achieved greater maximum size. Blow & Banner (1962) and Blow (1979) used *Dentoglobigerina tapuriensis* as an indicator of the Oligocene. It has been reported as first occurring at the same level as the extinction of Hantkeninidae, including in the GSSP section at Massignano in Italy (Coccioni et al., 1988; see also Premoli Silva & Spezzaferri, 1990). However we find low abundances of *D. tapuriensis* sensu stricto first occurring in the uppermost Eocene (e.g., Figs. 20.4a-b, 20.7a-b), but the species rapidly increases in abundance at a level slightly above the Eocene/Oligocene boundary (Wade & Pearson, 2008). For this reason we caution its use as a secondary zonal marker.

Dentoglobigerina cf. *tripartita* (Koch, 1926)

Fig. 21.1-7c

? *Globigerina bulloides* var. *tripartita* Koch *in* Koch, 1926, p. 742, fig. 21a, b ('middle Tertiary', Sadjau-Njak, southeast Bulongan, East Borneo).
Globigerina tripartita Koch *in* Blow, 1969, p. 322, pl. 16, fig. 6 (upper Eocene Zone P15, Lindi area, Tanzania). (? not Koch, 1926.)

Dentoglobigerina tripartita (Koch) *in* Blow, 1979, pl. 244, figs. 3, 4 (upper Eocene Zone P16, Lindi area, Tanzania). (Not Koch, 1926.)

Dentoglobigerina tripartita (Koch) *in* Olsson et al., 2006c (partim), p. 408–410, pl. 13.3, figs. 4, 15 (upper Eocene Zone E16, Nanggulan Fm., Java), 5 (reproduced from Blow, 1979, pl. 244, fig. 3), 6 (reproduced from Blow, 1969, pl. 16, fig. 6), 7,8 (upper Eocene Zone E15/16, TDP Site 11, Tanzania), 9–11 (upper Eocene Zone E15/16, Shubuta Clay, Mississippi), 14 (upper Eocene Zone E15, Istra-More Well 4, Adriatic Sea). (? Not pl. 13.3, figs. 1-3 = holotype; not pl. 13.3, figs. 12, 16 = *Dentoglobigerina galavisi*). (? not Koch, 1926.)

Remarks. The concept of *Dentoglobigerina tripartita* will be revised in the forthcoming Oligocene Atlas because the holotype has now been located. Eocene forms that have been referred to as *tripartita* following the concept of Blow (1969, 1979), including by us (Wade & Pearson, 2008) are here referred to as 'cf. *tripartita*' pending this revision (the specimens illustrated in these works by Blow are reproduced on Figure 21.1 and 21.2 for comparison with the new specimens). The species was revised by Olsson et al. (2006c) who illustrated a variety of Eocene specimens that we include here, although here we reassign two specimens illustrated in that work (pl. 13.3, figs. 12 and 16 in Olsson et al. 2006c) to *galavisi* based on the number of chambers in the final whorl and umbiical features. *Dentoglobigerina* cf. *tripartita* is distinguished from *galavisi* by possessing more rapidly expanding chambers, a more overarching and compressed final chamber and by having a tooth that generally points down the opposite suture. The test is generally more compact, with a tighter umbilicus and the chambers more closely embracing. Some specimens show transition to *Dentoglobigerina tripartita* sensu stricto (e.g., Fig. 21.6a-b) and we speculate that 'cf. *tripartita*' may have evolved into *D. tripartita* later in the Oligocene. Stable isotope data indicate a thermocline habitat, becoming deeper with increasing test size (Wade & Pearson, 2008; see Fig. 3).

Family Hantkeninidae Cushman, 1927

The Tanzanian Kilwa group contains abundant members of this family, divided between the genera *Cribrohantkenina* and *Hantkenina*. Their simultaneous extinction marks the Eocene/Oligocene boundary. A taxonomic key for distinguishing features of the five species of Hantkeninidae discussed in this paper is provided in Table 4.

Genus *Cribrohantkenina* Thalmann, 1942

Type species: *Hantkenina* (*Cribrohantkenina*) *bermudezi* Thalmann, 1942

Remarks. This genus was revised by Coxall and Pearson (2006). The presence of at least one areal aperture is required for a specimen to be assigned to this genus. The areal apertures may not be present on earlier chambers hence individuals would pass through a *Hantkenina nanggulanensis* stage in their ontogeny. Hence the genus is strictly a morphogenus; we retain it for consistency with a long history of published literature.

Cribrohantkenina inflata (Howe, 1928)

Figs. 22.1a-3b, 23.1a-21.

Hantkenina inflata Howe *in* Howe, 1928, p. 14, pl.14, fig. 2 (lower Oligocene [upper Eocene?], St. Stephens Bluff, Alabama).

Cribrohantkenina inflata (Howe) *in* Coxall & Pearson, 2006, p. 226–229, pl. 8.3, figs. 1-16 (various localities including SEMs of holotype).

Remarks. According to Coxall & Pearson (2006), *Cribrohantkenina* is monospecific. The critical feature for inclusion is the presence of at least one areal aperture; specimens similar in all other respects but lacking areal apertures are assigned to *Hantkenina nanggulanensis* (see above). Here we illustrate a variety of specimens of *C. inflata* to demonstrate the range of test architectures shown by mature specimens, including details of the areal aperture systems and tubulospines. The wall usually has a smooth appearance, with variable pore sizes, but can be distinctly cancellate or pustulose. The smooth surface is achieved by laying calcite on top of the inner cancellate structure. The pore sizes on the smooth surface varies considerably (Fig. 22.1e), but very small pores should not be confused with spine holes. Near the Eocene/Oligocene boundary we have noticed a high frequency of pustulose specimens, the pustules being laid down on top of the smooth surface (Fig. 22.3a-b). This is also seen in species of *Hantkenina* (Fig. 25.4a-b).

The primary aperture is usually a low arch or, when built around a tubulospine, two more or less symmetrical arches that join at the mid-line. The number of areal apertures in our material varies from 1 to 12. These

Table 4. Distinguishing features of the Hantkeninidae discussed in this paper.

Hantkenina and *Cribrohantkenina*	Aperture(s)	Tubulospines	Chamber inflation
C. inflata	Primary aperture is a low arch, sometimes bifurcate. At least one, usually multiple, areal apertures.	Mostly short and stumpy, to conical	Very inflated, final chamber usually broader than tall in edge view
H. alabamensis	Broad, open	Variable in length	Moderately inflated, usually taller than broad in edge view
H. compressa	Tall, slit, inverted 'Y' shape	Long and slender	Compressed
H. nanggulanensis	Broad, open	Mostly short and stumpy	Very inflated, final chamber usually broader than tall in edge view
H. primitiva	Tall, slit, inverted 'Y' shape	Long, usually absent on first chamber(s) of the final whorl	Compressed

apertures are round, oval or sometimes sub-rectangular, of variable size, and set within a field of smooth non-porous test wall. They are always bordered by a smooth lip and are generally arranged in rough symmetry about the equatorial plane, although occasionally an aperture will have no symmetrical counterpart (Figs. 23.1b, 23.11, 23.18b). Apertures that lie on the mid-line are often themselves irregularly symmetrical (Figs. 23.5b, 23.12, 23.20). We have observed minute, inward pointing pustules on the apertural lips (Figs. 22.1g, 22.2b). The tubulospines vary from being relatively long and thin to short and stubby or even conical. On the last chamber they are usually very short. They usually end in a small circular aperture (Fig. 22.1b), but are sometimes smoothly rounded, with no aperture.

Possible functions for the apertural system include feeding the relatively large cell (extreme by the standards of planktonic foraminifera) by improving the ingress / egress of food and waste products, harboring photosynthetic symbionts, or gamete dispersal. Patterns of striations on the test surface indicate that it was remodeled in life by externally flowing cytoplasm (Fig. 22.1d, 22.1f, 22.1g). As in species of *Hantkenina*, these striations are frequently seen running along the tubulospines, but they are also seen on the chamber surfaces and in diverging / converging patterns around the apertural system. The areal aperture system is similar to that seen in Miocene *Globigerinatella insueta* (Pearson, 1995).

The bilateral symmetry shown by the aperture systems raises an intriguing question regarding the mode of test formation in the species. According to Coxall et al. (2003), the Hantkeninidae are descended from an ancestor in the genus *Parasubbotina* that was not only trochospiral but also, like most trochospiral species, possessed chambers that differ substantially in form on the dorsal and ventral sides. The earliest members of the family Hantkeninidae (*Clavigerinella*

eocanica, Hantkenina singanoae, H. mexicana) are much more symmetrical across the periphery, but still apparently retain vestiges of trochospirality (i.e., slight differences between 'umbilical' and 'spiral' sides; Coxall et al., 2003; Pearson & Coxall, 2014), whereas later (geologically younger) species become essentially planispiral in appearance, with fully symmetrical chambers either side of the equatorial periphery. In evolutionary terms, however, the resulting planispiral coiling mode might be considered from these observations to be more apparent than real, because it has resulted from gradually increasing chamber symmetry and a lowering of the trochospiral until effective planispirality is achieved. The *C. inflata* specimens are interesting in that they show a wide range of apertural modifications, in which the shape of the primary aperture and the number, shape and arrangement of additional areal apertures differs from specimen to specimen. However in each case there is distinct (although imperfect) symmetry across the peripheral mid-line. From this it can be inferred that 1) the morphogenetic instruction for test formation, including the areal apertures, had an underlying genetic basis (i.e., it was not merely fortuitous where the apertures developed) and 2) those genetic instructions were applied symmetrically across the plane of coiling as the chamber formed. The fundamental pattern of test formation must, therefore, be considered as genuinely planispiral. From this it can be concluded that at some point in the evolution of the hantkeninid lineage, a fundamental change in morphogenetic programming must have occurred, but as earlier species lack areal apertures, it is impossible to determine when.

Random deviations from perfect symmetry that occur in the development of symmetrical traits have been called Fluctuating Asymmetry (FA; Van Valen, 1962). Fluctuating Asymmetry is widely thought to be related to developmental instability, which 'can be thought of

as variation around the expected (target) phenotype that should be produced by a specific genotype in a specific environment' (Leamy & Klingenberg, 2005). The vast majority of studies dealing with FA and developmental instability refer to multicellular organisms. It is interesting that foraminifera display bilateral symmetry and measurable FA, although the genetic basis of it are unknown, and it is also interesting that the degree of FA is (qualitatively) very high compared to typical asymmetries in multicellular organisms.

Stable isotope data indicate a shallow thermocline habitat, becoming deeper with increasing test size (Wade & Pearson, 2008; see Fig. 3).

Genus *Hantkenina* Cushman, 1924

Type species: *Hantkenina alabamensis* Cushman, 1924

Remarks. This genus was reviewed by Coxall and Pearson (2006). The Tanzanian sediments contains relatively common hantkeninids (Wade & Pearson, 2008), including all four uppermost Eocene morphospecies that are considered valid in the taxonomy of Coxall & Pearson (2006). These forms intergrade and it is not clear to what extent they might represent separate biological species. They all persist to the level of the Eocene/Oligocene boundary where they disapppear simultaneously (Wade & Pearson, 2008). Interestingly, a variety of specimens belonging to various morphospecies exhibit pustules on their test wall surface close to their extinction, as also described above under *Cribrohantkenina*. These pustules are only present in the final part of the stratigraphic range: Detailed study of TDP Site 12 shows that the interval of pustulose hantkeninids extends for ~240 kyr from Section TDP12/20/3 (65 m) to the extinction level in Section TDP 12/14/2 (45 m).

Hantkenina alabamensis Cushman, 1924

Fig. 24.1a-6b

Hantkenina alabamensis Cushman *in* Cushman, 1924, p. 3, pl. 1, figs. 1-6, pl. 2, fig. 5 (Eocene *Zeuglodon* bed, Cocoa Post Office, Alabama).
Hantkenina alabamensis Cushman *in* Coxall & Pearson, 2006, p. 230–232, pl. 8.4, figs. 1-16 (various localities including SEM of the holotype).

Remarks. Following Coxall & Pearson (2006) we include moderately inflated forms in this species. In large specimens the final chamber is often positioned firmly on the tubulospine of the preceding chamber, as is the case in the holotype. The tubulospines generally lean forward but on occasional specimens (Fig. 24.3) they can be radial.

Hantkenina compressa Parr, 1947

Fig. 24.7-12b

Hantkenina compressa Parr *in* Parr, 1947, p. 46, text-figs. 1-7, figs. 7-7a (probably upper Eocene, Browns Creek coastal section, Victoria, Australia).
Hantkenina compressa Parr *in* Coxall & Pearson, 2006, p. 233–236, pl. 8.6, figs. 1-21 (various localities).

Remarks. Following Coxall & Pearson (2006) we include in this species laterally compressed forms in which the tubulospines are more radially directed than is generally the case in *H. alabamensis*. Due to the more compressed shape, the aperture is usually a flanged slit. The morphospecies *H. alabamensis* and *H. compressa* seem to be linked by a continuous gradation of morphology. This species is also very similar to *H. primitiva* in its compressed morphology and tubulospine position, but has tubulospines on every chamber of the final whorl.

Hantkenina nanggulanensis Hartono, 1969

Fig. 25.1-4b

Hantkenina nanggulanensis Hartono *in* Hartono, 1969, p. 154, pl. 20, figs. 3-4 (upper Eocene, Kebon Agung, Nanggulan region, Java).
Hantkenina nanggulanensis Hartono *in* Coxall & Pearson, 2006, p. 246–250, pl. 8.11: figs. 1-18 (various localities).

Remarks. Following Coxall & Pearson (2006) we include large inflated forms in this species. They are distinguished from *Cribrohantkenina inflata* by the lack of areal apertures. As noted under *C. inflata*, a given test of that species may only show areal apertures on the final chamber, before the addition of which it would be assigned to *nanggulanensis*. Another subtle distintion between *inflata* and *nanggulanensis* is that the latter tends to have a more highly arched primary aperture (Table 4). There also seems to be a complete gradation of morphology between *H. nanggulanensis* and *H. alabamensis*. Stable isotope data indicate an upper thermocline habitat (Wade & Pearson, 2008; see Fig. 3).

Hantkenina primitiva Cushman & Jarvis, 1929

Fig. 25.5a-9b

Hantkenina alabamensis Cushman var. *primitiva* Cushman & Jarvis *in* Cushman & Jarvis, 1929, p. 16, pl. 3, figs. 2-3 (Eocene, Mt. Moriah beds, Vistabella Quarry, Trinidad).

Hantkenina primitiva Cushman and Jarvis *in* Coxall & Pearson, 2006, p. 250–252, pl. 8.12, figs. 1-20 (various localities including SEMs of the holotype).

Remarks. Following Coxall & Pearson (2006) we include in this species relatively small compressed forms that tend to lack tubulospines on the earlier chambers of the final whorl. In other respects they are similar to *H. alabamensis*.

Family Hedbergellidae Loeblich & Tappan, 1961

Genus *Pseudohastigerina* Banner & Blow, 1959

Type species: *Nonion micrus* Cole, 1927

Remarks. This genus was reviewed by Olsson and Hemleben (2006).

Pseudohastigerina micra (Cole, 1927)

Fig. 26.1–7

Nonion micrus Cole *in* Cole, 1927, p. 22, pl. 5, fig. 12 (middle Eocene, Guayabal Fm., Tampico, Mexico).

Pseudohastigerina micra (Cole) *in* Olsson & Hemleben, 2006, p. 422–424, pl. 14.3, figs. 11-24 (various localities including SEMs of the holotype).

Remarks. Our SEM observations show that some relatively large forms have a distinctly pinched periphery with a peripheral imperforate band, smooth umbilical shoulders and strongly curved sutures (see Figs. 26.3, 26.4, 26.6). The umbilicus tends to be crowded with minute pustules. These features can also be seen in the SEM illustration of the holotype in Olsson & Hemleben (2006). There is a distinct decrease in the size of *Pseudohastigerina micra* at the same level as the extinction of the Hantkeninidae (i.e., the Eocene/Oligocene boundary) (Wade & Pearson, 2008). This shift in size is also recognised at St Stephens Quarry, Alabama (Miller et al., 2008; Wade & Olsson, 2009) and elsewhere (Cordey et al., 1970) and serves as an alternative means of correlating the Eocene/Oligocene boundary when hantkeninids are rare or absent (Wade et al., 2011).

Pseudohastigerina naguewichiensis (Myatliuk, 1950)

Fig. 26.8a-11

Globigerinella naguewichiensis Myatliuk *in* Myatliuk, 1950, p. 281, pl. 4, figs. a, b (Oligocene, Chechva River, Lopanetskie layer, western Ukraine).

Pseudohastigerina naguewichiensis (Myatliuk) *in* Olsson & Hemleben, 2006, p. 424–426, pl. 14.3, figs. 1-10 (various localities).

Remarks. Blow (1979) provided a detailed description of *P. naguewichiensis* and related forms, at which time he distinguished two closely related subspecies, *P. naguewichiensis naguewichiensis* and *P. naguewichiensis barbadoensis*. The latter form was separated principally by the fact that it contains more abundant large pore pits and by the "more appressed, more close-set and somewhat more embracing chambers as seen in side view" (Blow 1979, p. 1190). We have not been able to distinguish the two forms adequately using these criteria and so regard them as synonyms. We agree with Olsson & Hemleben (2006) that the frequency of large pore pits is related to the degree of late-stage calcite encrustation which varies considerably between individuals. Stable isotope data indicate a surface mixed-layer habitat with relatively low δ^{13}C indicating incorporation of respired carbon into the test as is typical of small species (Wade & Pearson, 2008; see Fig. 3).

Genus *Turborotalia* Cushman & Bermúdez, 1949

Type species: *Globorotalia centralis* Cushman & Bermúdez, 1949

Remarks. This genus was reviewed by Pearson et al. (2006b). The key features of *Turborotalia* species discussed in this paper are presented in Table 5.

Turborotalia ampliapertura (Bolli, 1957b)

Fig. 27.1a-6

Globigerina ampliapertura Bolli *in* Bolli, 1957b, p. 108, pl. 22, figs. 4a-6c (lower Oligocene *Globigerina ampliapertura* Zone, Cipero Fm., Trinidad).

Turborotalia ampliapertura (Bolli) *in* Pearson et al., 2006c, p. 441–442, pl. 15.2, figs. 1-20 (various localities including new SEMs of the holotype).

Remarks. This species is distinguished from other species of *Turborotalia* by the almost globigeriniform morphology and tendency for possessing a wide, arched

Table 5. Distinguishing features of *Turborotalia* discussed in this paper.

Turborotalia	Test shape	Chambers in final whorl	Final chamber shape (edge view)	Aperture	Ornamentation
ampliapertura	Inflated globigeriniform	3½-4	Rounded	Asymmetrical, broad, high arch	Perforate wall with cylindrical pustules
cerroazulensis	High anguloconical	4½-5	Orthogonal to obtuse peripheral angle	Broad, high arch	Smooth perforate wall. Peripheral band / keel optional
cocoaensis	Low anguloconical	4-4½	Slightly acute peripheral angle	Broad, high arch	Smooth perforate wall. Peripheral band / keel optional
cunialensis	Lenticular	4½-5	Acute peripheral angle	Circular arch	Smooth perforate wall. Peripheral band / keel optional
increbescens	Inflated globorotaliiform	4-4½	Rounded	High arch	Perforate wall with cylindrical pustules.

and generally asymmetrical aperture. Specimens can be quite variable in morphology, grading in to the *increbescens* morphospecies. Pearson et al. (2006c) included Blow and Banner's (1962) Tanzanian species *Globigerina pseudoampliapertura* in synonymy with *ampliapertura*. The main distinction between these species according to Blow & Banner (1962) and Blow (1979) was based on the supposedly smoother wall texture of *pseudoampliapertura*. Pearson et al. (2006c) argued that the wall texture was variable, depending principally on the size of the specimen and the state of preservation. Our new SEMs of very well-preserved specimens demonstrate the variability of the wall, supporting the synonymy of the two taxa. Some specimens with relatively low umbilical apertures can resemble *Dentoglobigerina taci* n. sp. in general morphology. They are distinguished principally by the wall texture, which is relatively smooth and pustulose in *ampliapertura* (with cylindrical pustules; see Pl. 27.4b) and more reflective under the light microscope, but cancellate in *taci*, and by the sutures which are not incised in *ampliapertura*.

