

Chapter 15

WALL TEXTURES AND HIGHER TAXONOMY OF OLIGOCENE MICRO- AND MEDIOPERFORATE PLANKTONIC FORAMINIFERA

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ABSTRACT

New microstructural observations on the tests of microperforate and medioperforate planktonic foraminifera from the Oligocene are presented and comparisons are made with some Holocene specimens. Two types and two subtypes of wall texture are distinguished: the *glutinata*-type (in *Globigerinita* and *Tenuitella*; with the *danvillensis*-subtype in *Dipsidripella*), and the *ototara*-type (in most *Chiloguembelina*), with the *chipolensis*-subtype (in *Cassigerinella* and some *Chiloguembelina*). Given also the gross morphological differences

between the two major groups (trochospiral versus biserial or enrolled-biserial), these wall textures likely indicate separate evolutionary radiations from different groups of benthic foraminifera and so help define the higher taxonomy of the planktonic foraminifera. Accordingly, the following superfamilies are recognized in the chapters of this work: Globigerinitoidea and Guembelitriloidea. Their placement relative to other superfamilies of foraminifera is not yet known.

INTRODUCTION

Previous taxonomic atlases of the Paleogene Planktonic Foraminifera Working Group (Olsson and others, 1999; Pearson and others, 2006) followed Fleisher (1974) by recognizing a fundamental distinction between the ‘macroperforate’ wall texture (with pores >1 μm in diameter) which is typical of the Superfamily Globigerinoidea and the ‘microperforate’ wall texture (with pores <1 μm in diameter) found in other groups, including Families Guembelitriloidea, Chiloguembelinoidea, Heterohelicoidea and Cassigerinelloidea. Variant textures within the microperforate category were noted, including the supposedly monolamellar wall of some taxa and the presence or absence of pore mounds or costellae in others (e.g., Huber and others, 2006). Li and Radford (1991) introduced the term ‘medioperforate’ for wall textures with pores in the range 1-4 μm . This is a useful term because 1 μm is not always a meaningful cut-off point for distinguishing wall textures, including for example

in the Cassigerinelloidea which usually exhibit pores that are a little larger than 1 μm in diameter. Although such divisions are always to some extent arbitrary, the term medioperforate is here revised to indicate walls with pores in the range 1-2 μm because the range 2-4 μm includes large numbers of species that naturally group with the other macroperforates. The purpose of this work is to propose a more formal classification of Oligocene microperforate and medioperforate wall textures and to help delimit two groups of taxa that probably had independent origins in the benthos. This wall texture classification is intended to complement the macroperforate classification developed, among others, by Fleisher (1974, 1975), Steineck and Fleisher (1978), Hemleben and others (1999), Hemleben and Olsson (2006), and Chapter 3 (this volume).

Originally, planktonic foraminifera were divided into genera and higher taxa mainly on the basis of general test morphology, chamber shape, and apertural position (e.g. Galloway, 1933; Cushman, 1940, Bermúdez, 1952:

see reviews by Bolli and others, 1957:19, and Lipps, 1966). Because such features are now thought to have evolved independently many times, this resulted in what are now recognized as only distantly related groups being lumped together, creating polyphyletic higher taxa. In the 1960s, some authors attempted to establish a more natural classification by differentiating higher taxa based on wall textures as observed using the light microscope (e.g., Parker, 1962; Wade, 1964; Lipps 1966). This approach was accelerated with the SEM which revealed test surfaces in unprecedented detail (e.g., Fleisher, 1974, 1975; Steineck and Fleisher, 1978; Blow, 1979).

Fleisher (1974:1011-1012) proposed the 'microperforate' wall texture as a distinct category, exemplified by the genus *Globigerinita*. He described it as characterized by 'extremely small perforations' (i.e., pores) on an otherwise smooth surface, with small pustules common in some forms. Fleisher's newly described genus *Tenuitella* was assigned to the microperforate category and, following Jenkins (1965), he regarded *Globigerinita* and *Tenuitella* as closely related in an evolutionary sense, underlining the point that the wall texture could be used to identify natural groups. This was a significant development because species that are now included in these taxa had previously been assigned to various macroperforate genera such as *Globigerina*, *Turborotalia* and *Globorotalia*.

Steineck and Fleisher (1978) developed and formalized the wall texture classification of Fleisher (1974, 1975) and made a compelling case for the use of wall textures in identifying phylogenetically related groups. The 'microperforate' wall was one of five textures identified by them among Neogene planktonic foraminifera, the others being 'spinose' (exemplified by *Globigerina bulloides*), 'cancellate spinose' (exemplified by *Trilobatus trilobus*), 'cancellate' and, by inference, nonspinose (as exemplified by *Globoquadrina dehiscens*) and finely perforate-smooth (as exemplified by *Globorotalia cultrata*).

Blow (1969, 1979; the latter a posthumous work developed several years before the publication date) also pioneered SEM investigations but he did not recognize the microperforate wall as delineating a major subdivision in his classification of planktonic foraminifera and some of his genera contain both macro- and microperforate forms. He did nevertheless separate serial taxa such as *Chiloguembelina* and *Guembelitra* from the *Globigerinitoidea* and included them in the

Superfamily Heterohelicacea: these serial taxa are now acknowledged as being microperforate. (Note that the correct suffix for superfamilies of protists is -oidea not -acea "when workers treat them as animals for the purposes of nomenclature" which is the case in this work; see International Code of Zoological Nomenclature, 1999, Article 1.1.1, see also Article 29.2.) Blow (1969, 1979) also argued for an evolutionary link between *Globigerinita* and the modern species *Candeina nitida* and recognized an intermediate species as *C. praenitida*. Although this has been supported by genetic evidence it is doubtful on wall texture grounds (see discussion below).

Kennett and Srinivasan (1983) described and illustrated with high quality SEMs the microperforate wall texture of *Globigerinita*, *Tenuitella*, *Globigerinatella* and *Candeina*, and suggested that together they form a natural group. However their illustrations of the *Candeina* wall, while it is clearly microperforate (pores <1 µm), does not compare closely with the other genera, even in their own images (see Kennett and Srinivasan, 1983, pl. 57, fig. 8).

Loeblich and Tappan (1984, 1988) made the first attempt to use the microperforate wall to establish a higher taxonomy. They assigned all non-serial microperforate planktonic foraminifera to Family Candeinidae, which was then subdivided into Subfamilies Tenuitellinae, Globigerinitinae, and Candeininae. This arrangement implies that all non-serial microperforate foraminifera are part of a single clade which is a sister group to the macroperforates.

In their influential work on modern planktonic foraminifera, Hemleben and others (1989) avoided a formal higher taxonomy but divided modern species into spinose and nonspinose groups, with the microperforate forms (including *Tenuitella*, *Globigerinita*, *Candeina* and serial forms) forming a division of the nonspinose category (see also Spezzaferri, 1994).

Li and Radford (1991) summarized the stratigraphic and biogeographic distribution of Paleogene micro- and medioperforate species and argued that they belong to "several phylogenetically unrelated groups", of which they identified five. Two of Li and Radford's five groups (*Parvularugoglobigerina* and *Globoconusa*) are restricted to the Paleocene and one (*Cassigerinelloita*) to the Eocene and so are not considered further here. The remaining three (*Chiloguembelina*, *Cassigerinella*, and *Tenuitella*) persist into the Oligocene. In essence they recognized three of the wall types or subtypes of

Oligocene planktonic foraminifera that are formalized in this paper.

In the *Atlas of Paleocene Planktonic Foraminifera*, Olsson and others (1999; following Liu and Olsson, 