Stable isotope data indicate a relatively shallow habitat, but slightly cooler than small surface-dwellers like *Globoturborotalita* (Wade & Pearson, 2008; see Fig. 3). The relative abundance of this species increases through the Eocene/Oligocene transition, and can dominate assemblages in Tanzania (Wade & Pearson, 2008) and also assemblages from the South Pacific Gyre IODP Site U1367 (Wade, unpublished).

Turborotalia cerroazulensis (Cole, 1928)

Fig. 28.1a-4

Globigerina cerro-azulensis Cole *in* Cole, 1928, p. 217, pl. 32, figs. 11-13 (upper Eocene, Chapapote Fm., Mexico).

Turborotalia cerroazulensis (Cole) *in* Pearson et al., 2006c, p. 442–446, pl. 15.3, figs. 1-20 (various localities, including SEMs of the holotype).

Remarks. We follow Pearson et al. (2006c) in distinguishing this species from *T. cocoaensis* by the obtuse angle of the final chamber in edge view, although the distinction is arbitrary and our samples seem to contain a smooth gradation from quite globular, anguloconical specimens of *T. cerroazulensis* all the way through to compressed biconvex forms attributed to *T. cunialensis*. Pearson and Ezard (2014) have used morphometric clustering techniques to reveal two separate morphoclusters in upper Eocene turborotaliids in the Pacific Ocean, and similar clusters may exist in Tanzania but would require detailed morphometry of large populations to identify them. A noticeable feature of this group of species is the presence of an imperforate band on many specimens of all morphospecies, including quite anguloconical individuals referable to *T. cerroazulensis* (Fig. 28.1a-b). This species does not normally show an imperforate band or keel for most of its stratigraphic range (see Pearson et al., 2006c).

Turborotalia cocoaensis (Cushman, 1928)

Fig. 28.5a-13b

Globorotalia cocoaensis Cushman *in* Cushman, 1928., p. 75, pl. 10, figs. 3a-c (upper Eocene, Cocoa Sand, Choctaw County, Alabama).

Turborotalia cocoaensis (Cushman) *in* Pearson et al., 2006c, p. 446–450, pl. 15.4, figs. 1-12 (various localities including SEMs of the holotype).

Remarks. This species is distinguished from *Turborotalia cerroazulensis* by having a distinctly acute periphery on the final chamber and from *T. cunialensis* by having a less acute periphery and a relatively flat spiral

side (Pearson et al., 2006c). There is a preponderance of sinistrally coiled tests as observed by Pearson & Ezard (2014) in the Pacific Ocean. Stable isotope data indicate a thermocline habitat (Wade & Pearson, 2008; see Fig. 3).

Turborotalia cunialensis (Toumarkine and Bolli, 1970)

Fig. 29.1a-11

Globorotalia cerroazulensis cunialensis Toumarkine & Bolli *in* Toumarkine & Bolli, 1970, p. 144–145, pl. 1, figs. 37-39 (upper Eocene, Cunial quarry, Possagno area, Italy).

Turborotalia cunialensis (Toumarkine & Bolli) *in* Pearson et al., 2006c, p. 450–452, pl. 15.4, figs. 13-17 (various locations).

Remarks. Turborotalia cunialensis is a relatively rare form that occurs in the upper Eocene (Wade & Pearson, 2008). Pearson et al. (2006c) distinguish it from *cocoaensis* by its more acute periphery and biconvex morphology rather than the presence of an imperforate band or keel, because the latter can also be found in both *T. cerroazulensis* and *T. cocoaensis* (Fig. 28.8, 28.12) and can be absent in *T. cunialensis* (Fig. 29.6). Stable isotope data indicate a thermocline habitat (Wade & Pearson, 2008; see Fig. 3).

Turborotalia increbescens (Bandy, 1949)

Pl. 27.7a-8b

Globigerina increbescens Bandy *in* Bandy, 1949, p. 120, pl. 23, figs. 3a-c (upper Eocene, Little Stave Creek, Alabama).

Turborotalia increbescens (Bandy) *in* Pearson et al., 2006c, p. 453–454, pl. 15.6, figs. 1-15 (various localities including SEMs of the holotype).

Remarks. This species is distinguished from *T. ampliapertura* by its narrower umbilicus and more globorotaliform morphology with a more extraumbilical aperture. Along with *T. ampliapertura*, it survived the extinction of the *cerroazulensis* group and the E/O boundary but is rare in the Oligocene part of the section (Wade & Pearson, 2008). Stable isotope data are virtually indistinguishable from *T. ampliapertura* (Wade & Pearson, 2008; see Fig. 3).

Family Truncorotaloididae Loeblich & Tappan, 1961

Type genus: *Acarinina* by synonymy with *Truncorotaloides*

Genus *Acarinina* Subbotina, 1953

Type species: *Acarinina acarinata* Subbotina, 1953

Remarks. This genus was revised by Berggren et al. (2006). It was traditionally thought of as a Paleocene - middle Eocene genus, but some inconspicuous forms survived into the late Eocene and, as argued here, the Oligocene.

Acarinina collactea (Finlay, 1939)

Fig. 30.1a-b

Globorotalia collactea Finlay *in* Finlay, 1939, p. 327, pl. 29, figs. 164, 165 (middle Eocene, Hampden Beach, North Otago, New Zealand).

Acarinina collactea (Finlay) *in* Berggren et al., 2006, p. 276–280, pl. 9.8, figs. 1-16 (various localities, including SEMs of holotype and paratype).

Remarks. The <125 µm size fraction indicates the presence of rare but distinctive small muricate forms which we ascribe to the genus *Acarinina* and interpret as being *in situ*. The biconvex, low trochospiral form illustrated has a bulla and blunted muricae (slightly corroded showing the internal structure; similar to the illustrations of Hemleben and Olsson (2006, pl. 4.8, figs. 9, 14) and is similar in gross morphology and size to Finlay's taxon except that the spiral sutures are more strongly curved than is typical for *A. collactea*. According to Berggren et al. (2006), *A. collactea* survived into the upper Eocene but its last global appearance datum was poorly constrained in that study. This occurrence suggests that *A. collactea* (and hence the genus *Acarinina*) survived at least to the earliest Oligocene. It may have been overlooked because of its small size and rarity.

Superfamily Heterohelicoidea Cushman, 1927

Family Chiloguembelinidae Reiss, 1963

Type genus: *Chiloguembelina* Loeblich & Tappan, 1956

Genus: *Chiloguembelina* Loeblich & Tappan, 1956

Type species: *Guembelina midwayensis* Cushman, 1940

Remarks. This genus was revised by Huber et al. (2006).

Chiloguembelina cubensis (Palmer, 1934)

Fig. 30.3a-b

Guembelina cubensis Palmer *in* Palmer, 1934, p. 74, figs. 1-6 (lower Oligocene, Palmer Station Well 1163, Santa Clara province, Cuba).

Chiloguembelina cubensis (Palmer) *in* Huber et al., 2006, p. 473–474, pl. 16.3, figs. 23-24 (middle Eocene Zone E10, TDP Site 13, Mkazambo, Tanzania).

Remarks. This species of *Chiloguembelina* is characterized by a surface ornamentation of longitudinal striations (Huber et al., 2006; Miller et al., 2008).

Genus: *Streptochilus* Brönnimann & Resig, 1971, p. 1288

Type species: *Bolivina tokelauae* Boersma, 1969

Remarks. This genus was revised by Huber et al. (2006). Pending further investigation we follow Huber et al. (2006) by including it in Family Chiloguembelinidae although we note that more recent genetic evidence suggests it may be a junior synonym of the benthic biserial genus *Bolivina* in Family Bolivinidae (Darling et al., 2009, p. 12631).

Streptochilus martini (Pijpers)

Fig. 30.4-6c

Textularia martini Pijpers *in* Pijpers, 1933, p. 57, figs. 6-10 (upper Eocene, Bonaire, Dutch West Indies).

Streptochilus martini (Pijpers) *in* Huber et al., 2006, p. 477–478, pl. 16.3, figs. 1-2 (holotype of *Chiloguembelina victoriana* Beckmann, 1957), pl. 16.3, figs. 3, 6 (upper Eocene, Atlantic City Borehole, New Jersey, ODP Hole 150X), pl. 16.3, figs. 4, 5 (middle Eocene Zone P9, Aragon Fm., Tampico, Mexico), pl. 16.3, figs. 7, 8 (upper Eocene Zone P15, lower Kitunda slopes, Lindi, Tanzania).

Remarks. We follow Huber et al. (2006) in our identification of this species, which has reniform chambers and a loop-like aperture. Huber et al. (2006) noted that some low-latitude specimens may show macroperforation ($>$ 1 μm in diameter). The specimen illustrated as Figure 30.4a-b is technically macroperforate.

Family Globigerinitidae Bermúdez, 1961

Type genus: *Globigerinita* Brönnimann, 1951

Genus *Tenuitella* Fleisher, 1974

Type species: *Globorotalia gemma* Jenkins, 1966

Remarks. This genus was revised by Huber et al. (2006).

Tenuitella gemma (Jenkins, 1966)

Fig. 30.2a-b

Globorotalia gemma Jenkins *in* Jenkins, 1966, p. 1115, fig. 11, nos. 97–103 (lower Oligocene *Globigerina brevis* Zone, DSDP Site 350, Cape Basin, South Atlantic Ocean).

Tenuitella gemma (Jenkins, 1966) *in* Huber et al., 2006, p. 488–489, pl. 16.7, figs. 15-20 (various localities including SEM of holotype).

Remarks. We follow Huber et al. (2006) in identifying this species which is a rare component of the fine fraction in our material. Dedicated searching has yielded just a few specimens.

Superfamily Unknown

Family Cassigerinellidae Bolli et al., 1957

Type genus: *Cassigerinella* Pokorný, 1955

Genus *Cassigerinella* Pokorný, 1955

Type species: *Cassigerinella boudecensis* Pokorný, 1955 (=junior subjective synonym of *Cassigerinella chipolensis* Cushman and Ponton, 1932).

Remarks. This genus was revised by Li (1986) and Pearson & Wade (2009).

Cassigerinella chipolensis (Cushman & Ponton, 1932)

Fig. 30.7a-8

Cassidulina chipolensis Cushman & Ponton *in* Cushman & Ponton, 1932, p. 98, pl. 15, figs. 2a-c (lower Miocene Chipola Fm., Alum Bluff Group, Calhoun County, Florida).

Cassigerinella chipolensis (Cushman & Ponton) *in* Li, 1986, p. 6, pl. 3, figs. 7-11; pl. 4, figs. 1-17 (lower Oligocene Zone P21, Cipero Fm., Trinidad).

Cassigerinella chipolensis (Cushman & Ponton) *in* Pearson & Wade, 2009, p. 198–200, pl. 1, figs. 1a-2f (upper Oligocene Zone O6 [=O7 in Wade et al., 2011], Cipero Fm., Trinidad), pl. 1, figs. 3a-3b (upper Oligocene Zone O5, Juana Diaz Fm., Puerto Rico).

Cassigerinella boudecensis Pokorný *in* Pokorný, 1955, p. 138, figs. 1-3 ('middle' Oligocene, Pausramer Marl, Czech Republic).

Remarks. The specimens we illustrate have a very smooth wall, similar to the holotype.

CONCLUSION

We have drilled three core-holes through the Eocene/Oligocene boundary in Tanzania. We have taken the opportunity provided by the exceptional state of preservation of planktonic foraminifera to illustrate test morphologies and revise species concepts including for a range of species originally described from Tanzania by Blow & Banner (1962) and Blow (1979).We have found it necessary to name three new species to fully document the observed range of variation. This monograph is intended as a contribution towards the wider goal of updating the taxonomy of all Paleogene planktonic foraminifera by the Paleogene Planktonic Foraminifera Working Group. We hope our extensive illustration and discussion of taxonomic concepts will enable others to form a clearer picture of assemblage variation through the Eocene/Oligocene transition in more typical, less well-preserved material. We also hope that it will contribute to a solid foundation for geochemical proxy work based on planktonic foraminifera for this important phase in Earth's climate history.

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Figure 4. *Catapsydrax unicavus*. **1a-d**, new SEM of holotype of *Globigerinita unicava primitiva* Blow & Banner (1d, detail of calcite crust). **2a-c**, lower Oligocene Zone O1, Sample TDP17/21/1, 25–35 cm (2c, detail of calcite crust). **3a-b**, lower Oligocene Zone O1, Sample TDP12/9/2, 23–36 cm. **4**, lower Oligocene Zone O1, Sample TDP12/9/2, 23–36 cm. **5a-c**, upper Eocene Zone E15/16, Sample TDP12/20/3, 74–83 cm (5b, detail of cancellate wall on final chamber; 5c, detail of calcite crust on bulla). Scale bars: 100 μm (whole specimens) and 10 μm (close-up images).
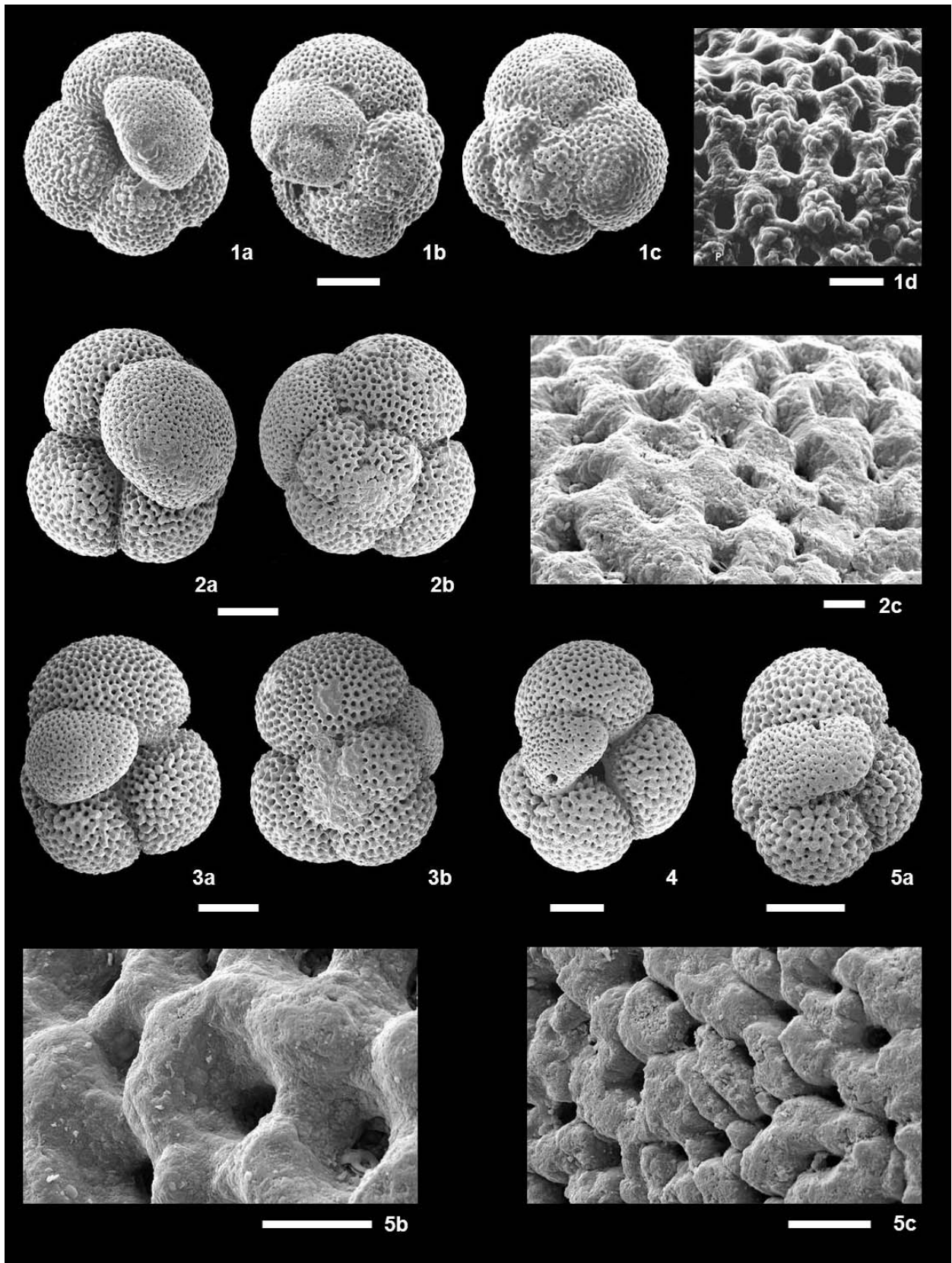
Figure 5. Various Globigerinidae. **1–2**, *Globigerina officinalis* (1, holotype of *Globigerina praebulloides leroyi* Blow & Banner, reproduced from Olsson et al., 2006b, pl. 6.1, fig. 15; 2, lower Oligocene Zone O1, Sample TDP11/19/1, 10–20 cm). **3-5d**, *Globorotaloides* forma *permicrus* (3, upper Eocene Zone E15/16, Sample TDP12/36/2, 60–70 cm; 4, lower Oligocene Zone O1, Sample TDP17/17/3, 40–52 cm; 5a-d, new SEMs of holotype of *Globorotalia* (*Turborotalia*) *permicra* Blow & Banner). **6–8**, *Globorotaloides quadrocameratus*, (6, upper Eocene Zone E15/16, Sample TDP12/36/2, 60–70 cm, specimen showing transitional features to *Globorotaloides* forma *permicrus*; 7a-b, upper Eocene Zone E15/16, Sample TDP12/14/3, 87–95 cm; 8, lower Oligocene Zone O1, Sample TDP12/9/2, 23–26 cm). **9-10c**, *Globoturborotalita* cf. *G. woodi* (9, lower Oligocene Zone O1, Sample TDP17/23/1, 0–15 cm; 10a-c lower Oligocene Zone O1, Sample TDP11/19/1, 60–75 cm). Scale bars: 100 μm (whole specimens) and 10 μm (close up image).
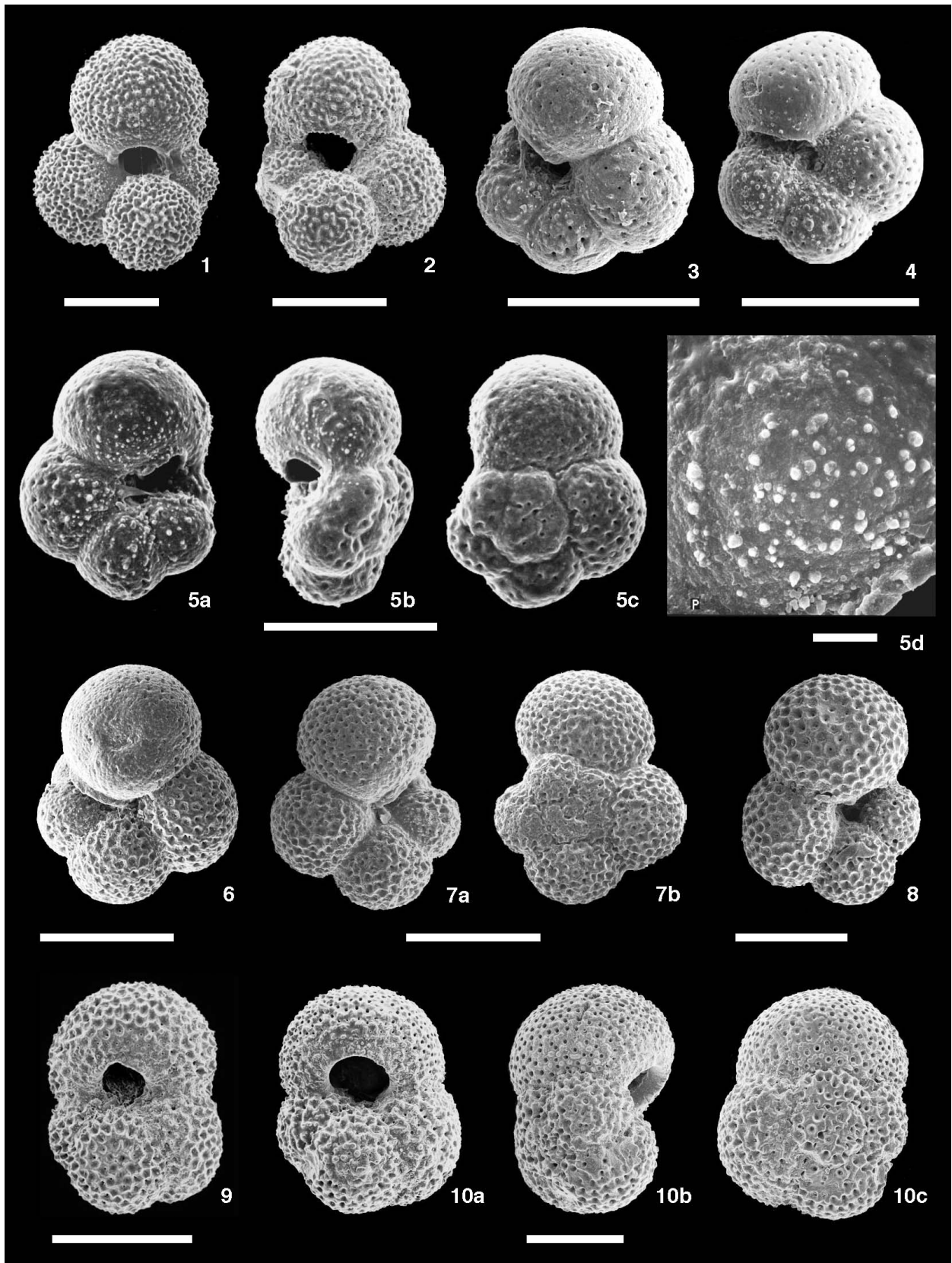
Figure 6. *Globoturborotalita barbula* n. sp. from Tanzania and Java. **1a-f,** Holotype (NHMUK PM PF 71143), upper Eocene Zone E15/16, Sample TDP17/40/2, 0–12 cm (1a, umbilical view, 1b, edge view, 1c, spiral view, 1d, oblique spiral view; 1e, detail of spiral side showing barbules, 1f, detail of suture between antepenultimate and penultimate chambers as seen in umbilical view). **2a-b,** Paratype (NHMUK PM PF 71144), upper Eocene Zone E15/16, Sample TDP12/42/1, 36–46 cm (2a, oblique umbilical view, 2b spiral view). **3a-b,** Paratype (NHMUK PM PF 71145), upper Eocene Zone E15/16, Sample TDP12/42/1, 36–46 cm (3a, oblique umbilical view, 3b spiral view). **4a-b,** Paratype (NHMUK PM PF 71146), upper Eocene Zone E15/16, Sample TDP12/42/1, 36–46 cm (5a, umbilical view, 5b, detail of wall on second chamber in final whorl). **5a-b,** Paratype (NHMUK PM PF 71147), Kali Kunir, Java, Indonesia, upper Eocene Zone E16, Sample NKK1-52, 70–78 cm (5a, detail of wall on second chamber in final whorl; barbules are visible despite adhering clay; 5b, umbilical view). Scale bars: 100 μm (whole specimens) and 10 μm (close-up images).
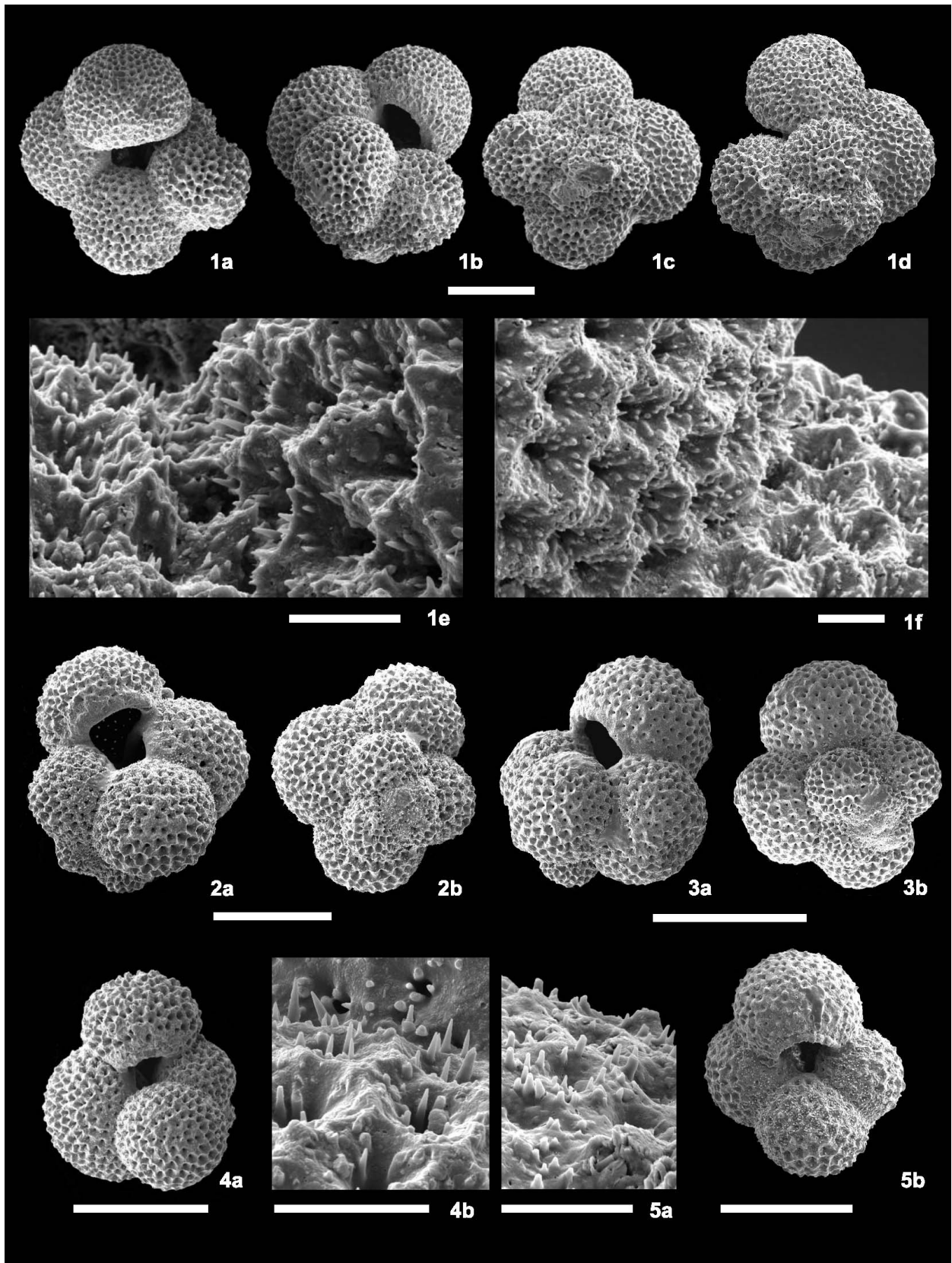
Figure 7. *Globoturborotalita barbula* n. sp. **1a-d,** Paratype, upper Eocene Zone E15/16, Sample TDP17/41/1, 8–18 cm (1a, oblique umbilical view, 1b, spiral view, 1c, detail of suture between first and second chamber in final whorl as seen in spiral view, 1d, high magnification detail of suture between first and second chamber in final whorl as seen in spiral view), **2**, Paratype, upper Eocene Zone E15/16, Sample TDP17/41/1, 8–18 cm (onlique edge view, enlarged to show extent of barbules along sutures). **3**, Paratype, upper Eocene Zone E15/16, Sample TDP17/41/1, 8–18 cm (broken wall in cross section to show barbules rooted in superficial layer). **4a-b,** Paratype, upper Eocene Zone E15/16, Sample TDP17/41/1, 8–18 cm (4a, oblique edge view, 4b, detail of first chamber in final whorl as seen in oblique edge view). **5,** Paratype, upper Eocene Zone E15/16, Sample TDP17/41/1, 8–18 cm, (detail of broken wall in cross section showing true spine embedded in wall, fractured across cleavage plane indicating that it is a single crystal). Scale bars: 100 μm (whole specimens) and 10 μm (close-up images).
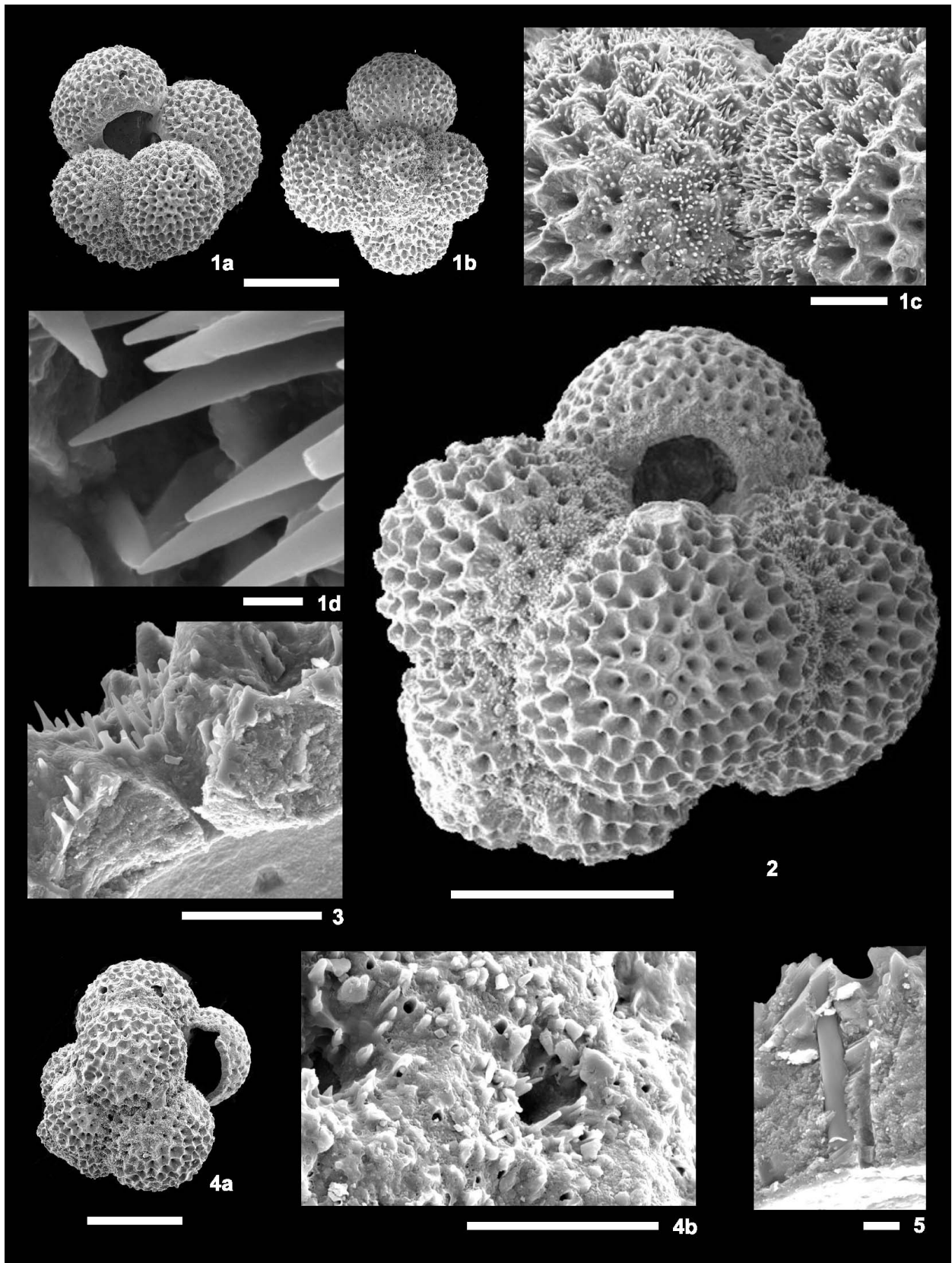
Figure 8. *Globoturborotalita barbula* n. sp. **1a-d,** Paratype (NHMUK PM PF 71151), upper Eocene Zone E15/16, Sample TDP17/40/2, 0–12 cm. **2a-d,** Paratype (NHMUK PM PF 71152), upper Eocene Zone E15/16, Sample TDP17/40/2, 0–12 cm. **3a-d,** Paratype (NHMUK PM PF 71153), upper Eocene Zone E15/16, Sample TDP12/42/1, 36–46 cm. **4a-b,** Paratype, upper Eocene Zone E15/16, Sample TDP17/40/2, 0–12 cm. **5a-c,** Paratype (NHMUK PM PF 71154), upper Eocene Zone E15/16, Sample TDP17/40/2, 0–12 cm (5c, detail of aperture showing smooth lip and relict lip and barbule development on earlier chamber shoulders). **6,** Paratype (NHMUK PM PF 71155), upper Eocene Zone E15/16, Sample TDP17/40/2, 0–12 cm (variety with open umbilicus and 4 chambers in the final whorl). **7,** Paratype (NHMUK PM PF 71156), upper Eocene Zone E15/16, Sample TDP17/40/2, 0–12 cm (variety with low trochospiral and globigeriniform morphology). **8,** Paratype (NHMUK PM PF 71157), upper Eocene Zone E15/16, Sample TDP17/40/2, 0–12 cm (variety with very high trochospiral). Scale bars: 100 μm (whole specimens) and 10 μm (close-up images).
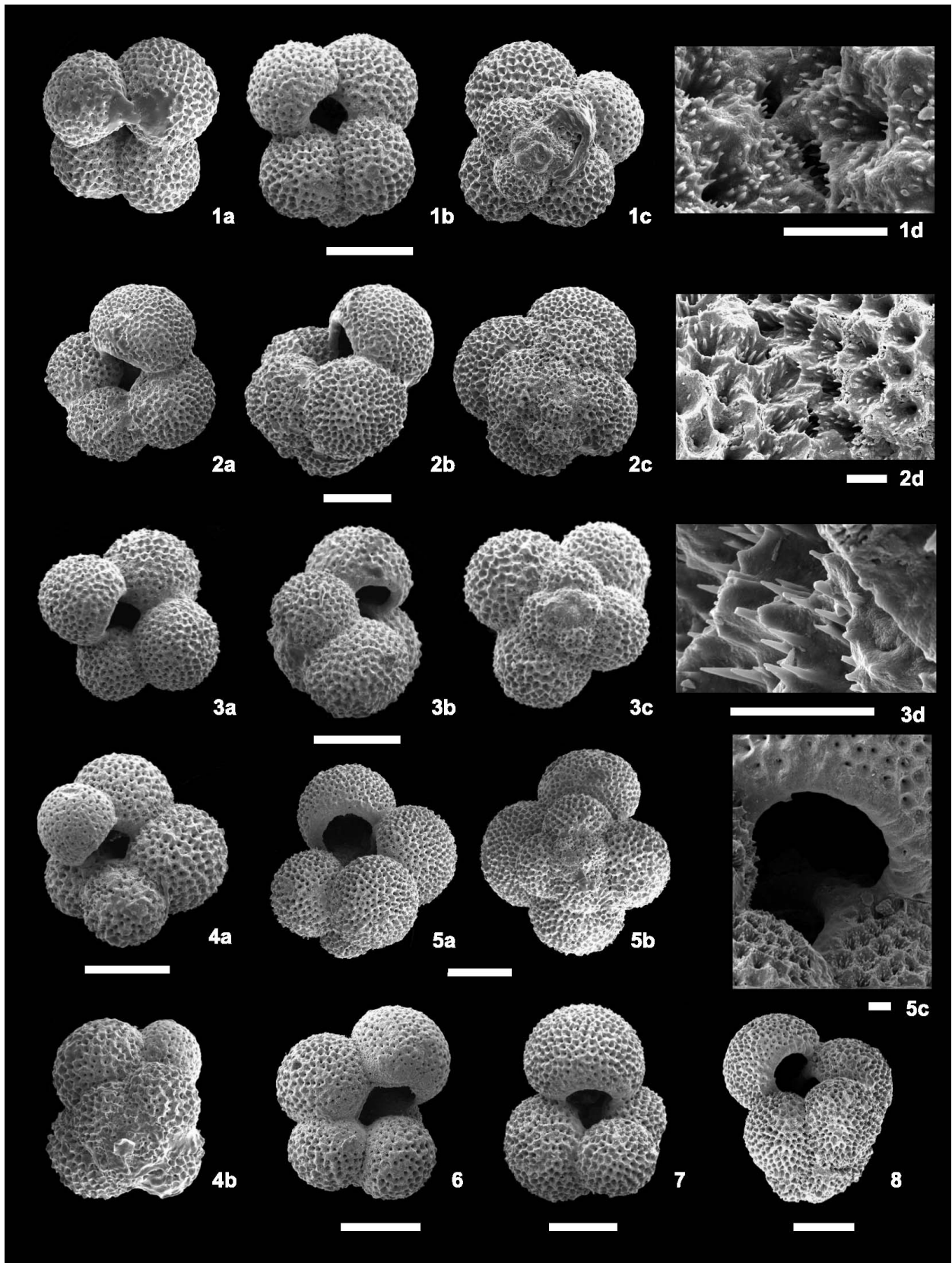
Figure 9. Various *Globoturborotalita*. **1**, **2,** *Globoturborotalita gnaucki* (1, holotype of *Globigerina ouachitaensis gnaucki* Blow and Banner, reproduced from Olsson et al., 2006b, pl. 6.4, fig. 3; 2, upper Eocene Zone E15/16, Sample TDP12/14/1, 81–83 cm). **3–12,** *Globoturborotalita martini* (3, holotype of *Globigerinita martini martini* Blow and Banner, reproduced from Olsson et al., 2006b, pl. 6.2, fig. 8; 4, lower Oligocene Zone O1, Sample TDP12/14/1, 81–83 cm; 5a-d, new SEMs of holotype of *Globigerinita martini scandretti* Blow and Banner [5d, detail of cancellate wall texture]; 6a-b, upper Eocene Zone E15/16, Sample TDP12/40/3, 88–96 cm; 7–8, lower Oligocene Zone O1, Sample TDP12/14/1, 81–83 cm; 9–11, upper Eocene Zone E15/16, Sample TDP12/36/2, 60–70 cm; 12, lower Oligocene Zone O1, Sample TDP12/9/2, 23–26 cm). Scale bars: 100 μm (whole specimens) and 10 μm (close-up image).
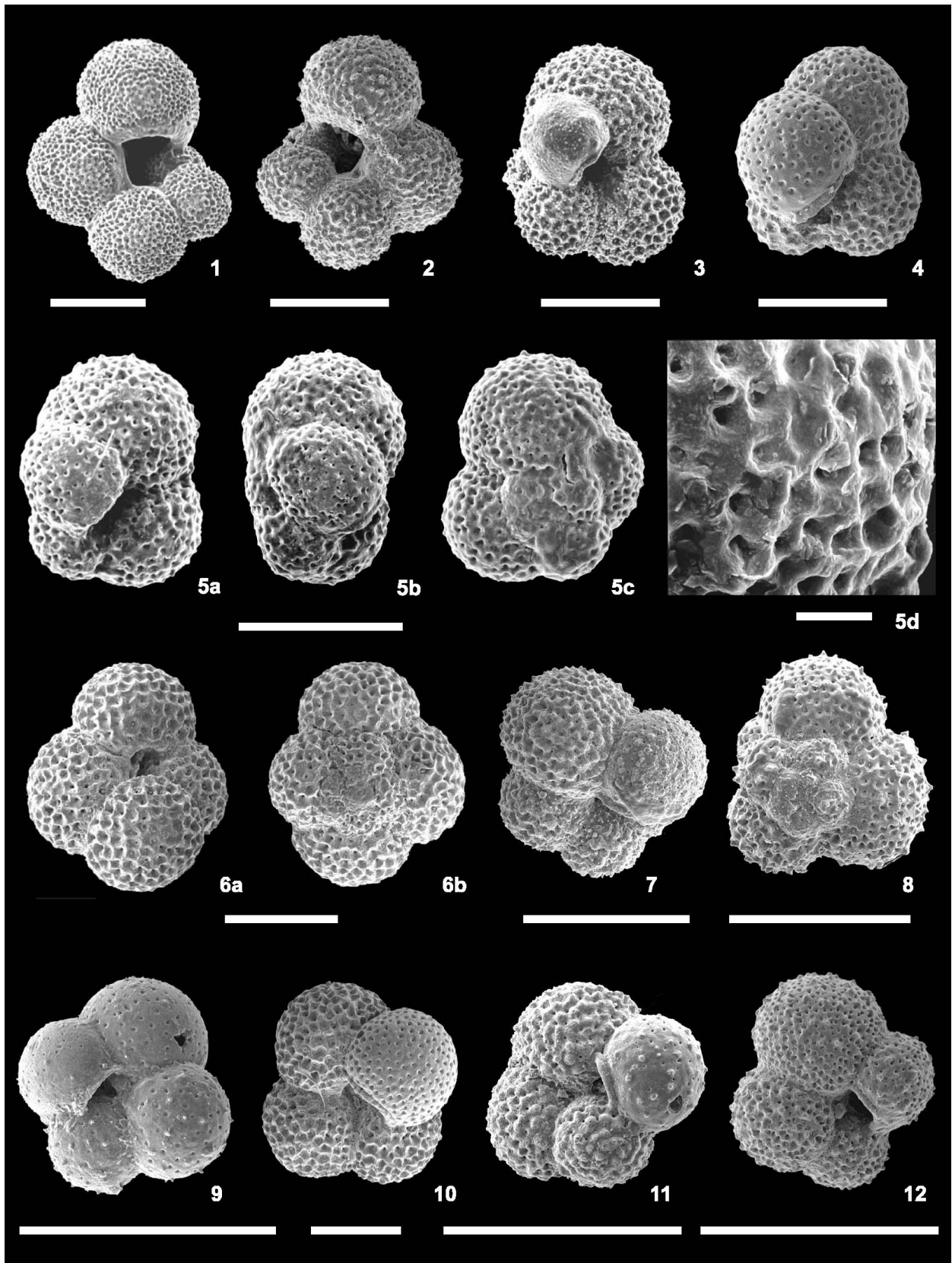
Figure 10. Various Globigerinidae. **1–2**, *Globoturborotalita ouachitaensis* (1a-c, upper Eocene Zone E15/16, Sample TDP12/36/1, 34–44 cm, 2, upper Eocene Zone E15/16, Sample TDP17/42/2, 61–78 cm). **3-4c**, *Subbotina corpulenta* (3, upper Eocene Zone E15/16, Sample TDP12/21/3, 48–56 cm, 4a-c, lower Oligocene Zone O1, Sample TDP17/21/1, 25–35 cm). **5a-8b**, *Subbotina eocaena* (5a-c, upper Eocene Zone E15/16, Sample TDP12/36/1, 10–20 cm, 6, Sample lower Oligocene Zone O1, Sample TDP12/9/2, 23–26 cm, 7a-b, upper Eocene Zone E15/16, Sample TDP12/36/1, 10–20 cm, specimen showing transition to *Subbotina tecta* n. sp., 8a-b, lower Oligocene Zone O1, Sample TDP17/11/1, 0–10 cm). Scale bars: 100 μm.
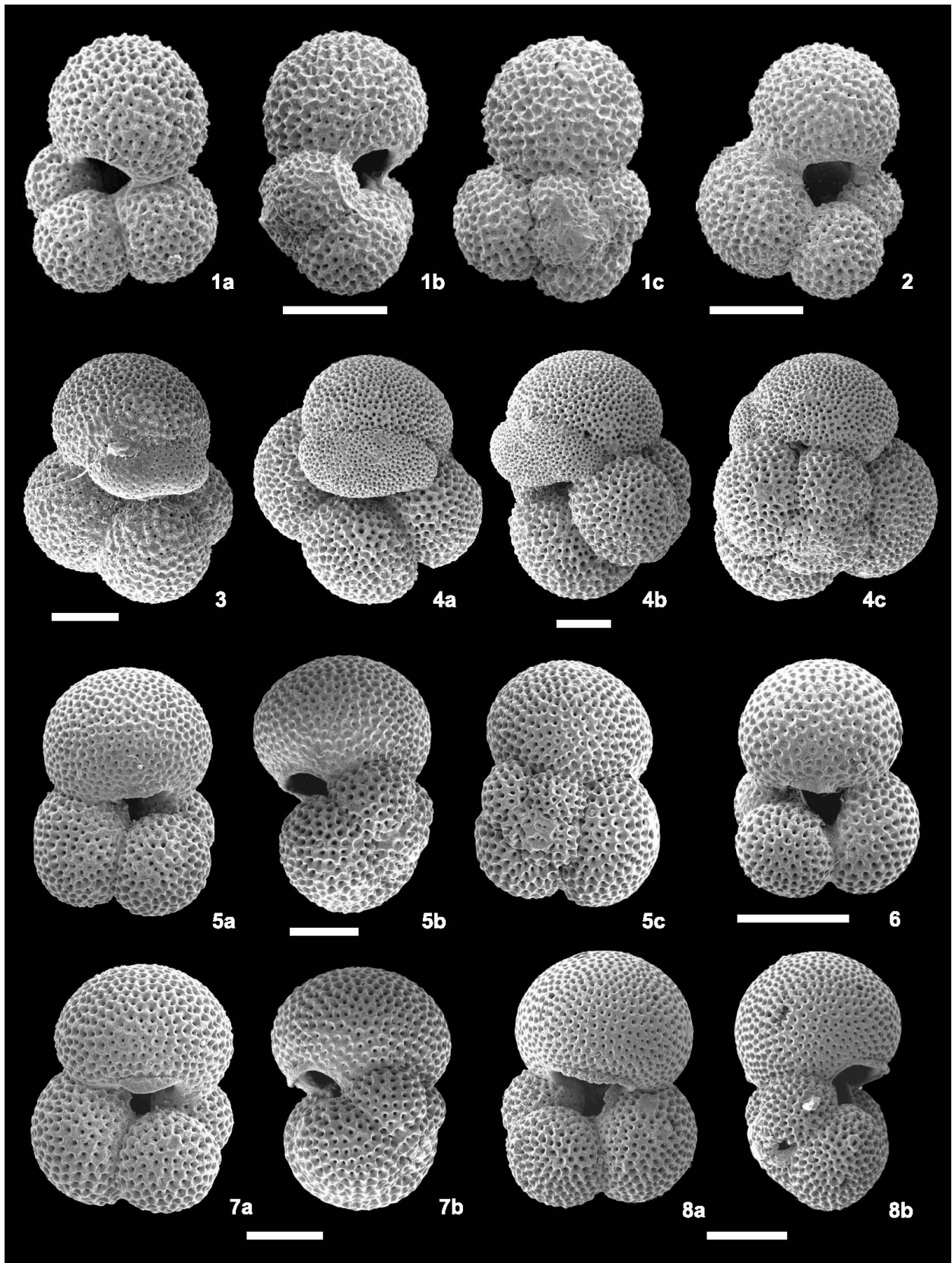
Figure 11. *Subbotina gortanii*. **1a-d**, holotype of *Globigerina turritilina praeturritilina* Blow & Banner, reproduced from Olsson et al., 2006b, pl. 6.10, fig. 11, note correction of scale. **2a-d**, holotype of *Globigerina turritilina turritilina* Blow & Banner (2a-c, reproduced from Olsson et al., 2006b, pl. 6.10, fig. 2, note correction of scale; 2d new image of wall texture). **3**, upper Eocene Zone E15/16, Sample TDP 17/41/1, 8–18 cm. **4a-b**, lower Oligocene Zone O1, Sample TDP12/9/2, 23–36 cm; **5,** lower Oligocene Zone O1, Sample TDP11/11/1, 0–10 cm; **6a-b**, upper Eocene Zone E15/16, Sample TDP12/36/1, 10–20 cm; **7, 8**, lower Oligocene Zone O1, Sample TDP17/11/1, 0–10 cm. Scale bars: 100 μm (whole specimens) and 10 μm (close-up images).
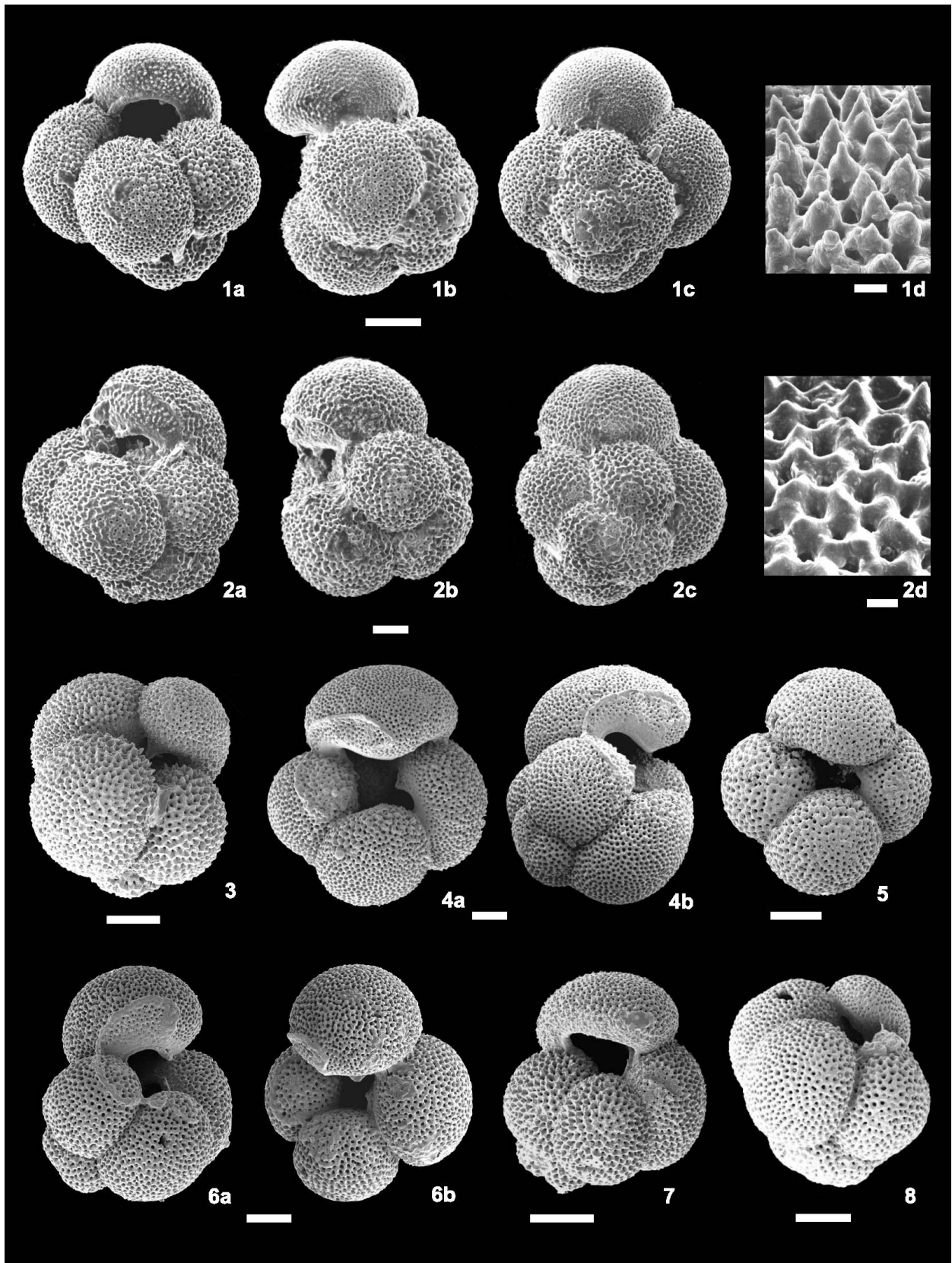
Figure 12. *Subbotina tecta* n. sp. **1a-f**, Holotype (NHMUK PM PF 71158), upper Eocene Zone E15/16, Sample TDP12/42/1, 36–46 cm. **2a-d**, Paratype (NHMUK PM PF 71159), upper Eocene Zone E15/16, Sample TDP12/42/1, 36–46 cm. **3a-d**, Paratype (NHMUK PM PF 71160), upper Eocene Zone E15/16, Sample TDP12/42/1, 36–46 cm. Scale bars: 100 μm (whole specimens) and 10 μm (close-up images).
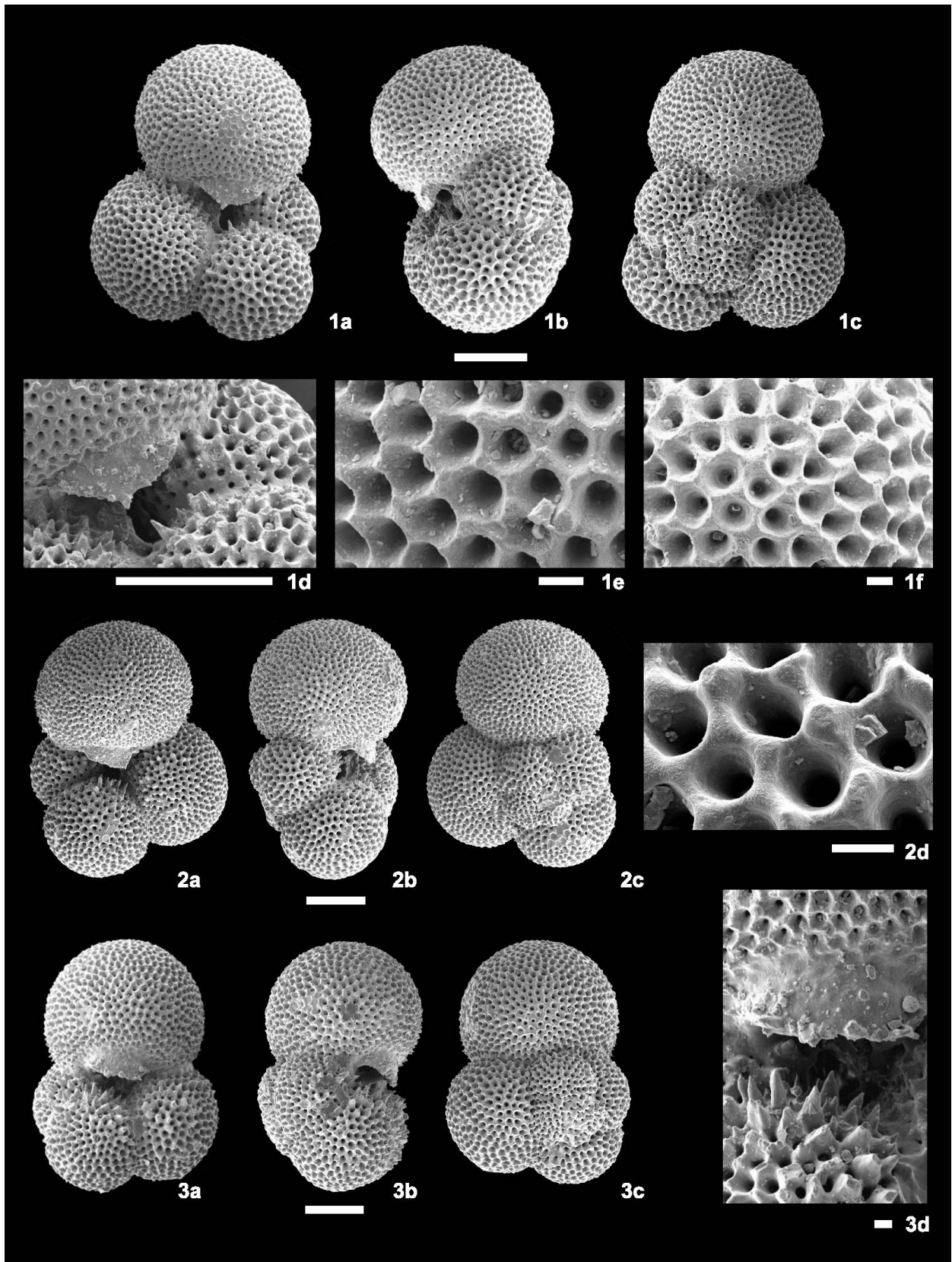
Figure 13. *Subbotina tecta* n. sp. **1a-c**, Paratype (NHMUK PM PF 71161), upper Eocene Zone E15/16, Sample TDP17/37/2, 32–49 cm. **2a-b**, Paratype (NHMUK PM PF 71162), upper Eocene Zone E15/16, Sample TDP17/41/1, 8–18 cm, **3a-c**, Paratype (NHMUK PM PF 71163), upper Eocene Zone E15/16, TDP12/24/1, 42–50 cm, Zone E15/16, upper Eocene. **4a-c**, Paratype, upper Eocene Zone E15/16, Sample TDP12/42/1, 36–46 cm. **5**, Paratype, upper Eocene Zone E15/16, Sample TDP17/42/2, 61–78 cm, Zone E15/16, upper Eocene. **6a-b**, Paratype, upper Eocene Zone E15/16, Sample TDP12/32/1, 15- 24 cm, Zone E15/16, upper Eocene (6b, detail of lip). **7a-b**, Paratype (NHMUK PM PF 71164), upper Eocene Zone E15/16, Sample TDP17/41/1, 8–18 cm (7b, detail of lip from slightly oblique edge view). Scale bars: 100 μm (whole specimens) and 10 μm (close-up images).
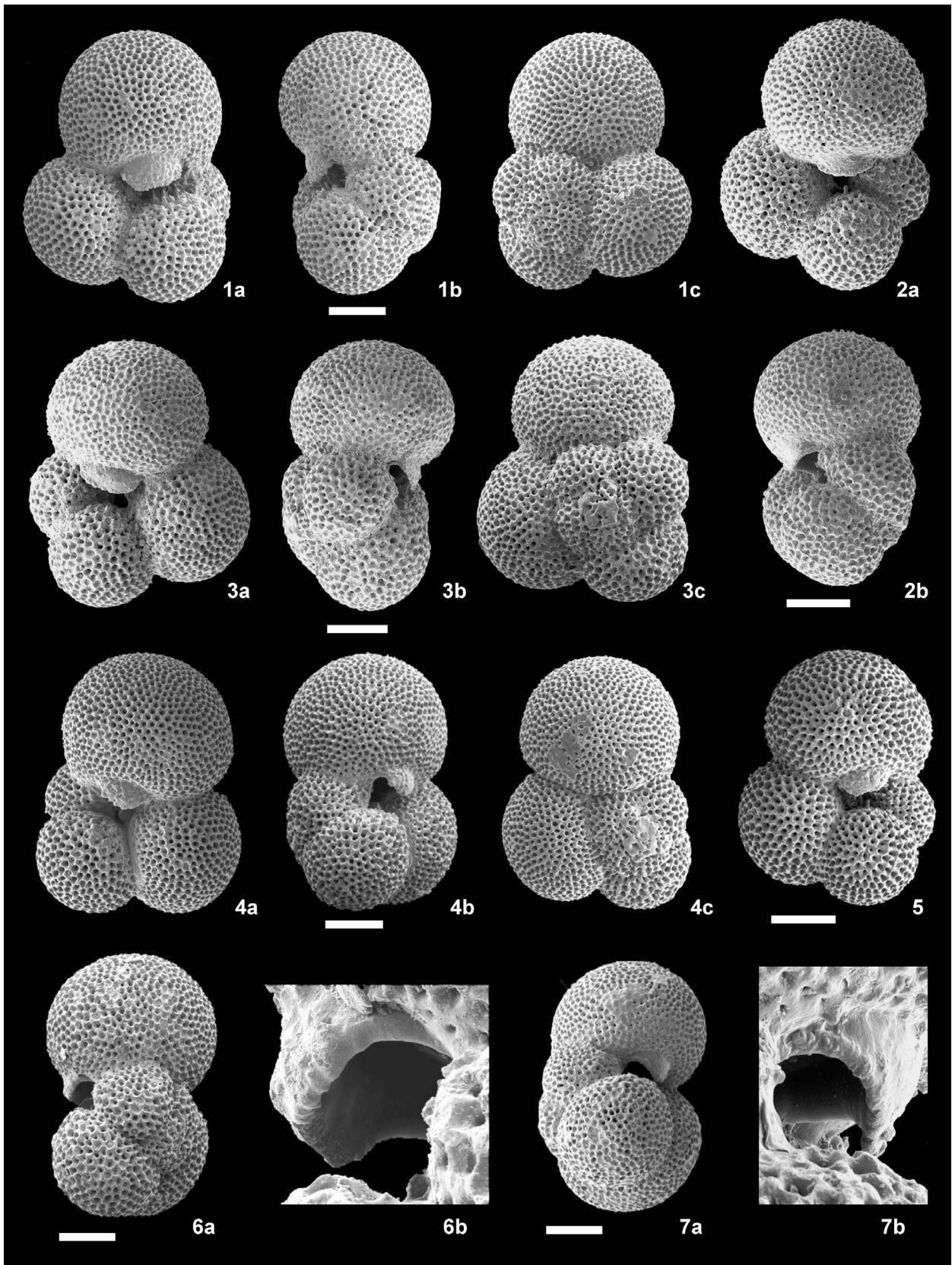
Figure 14. *Subbotina* sp. **1**, lower Oligocene Zone O1, Sample TDP17/11/1, 0–10 cm. **2a-b,** lower Oligocene Zone O1, Sample TDP17/32/1, 10–25 cm. **3,** lower Oligocene Zone O1, Sample TDP17/30/1, 30–38 cm. **4a-b,** lower Oligocene Zone O1, Sample TDP12/9/2, 23–36 cm (4b, detail of wall showing spine holes). **5**, lower Oligocene Zone O1, Sample TDP17/32/1, 10–25 cm. **6a-b,** lower Oligocene Zone O1, Sample TDP12/9/2, 23–36 cm (6b, detail of wall showing spine hole). **7,** upper Eocene Zone E15/16, Sample TDP12/42/1, 36–46 cm. **8a-b**, lower Oligocene Zone O1, Sample TDP11/11/1, 0–10 cm. **9a-b,** lower Oligocene Zone O1, Sample TDP17/30/1, 30–38 cm. Scale bars: 100 μm (whole specimens) and 10 μm (close-up images).
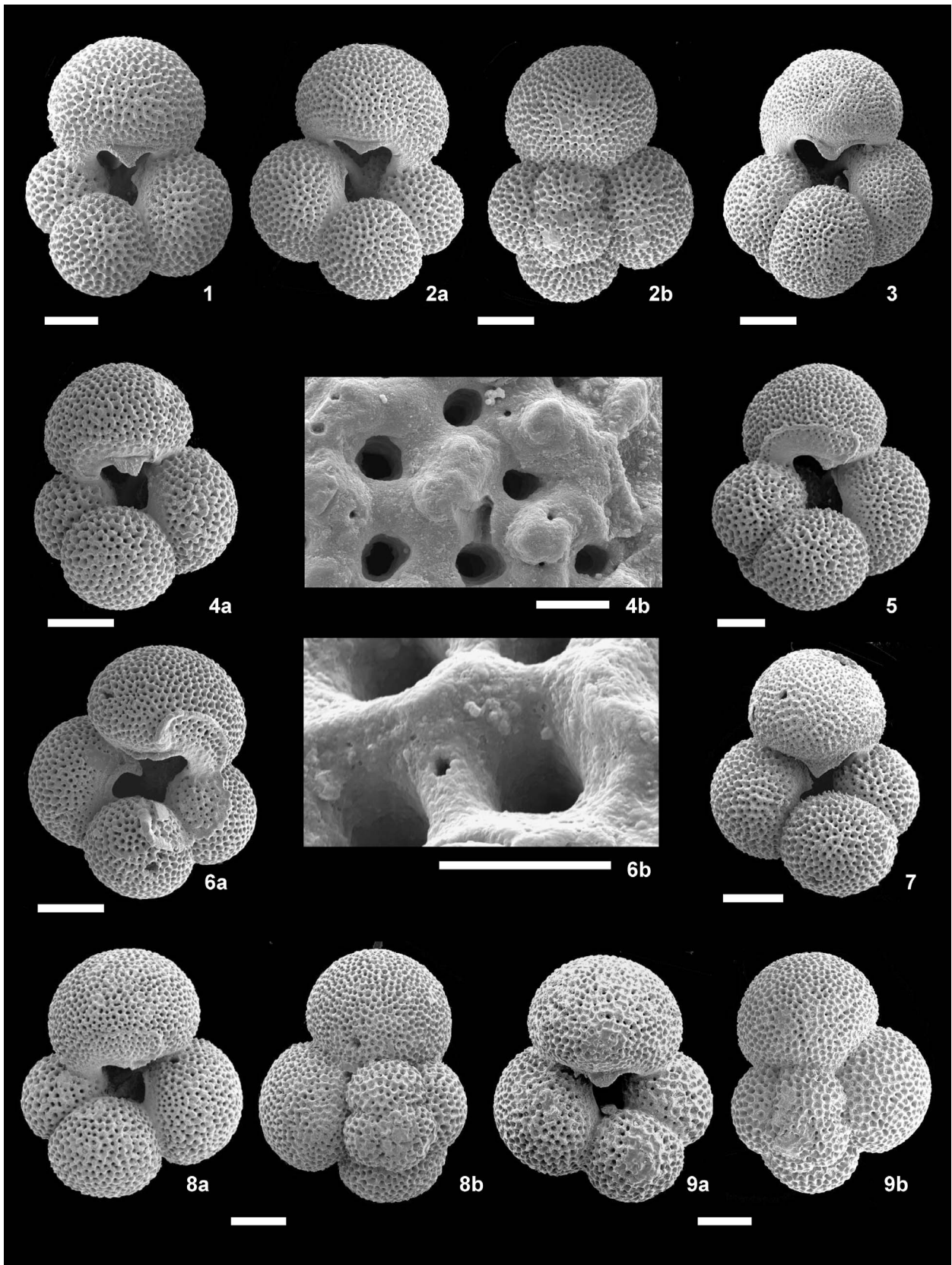
Figure 15. *Dentoglobigerina galavisi*. **1a-c**, holotype of Bermúdez (1961), upper Eocene Jackson Fm., Mississippi, SEM reproduced from Olsson et al., 2006c, pl. 13.1–3. **2**, upper Eocene Zone E15/16, Sample TDP12/27/1, 35–45 cm. **3a-c**, upper Eocene Zone E15/16, Sample TDP12/46/2, 56–66 cm. **4**, lower Oligocene Zone O1, Sample TDP17/32/1, 10–25 cm. **5a-6**, upper Eocene Zone E15/16, Sample TDP12/27/1, 35–45 cm. **7a-b**, lower Oligocene Zone O1, Sample TDP12/7/1, 0–10 cm (8b, detail of wall showing possible spine hole). **8a-b**, upper Eocene Zone E15/16, Sample TDP12/32/1, 15–24 cm. Scale bars: 100 μm (whole specimens) and 10 μm (close-up image).
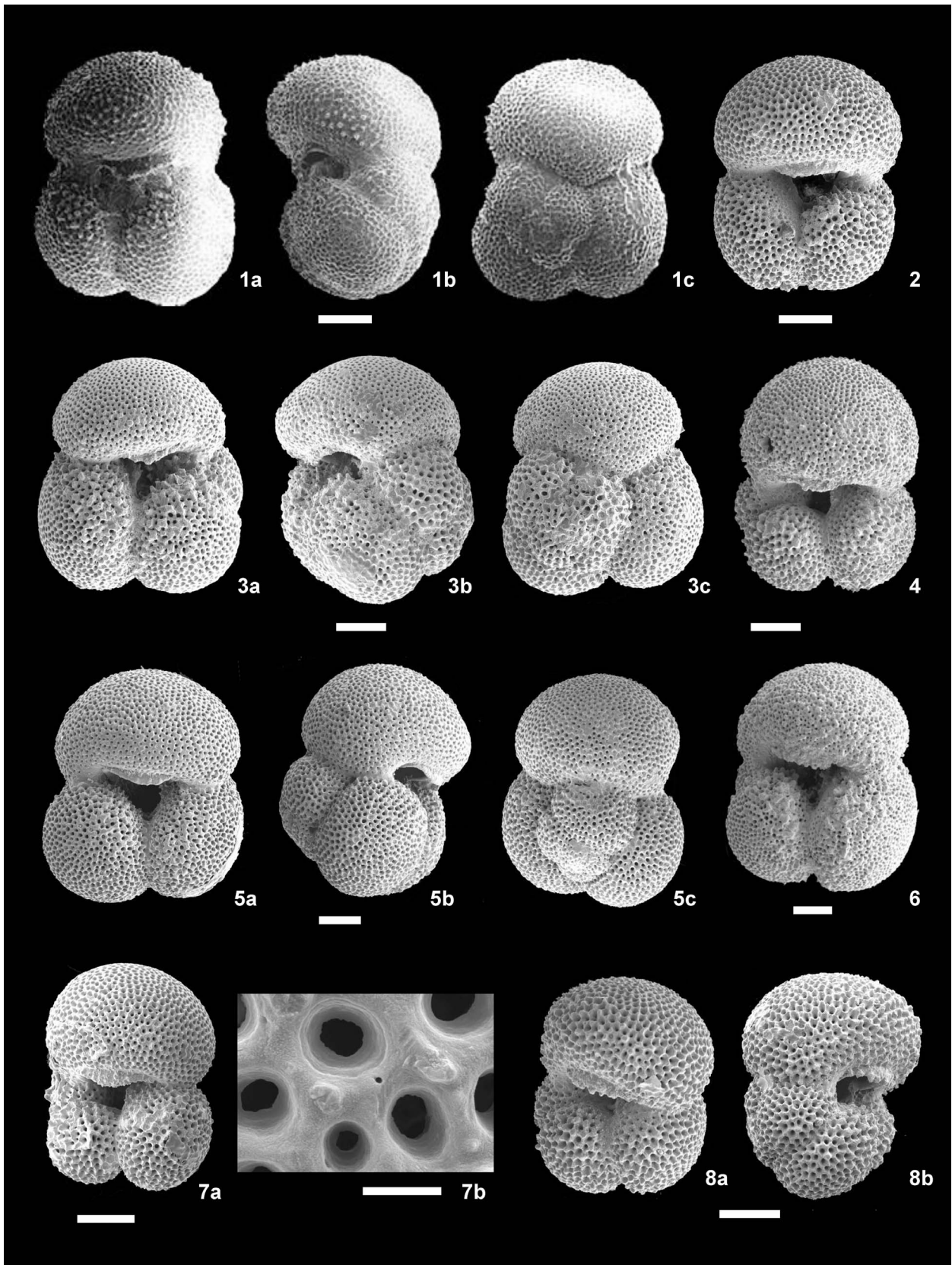
Figure 16. *Dentoglobigerina prasaepis*. **1a-d**, holotype of *Globigerina prasaepis* Blow, 1969. **2a-c**, lower Oligocene Zone O1, Sample TDP17/17/3, 40–52 cm. **3**, lower Oligocene Zone O1, Sample TDP17/16/1, 10–23 cm. **4a-c**, lower Oligocene Zone O1, Sample TDP17/17/3, 40–52 cm. **5**, lower Oligocene Zone O1, Sample TDP12/9/2, 23–26 cm. **6a-b**, lower Oligocene Zone O1, Sample TDP17/14/1, 0–14 cm. **7**, lower Oligocene Zone O1, Sample TDP17/11/5, 10–20 cm. **8**, Sample TDP17/42/2, 61–78 cm (specimen transitional to *D. venezuelana,* similar to form illustrated as *D. venezuelana* by Fox & Wade, 2013, fig. 8.6). Scale bars: 100 μm (whole specimens) and 10 μm (close-up image).
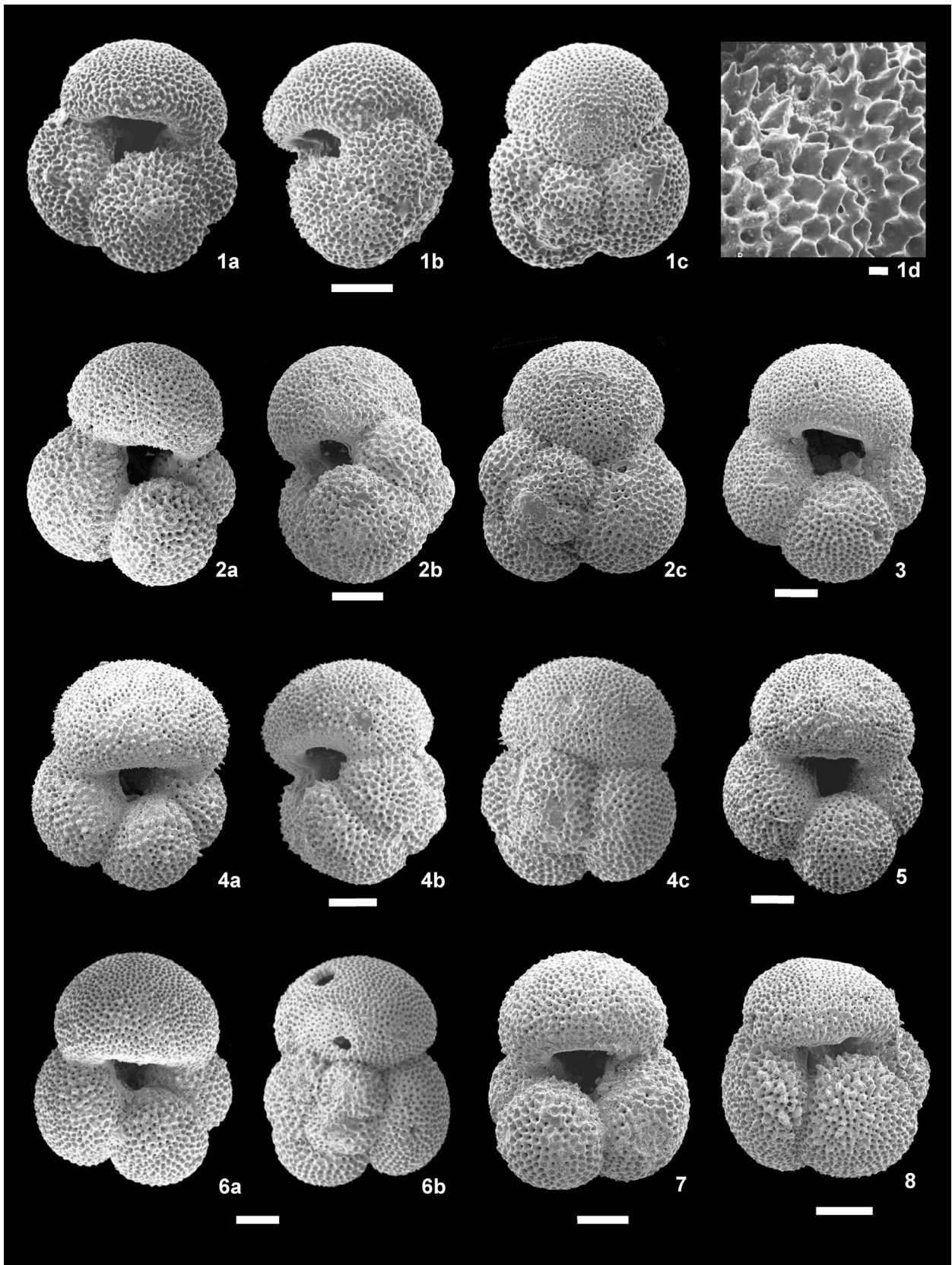
Figure 17. *Dentoglobigerina pseudovenezuelana*. **1a-d**, SEMs of holotype of *Globigerina yeguaensis pseudovenezuelana* Blow & Banner, reproduced from Olsson et al., 2006c, pl. 13.2, figs. 1-3, 5. **2a-c**, upper Eocene Zone E15/16, Sample TDP17/42/2, 61–78 cm. **3**, lower Oligocene Zone O1, Sample TDP17/32/1, 10–25 cm (specimen showing transition to *D. galavisi*). **4a-5b**, upper Eocene Zone E15/16, Sample TDP17/42/2, 61–78 cm. **6a-d**, lower Oligocene Zone O1, Sample TDP12/9/2, 23–36 cm (note probable spine holes). Scale bars: 100 μm (whole specimens) and 10 μm (close-up images).
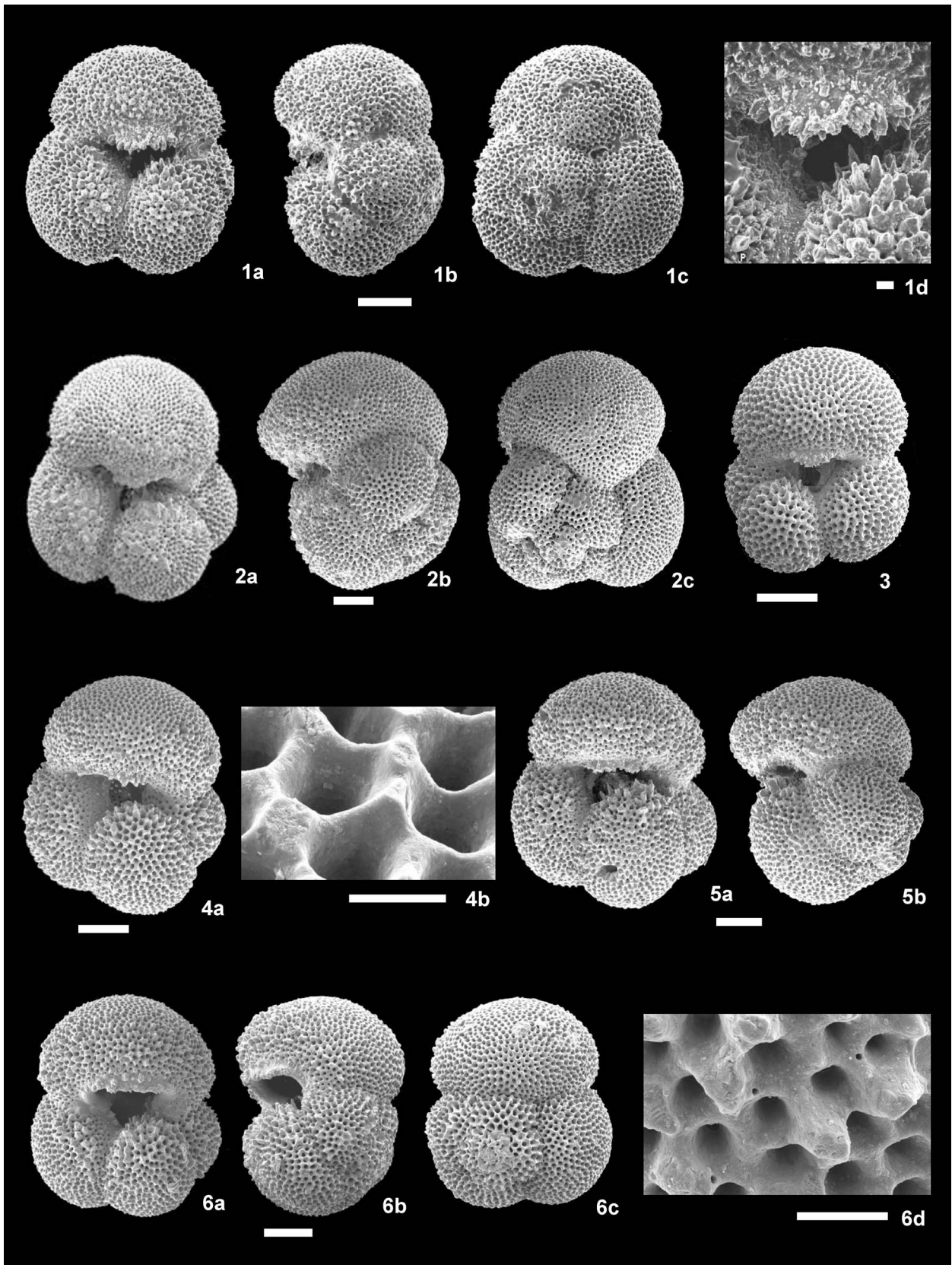
Figure 18. *Dentoglobigerina taci* n. sp. **1a-c**, Holotype (NHMUK PM PF 71165), lower Oligocene Zone O1, Sample TDP17/30/1, 30–38 cm. **2a-c**, Paratype (NHMUK PM PF 71166), lower Oligocene Zone O1, Sample TDP17/30/1, 30–38 cm (note possible spine holes). **3a-b**, Paratype, upper Eocene Zone E15/16, Sample TDP12/36/1, 10–20 cm. **4 a-c**, Paratype (NHMUK PM PF 71167), lower Oligocene Zone O1, Sample TDP17/30/1, 30–38 cm. **5a-d**, Paratype, upper Eocene Zone E15/16, Sample TDP12/36/1, 10–20 cm (note pustulose ornamentation and possible spine holes; specimen destroyed in wall texture study). Scale bars: 100 μm (whole specimens) and 10 μm (close-up images).
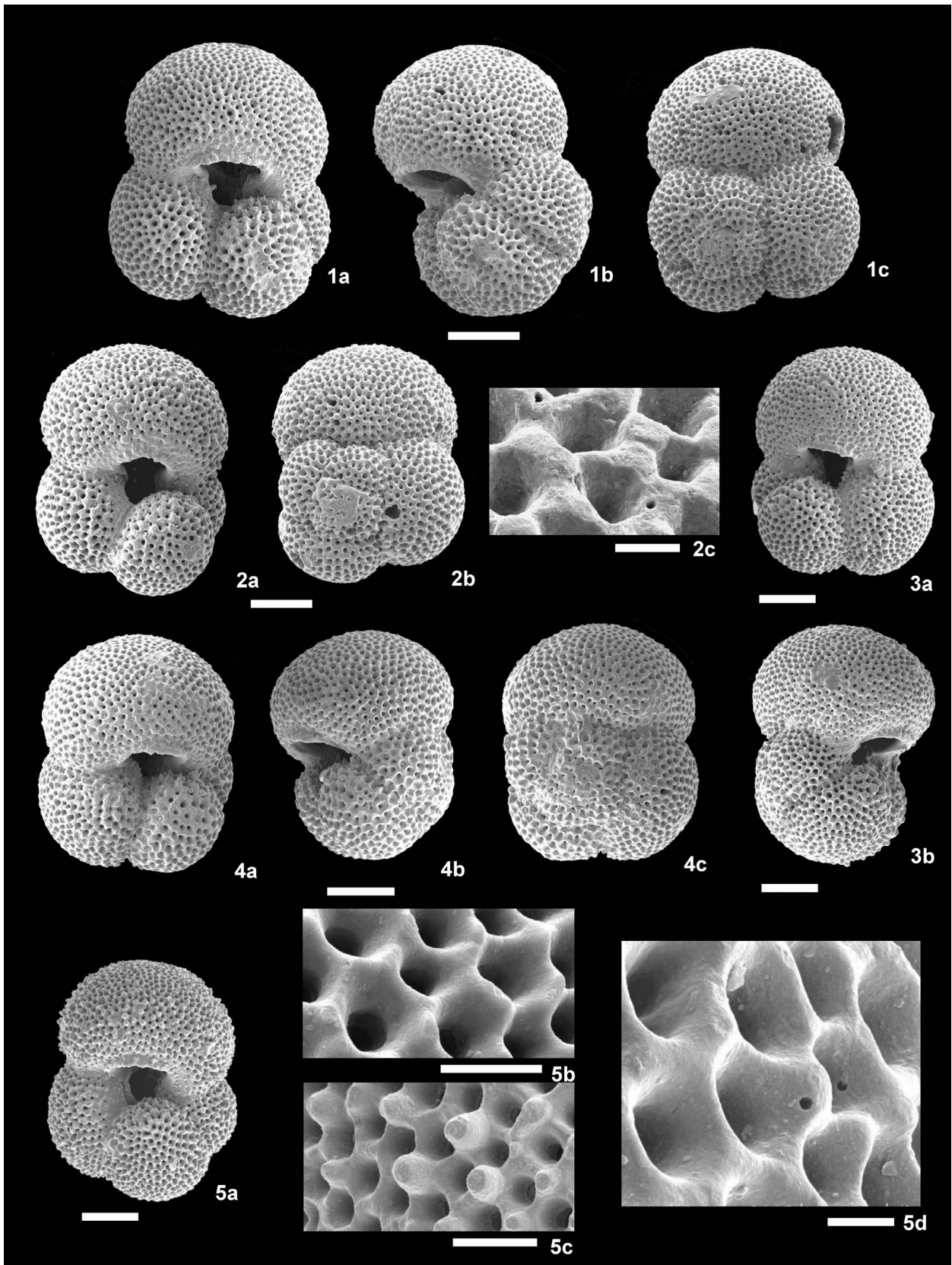
Figure 19. *Dentoglobigerina taci* n. sp. **1a-c**, Paratype (NHMUK PM PF 71168), lower Oligocene Zone O1, Sample TDP17/17/3, 40–52 cm. **2**, Paratype (NHMUK PM PF 71169), lower Oligocene Zone O1, Sample TDP17/17/3, 40–52 cm. **3a-c**, Paratype (NHMUK PM PF 71170), lower Oligocene Zone O1, Sample TDP17/16/1, 10–23 cm. **4**, Paratype (NHMUK PM PF 71171), lower Oligocene Zone O1, Sample TDP17/13/1, 39–53 cm. **5**, Paratype, lower Oligocene Zone O1, Sample TDP17/11/1, 0–10 cm. **6**, Paratype, lower Oligocene Zone O1, Sample TDP17/11/5, 10–20 cm. **7**, Paratype (NHMUK PM PF 71172), lower Oligocene Zone O1, Sample TDP17/21/1, 25–35 cm. **8**, Paratype (NHMUK PM PF 71173), lower Oligocene Zone O1, Sample TDP17/16/1, 10–23 cm. **9a-d**. Paratype (NHMUK PM PF 71174), lower Oligocene Zone O1, Sample TDP17/16/1, 10–23 cm. Scale bars: 100 μm (whole specimens) and 10 μm (close-up image).
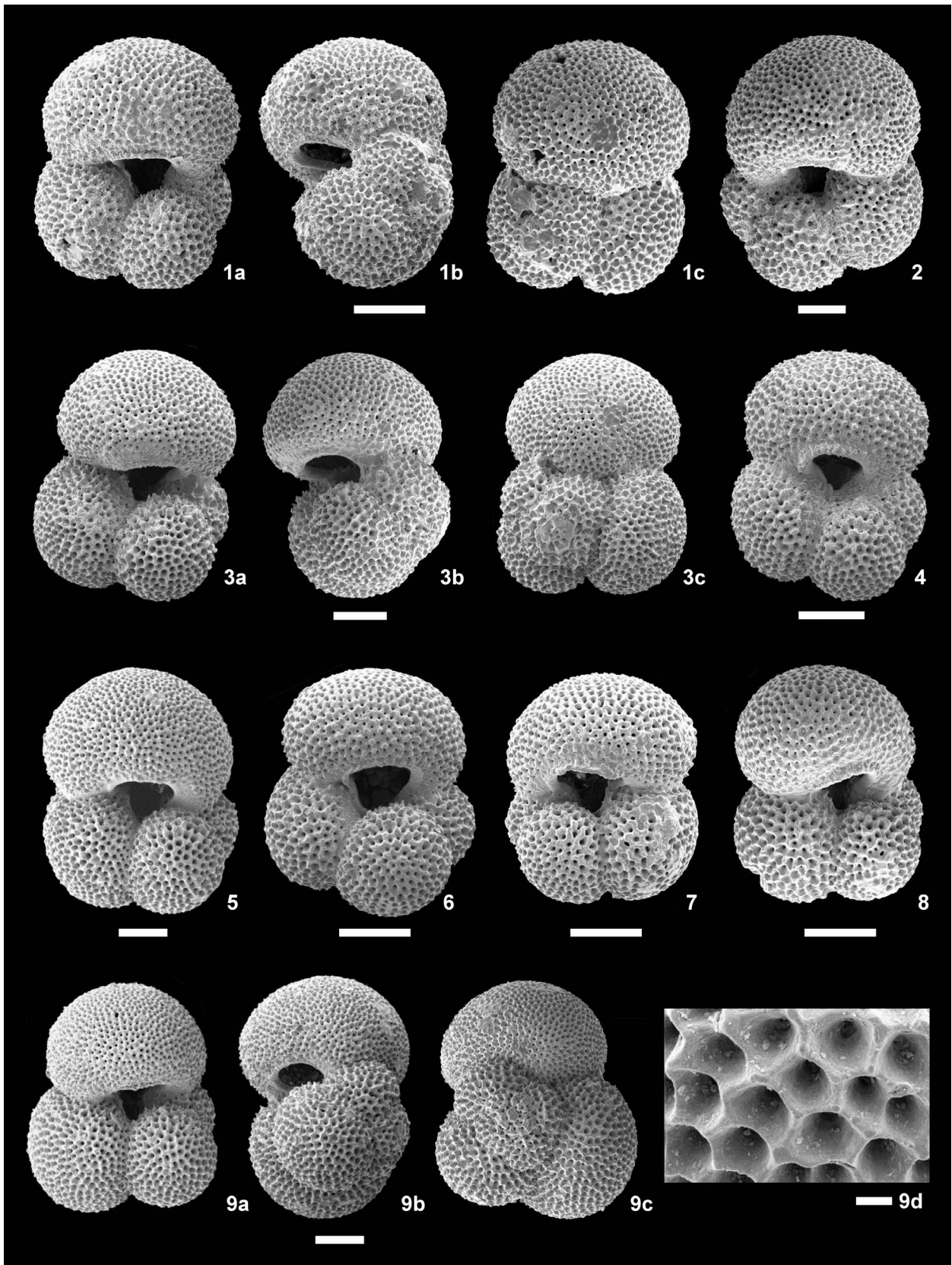
Figure 20. *Dentoglobigerina tapuriensis*. **1a-d**, New SEMs of holotype of *Globigerina tripartita tapuriensis* Blow & Banner. **2a-c**, lower Oligocene Zone O1, Sample TDP12/9/2, 23–36 cm. **3**, lower Oligocene Zone O1, Sample TDP17/21/1, 25–35 cm. **4a-b**, upper Eocene Zone E15/16, Sample TDP12/36/1, 10–20 cm. **5**, lower Oligocene Zone O1, Sample TDP17/32/1, 10–25 cm. **6**, lower Oligocene Zone O1, Sample TDP17/8/1, 22–34 cm. **7a-b**, upper Eocene Zone E15/16, Sample TDP17/37/2, 32–49 cm (note possible spine holes). **8**, lower Oligocene Zone O1, Sample TDP17/30/1, 30–38 cm (specimen transitional to *D. taci* n. sp.). **9**, lower Oligocene Zone O1, Sample TDP17/16/1, 10–23 cm (specimen transitional to *D. taci* n. sp.). Scale bars: 100 μm (whole specimens) and 10 μm (close-up images).
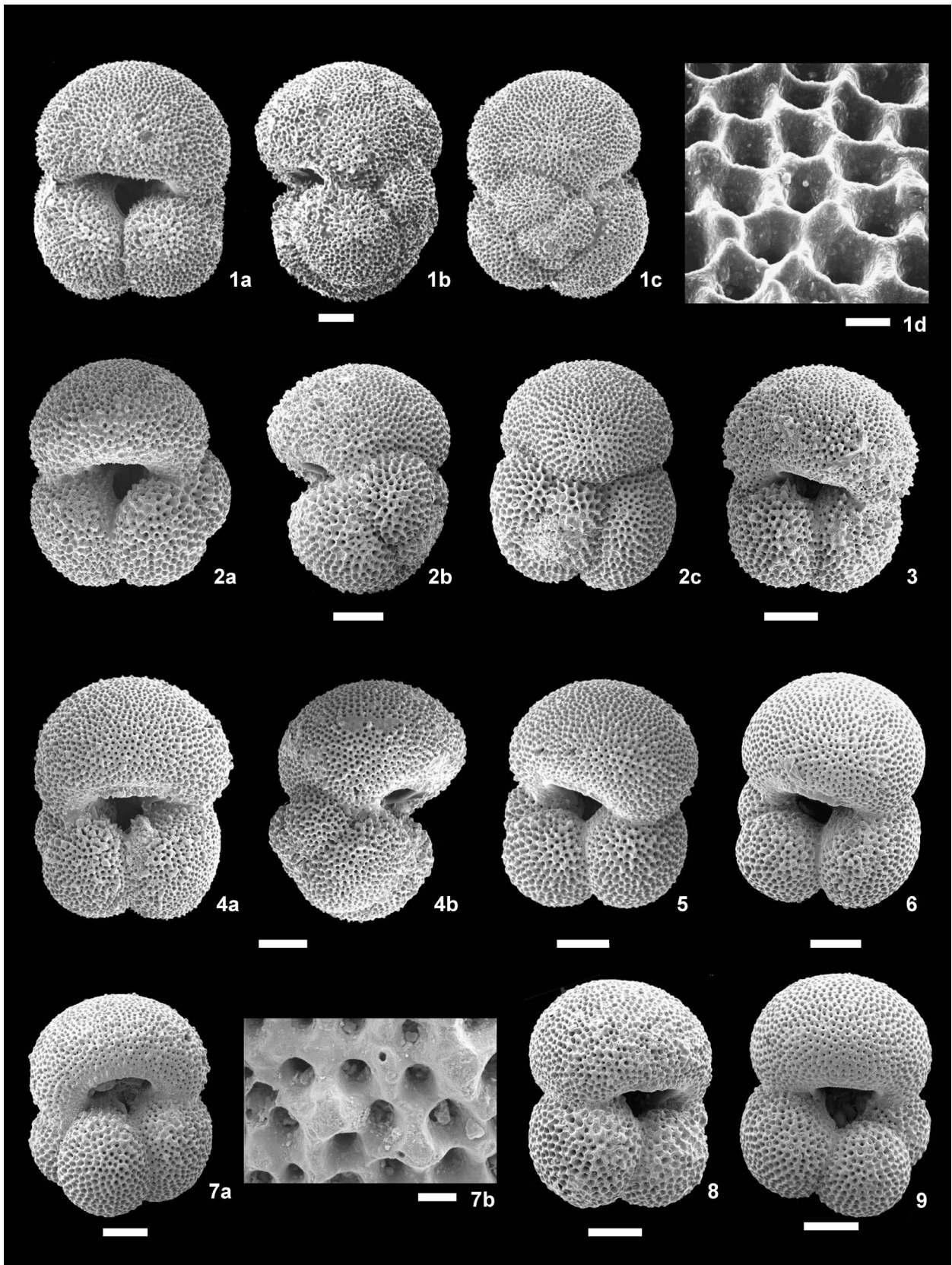
Figure 21. *Dentoglobigerina* cf. *tripartita*. **1**, reproduced from Blow, 1969, pl. 16, fig. 6. **2**, reproduced from Blow, 1979, pl. 244, fig. 4. **3a-b**, TDP12/42/1, 36–46 cm, reproduced from Olsson et al., 2006c, pl. 13.3, figs. 7-8. **4a-e**, upper Eocene Zone E15/16, Sample TDP12/42/1, 36–46 cm (note variation in wall texture especially 4e, possible spine holes with spines possibly still embedded in some of them) **5**, upper Eocene Zone E15/16, Sample TDP12/42/1, 36–46 cm. **6a-b**, upper Eocene Zone E15/16, Sample TDP12/36/2, 66–70 cm. **7a-c**, upper Eocene Zone E15/16, Sample TDP12/42/1, 36–46 cm. Scale bars: 100 μm (whole specimens) and 10 μm (close-up images).
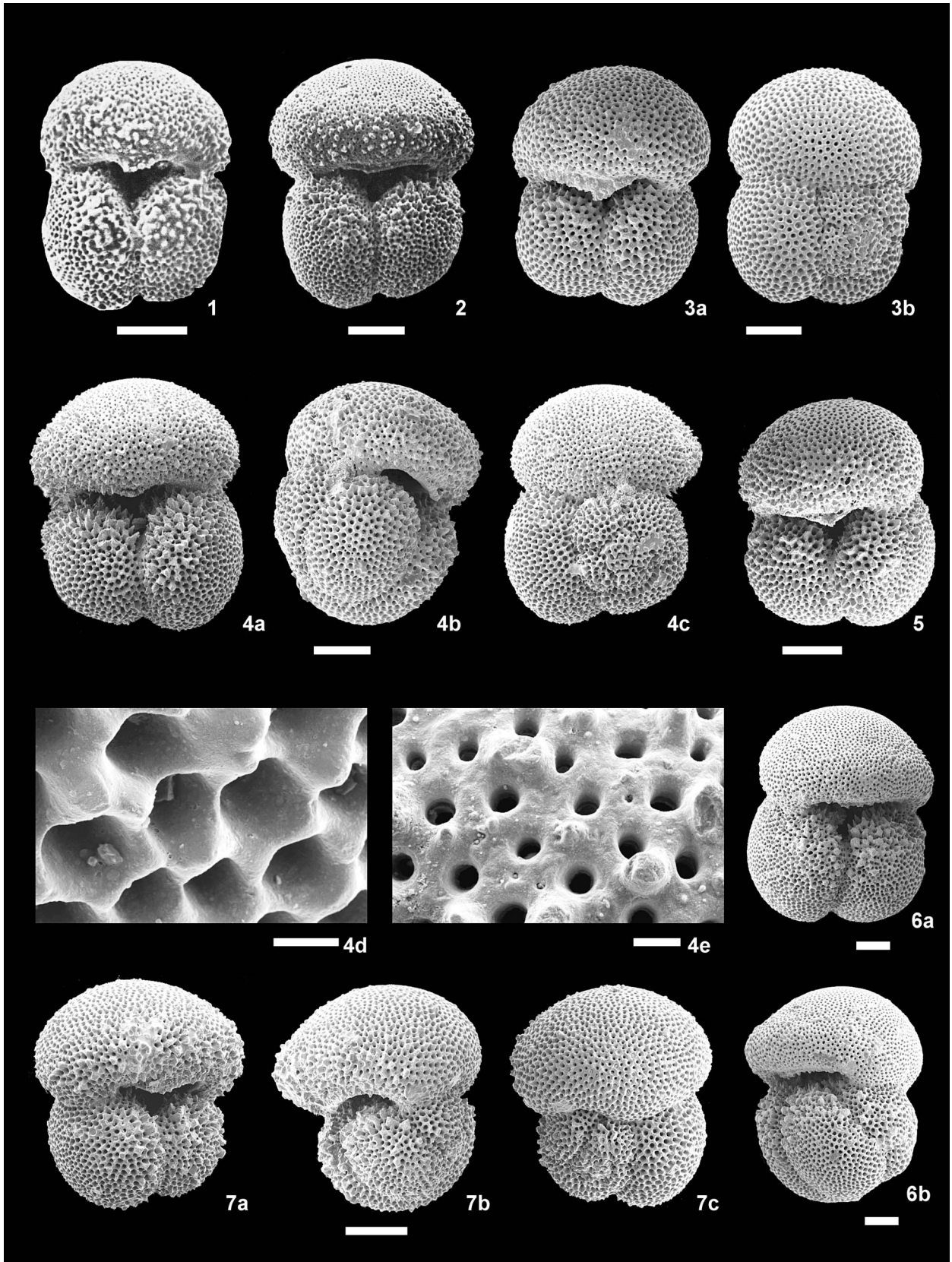
Figure 22. *Cribrohantkenina inflata*. **1a-g**, upper Eocene Zone E15/16, Sample TDP12/42/1, 36–46 cm (1d, detail of umbilical area showing pores kept open despite successive layers of calcite forming concentric terraces; 1e, detail of wall showing variable pore size and shape; 1f, detail of wall showing striation; 1g, detail of apertural area showing smooth face with splayed striations. **2a-b**, upper Eocene Zone E15/16, Sample TDP12/21/3, 0–10 cm (2b, detail of areal apertures showing sharp pustules). **3a-b**, upper Eocene Zone E15/16, Sample TDP17/37/3, 15–30 cm (3b, detail of heavily pustulose surface). Scale bars: 100 μm (whole specimens) and 10 μm (close-up images).
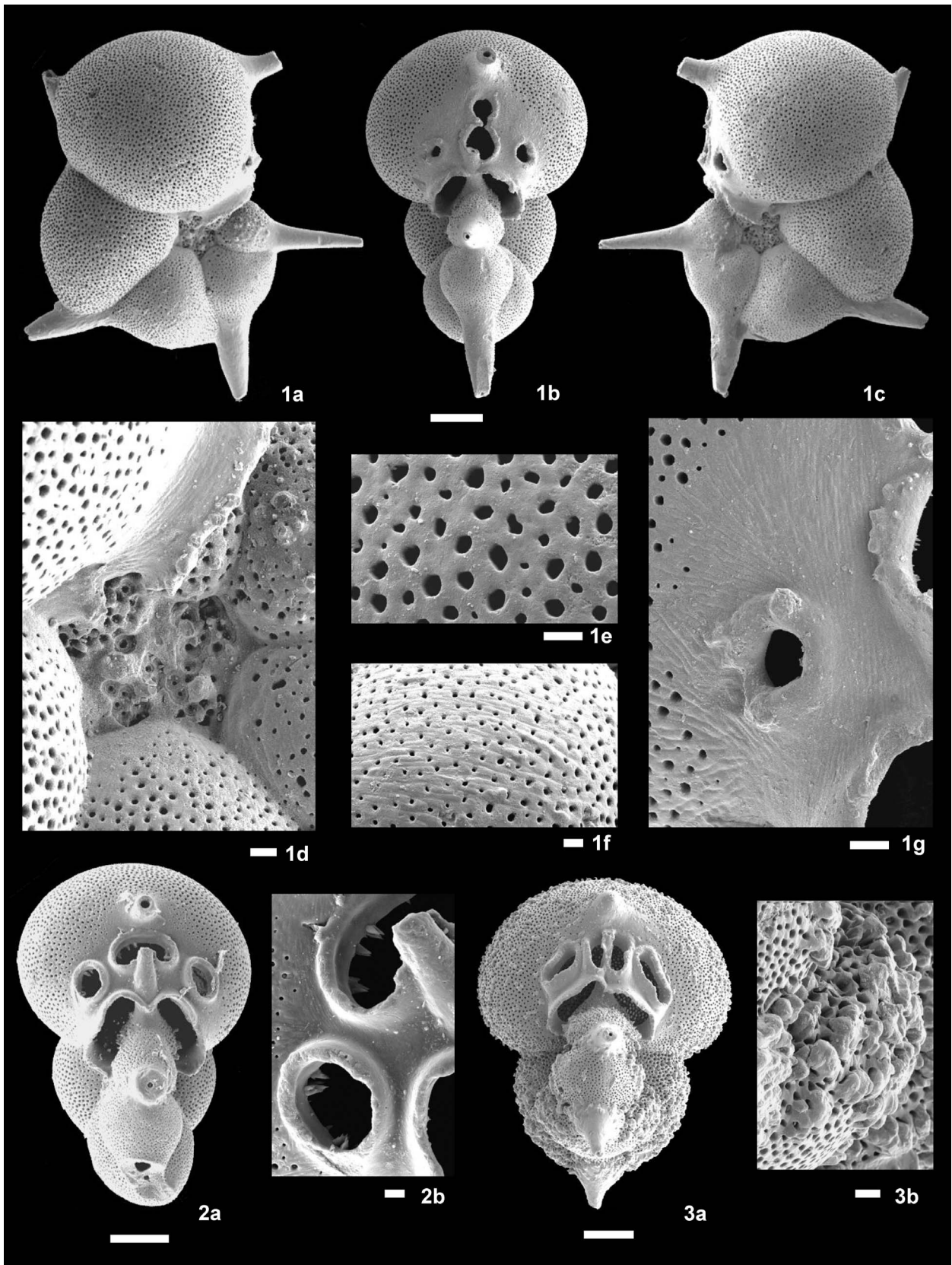
Figure 23. *Cribrohantkenina inflata*, to a common scale, illustrating variations in the apertural system. **1a-b**, upper Eocene Zone E15/16, Sample TDP12/42/1, 36–46 cm. **2–4**, upper Eocene Zone E15/16, Sample TDP12/36/3, 67–81 cm. **5a-b**, upper Eocene Zone E15/16, Sample TDP17/42/2, 61–78 cm. **6–8**, upper Eocene Zone E15/16, Sample TDP12/36/3, 67–81 cm. **9**, upper Eocene Zone E15/16, Sample TDP12/14/1, 92–100 cm. **10a-b**, upper Eocene Zone E15/16, Sample TDP12/25/1, 0–10 cm. **11–13**, upper Eocene Zone E15/16, Sample TDP17/37/2, 32–49 cm. **14a-b**, upper Eocene Zone E15/16, Sample TDP17/42/2, 61–78 cm. **15**, upper Eocene Zone E15/16, Sample TDP17/41/1, 8–18 cm. **16-17**, upper Eocene Zone E15/16, Sample TDP12/42/1, 36–46 cm. **18a-b**, upper Eocene Zone E15/16, Sample TDP17/37/3, 15–30 cm. **19** upper Eocene Zone E15/16, Sample TDP12/21/3, 10–20 cm. **20**, upper Eocene Zone E15/16, Sample TDP12/27/1, 35–45 cm. **21**, upper Eocene Zone E15/16, Sample TDP12/42/1, 36–46 cm. Scale bars: 100 μm.
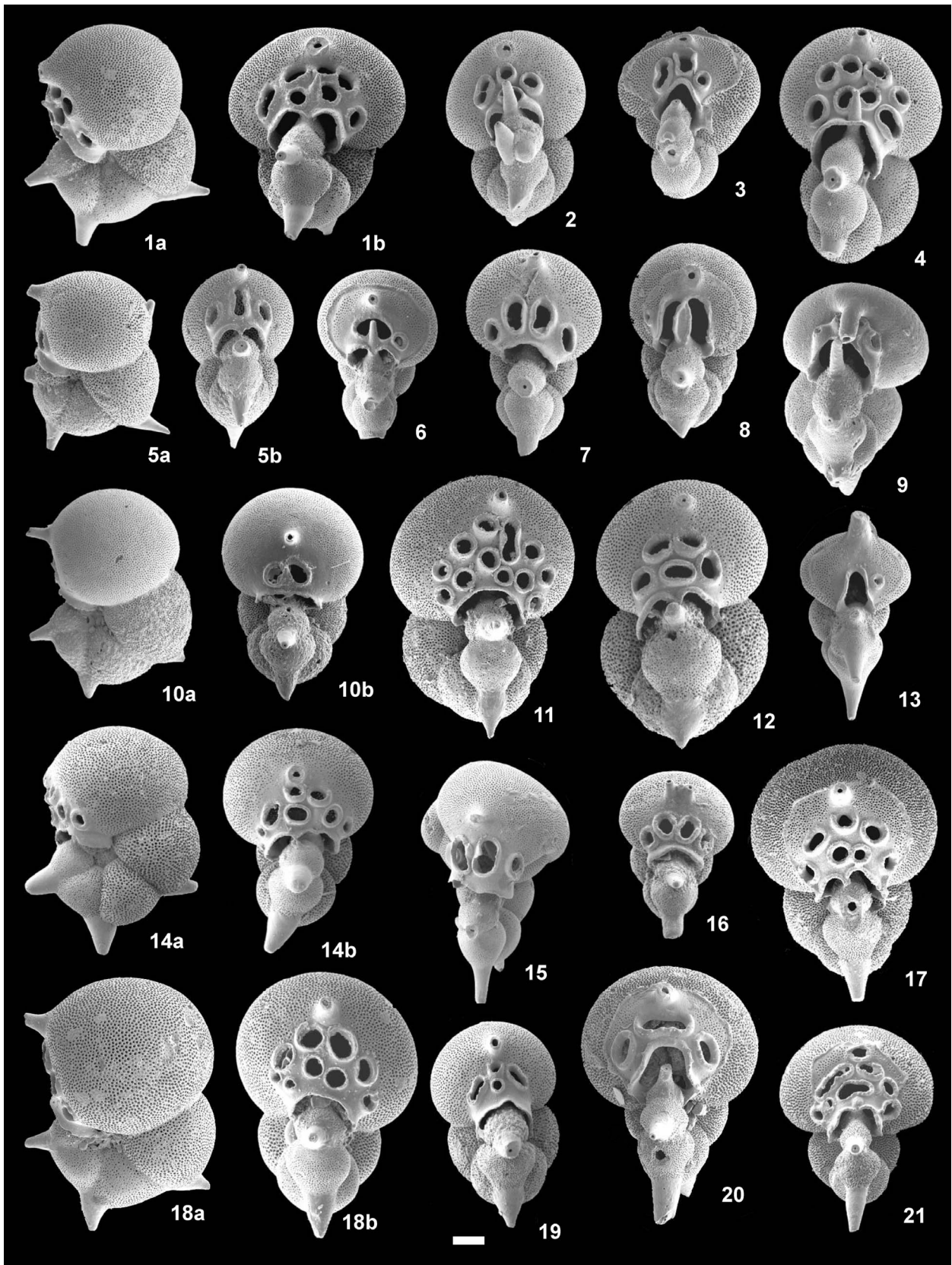
Figure 24. Various *Hantkenina*. **1a-6b**, *Hantkenina alabamensis* (1a-2, upper Eocene Zone E15/16, Sample TDP17/42/2, 61–78 cm; 3, upper Eocene Zone E15/16, Sample TDP12/14/1, 81–83 cm; 4a-b, upper Eocene Zone E15/16, Sample TDP11/30/1, 70–80 cm; 5, upper Eocene Zone E15/16, Sample TDP17/42/2, 61–78 cm; 6a-b, upper Eocene Zone E15/16, Sample TDP17/42/2, 61–78 cm). **7-12b**, *Hantkenina compressa* (7, upper Eocene Zone E15/16, Sample TDP17/40/2, 0–12 cm; 8a-b, upper Eocene Zone E15/16, Sample TDP17/42/2, 61–78 cm; 9, upper Eocene Zone E15/16, Sample TDP12/42/1, 36–46 cm; 10a-11b, upper Eocene Zone E15/16, Sample TDP17/40/2, 0–12 cm; 12a-b, upper Eocene Zone E15/16, Sample TDP17/42/2, 61–78 cm). Scale bars: 100 μm.
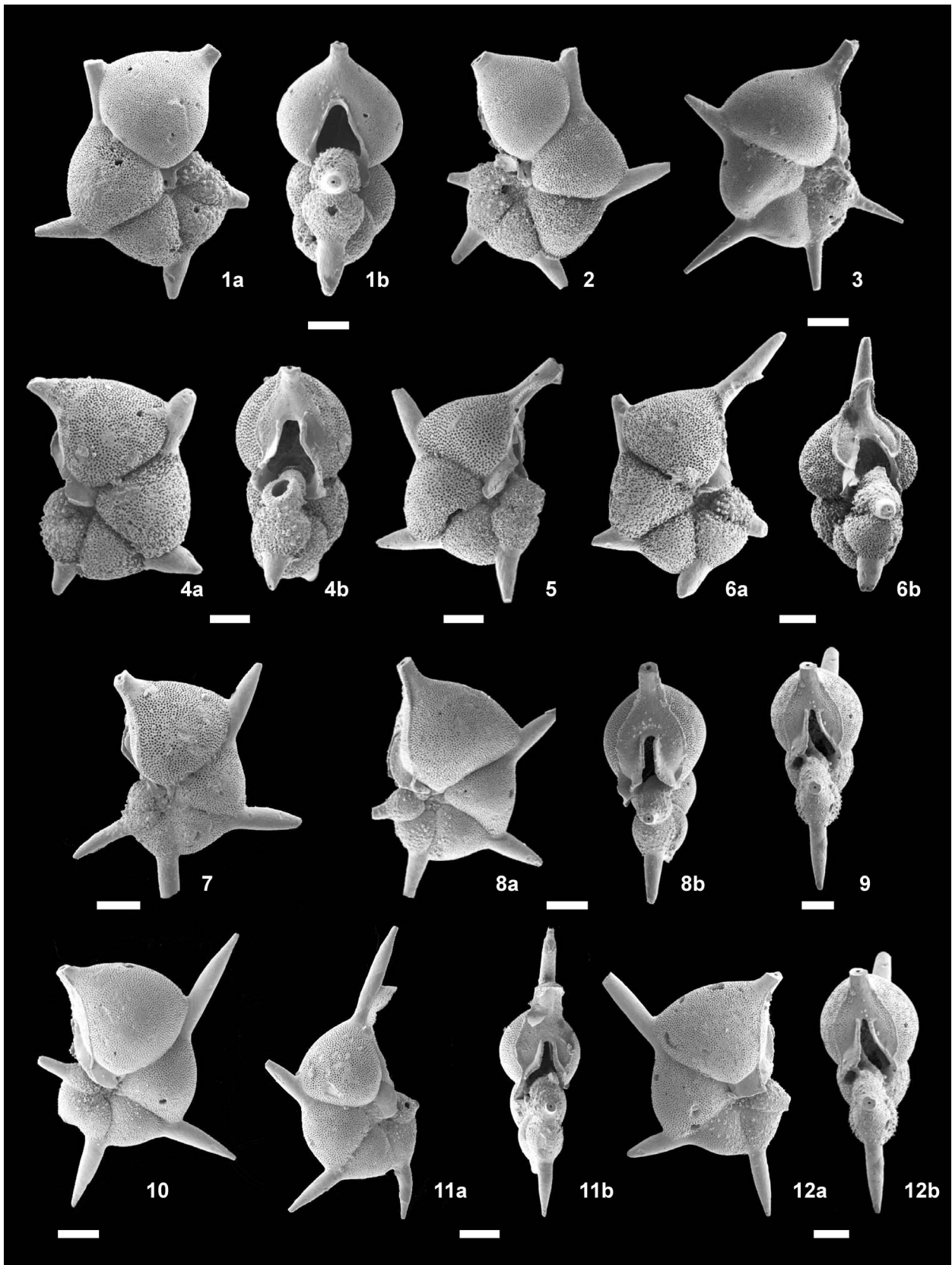
Figure 25. Various *Hantkenina*. **1-4b**, *Hantkenina nanggulanensis* (1, upper Eocene Zone E15/16, Sample TDP11/40/1, 0–10 cm; 2a-c; upper Eocene Zone E15/16, Sample TDP17/40/2, 0–12 cm; 3-4b, upper Eocene Zone E15/16, Sample TDP17/37/2, 32–49 cm). **5a-9b**, *Hantkenina primitiva*, upper Eocene Zone E15/16, Sample TDP17/42/2, 61–78 cm. Scale bars: 100 μm (whole specimens) and 10 μm (close-up images).
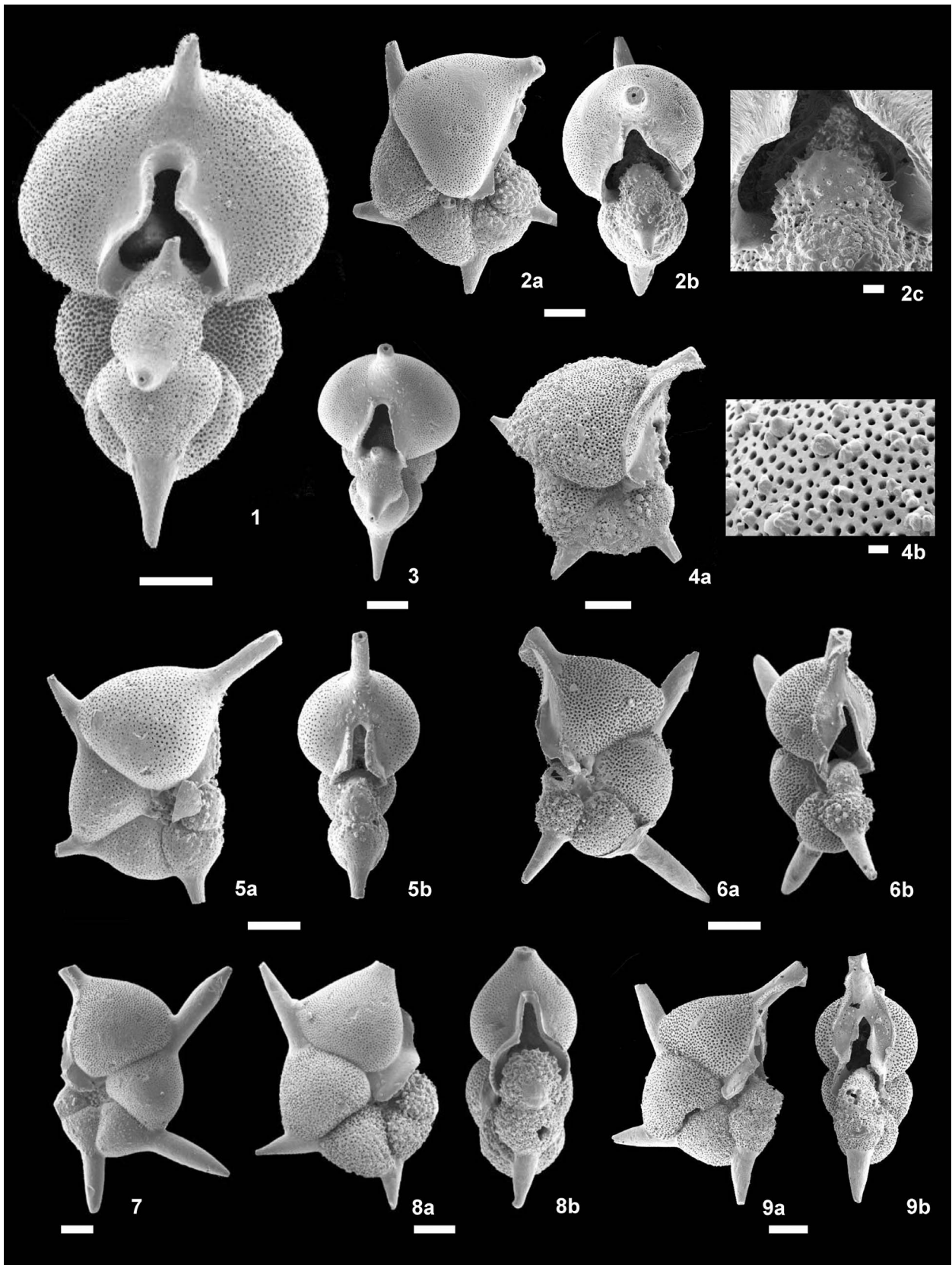
Figure 26. Various *Pseudohastigerina*. **1–7**, *Pseudohastigerina micra* (1, upper Eocene Zone E15/16, Sample TDP12/36/1, 0–10 cm; 2, upper Eocene Zone E15/16, Sample TDP17/44/2, 0–12 cm; 3–4, upper Eocene Zone E15/16, Sample TDP12/18/2, 61–72 cm; 5a-b, upper Eocene Zone E15/16, Sample TDP17/40/2, 0–12 cm; 6, upper Eocene Zone E15/16, Sample TDP12/18/2, 61–72 cm, 7, upper Eocene Zone E15/16, Sample TDP17/40/2, 0–12 cm). **8a-11**, *Pseudohastigerina naguewichiensis* (8a-b, lower Oligocene Zone O1, Sample TDP11/19/1, 60–75 cm, 9a-b, lower Oligocene Zone O1, Sample TDP11/25/3, 10–20 cm [9a, reillustrated from Olsson & Hemleben, 2006, plate 14.3, fig. 9]; 10, upper Eocene Zone E15/16, Sample TDP17/40/2, 0–12 cm, 11, lower Oligocene Zone O1, Sample TDP 11/25/3, 10–20 cm [reillustrated from Olsson & Hemleben, 2006, plate 14.3, fig. 5]). Scale bars: 100 μm.
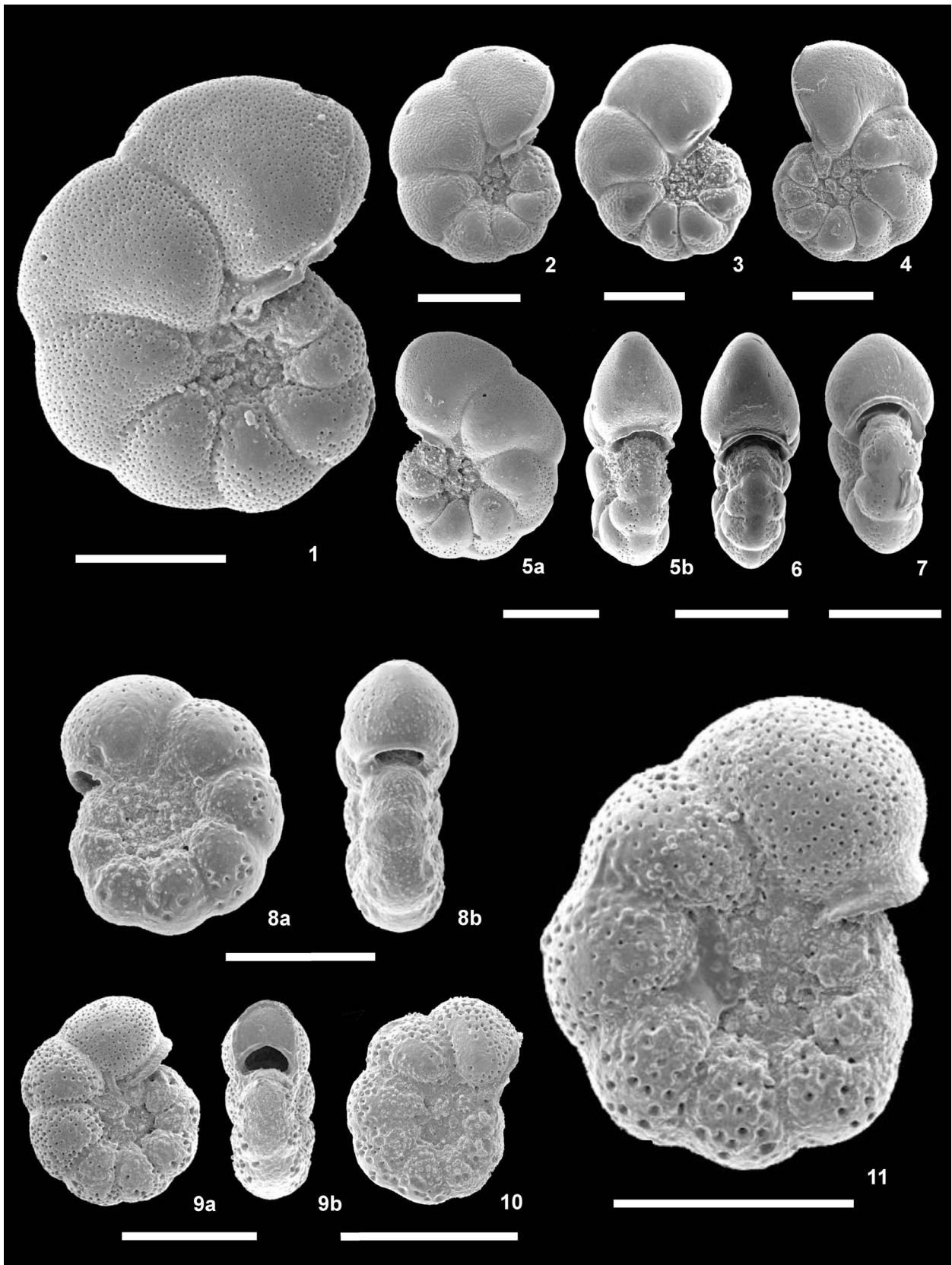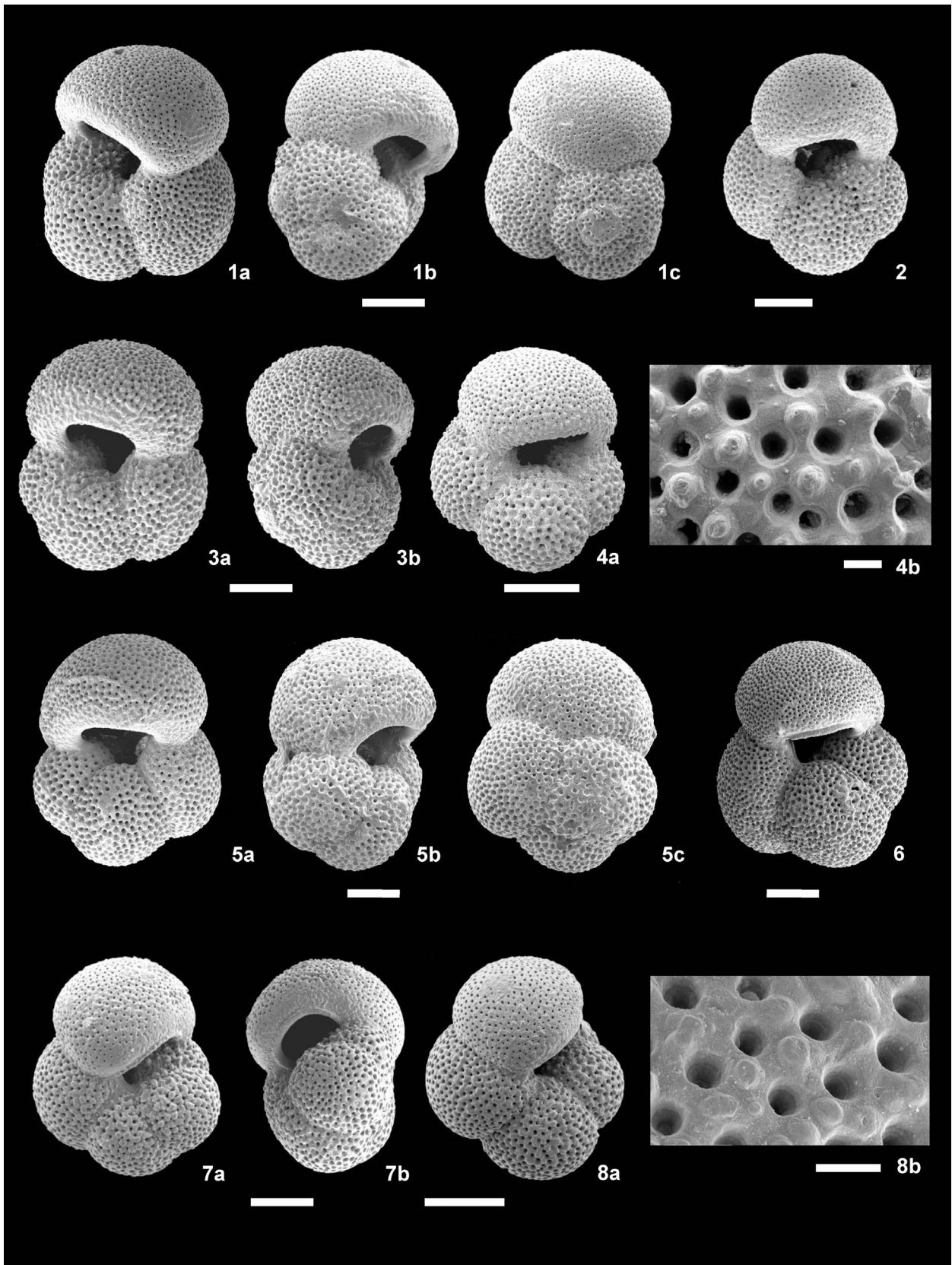
Figure 27. Various *Turborotalia*. **1a-6**, *Turborotalia ampliapertura* (1a-c, lower Oligocene Zone O1, Sample TDP17/17/3, 40–52 cm; 2-3b, lower Oligocene Zone O1, Sample TDP17/11/1, 0–10 cm; 4a-6, lower Oligocene Zone O1, Sample TDP17/17/3, 40–52 cm). **7a-8b**, *Turborotalia increbescens* (7a-b, lower Oligocene Zone O1, Sample TDP12/7/1, 0–10 cm; 8a-b, lower Oligocene Zone O1, sample TDP17/11/1, 0–10 cm). Scale bars: 100 μm (whole specimens) and 10 μm (close-up images).

Figure 28. Various *Turborotalia*. **1a-4**, *Turborotalia cerroazulensis* (1a-b, upper Eocene Zone E15/16, Sample TDP11/25/3, 10–20 cm (reproduced from Pearson et al., 2006c, pl. 15.3, figs. 19-20); 2a-b, upper Eocene Zone E15/16, Sample TDP17/42/2, 61–78 cm; 3-4, upper Eocene Zone E15/16, Sample TDP12/36/3, 67–81 cm). **5a-13b**, *Turborotalia cocoaensis* (5a-b, upper Eocene Zone E15/16, Sample TDP17/42/2, 61–78 cm; 6, upper Eocene Zone E15/16, Sample TDP12/36/3, 67–81 cm; 7, upper Eocene Zone E15/16, Sample TDP12/42/1, 36–46 cm; 8 upper Eocene Zone E15/16, Sample TDP12/44/1, 51–61 cm; 9, upper Eocene Zone E15/16, Sample TDP12/46/2, 56–66 cm; 10, upper Eocene Zone E15/16, Sample TDP12/45/3, 30–40 cm; 11-12, upper Eocene Zone E15/16, Sample TDP12/42/1, 36–46 cm; 13a-b, Sample TDP17/41/1, 8–18 cm). Scale bars: 100 µm.
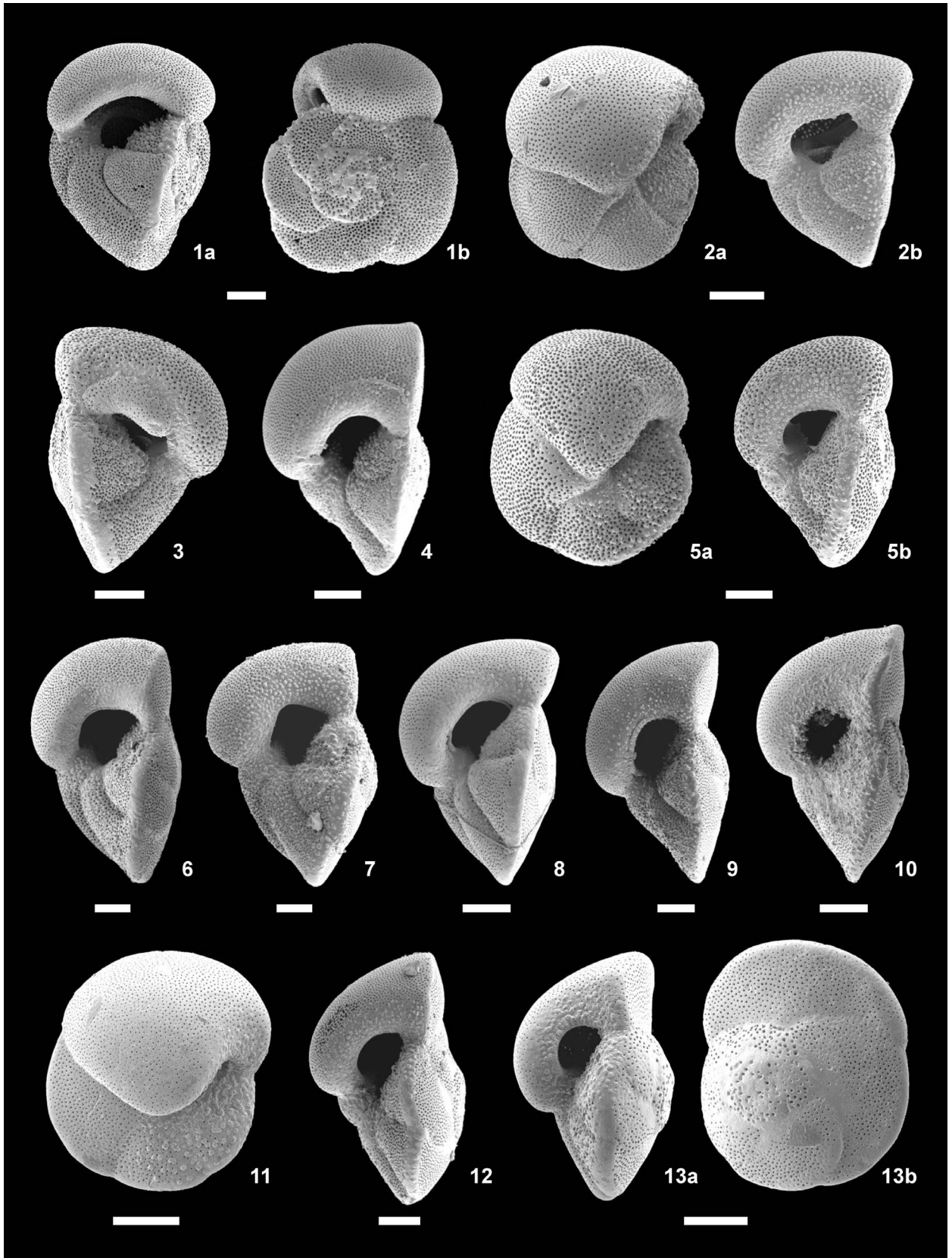
Figure 29. *Turborotalia cunialensis*. **1a-b**, upper Eocene Zone E15/16, Sample TDP11/40/1, 0–10 cm; **2a-b**, upper Eocene Zone E15/16, Sample TDP17/41/1, 8–18 cm; **3a-b**, upper Eocene Zone E15/16, Sample TDP11/30/1, 70–80 cm; **4a-5**, upper Eocene Zone E15/16, Sample TDP17/41/1, 8–18 cm; **6**, upper Eocene Zone E15/16, Sample TDP12/45/3, 30–40 cm; **7-9**, upper Eocene Zone E15/16, Sample TDP17/37/3, 15–30 cm; **10a-c**, upper Eocene Zone E15/16, Sample TDP12/46/2, 56–66 cm; **11**, upper Eocene Zone E15/16, Sample TDP12/45/3, 30–40 cm). Scale bars: 100 μm (whole specimens) and 10 μm (close-up images).
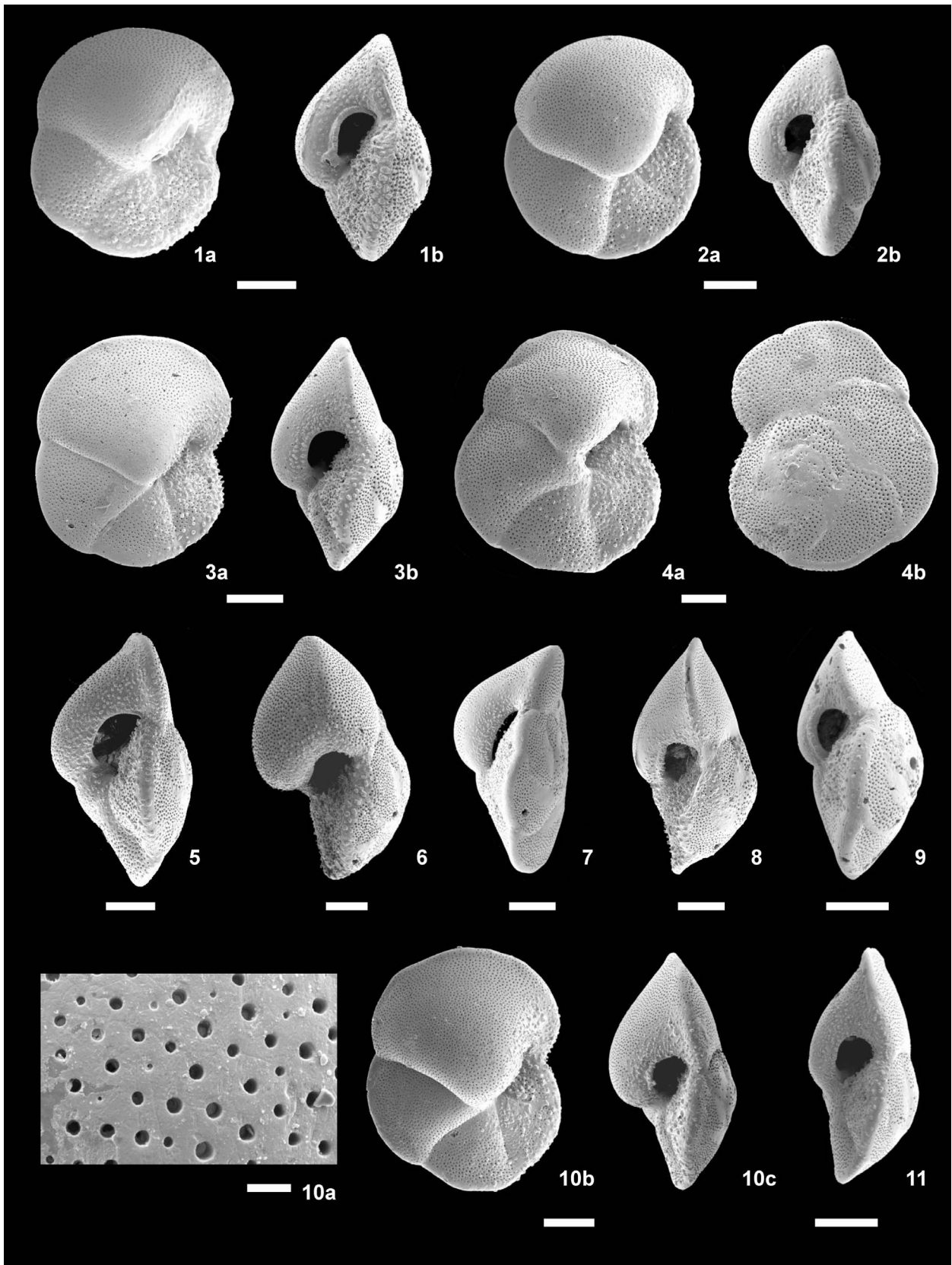
Figure 30. Various species. **1a-b**, *Acarinina collactea*, lower Oligocene Zone O1, Sample TDP11/19/1, 0–10 cm (1b, detail of wall showing eroded muricae). **2a-b**, *Tenuitella gemma*, lower Oligocene Zone O1, Sample TDP12/14/1, 81–83 cm. **3a-b**, *Chiloguembelina cubensis*, lower Oligocene Zone O1, Sample TDP17/11/1, 0–10 cm. **4a-6c**, *Streptochilus martini*, upper Eocene Zone E15/16, Sample TDP17/40/2, 0–12 cm (4, note macro-perforations; 6c, microperforate wall). **7a-8**, *Cassigerinella chipolensis*, (7a-c, lower Oligocene Zone O1, Sample TDP12/11/3, 40–48 cm; 8, lower Oligocene Zone O1, Sample TDP12/13/1, 59–67 cm). Scale bars: 100 μm (whole specimens) and 10 μm (close-up images).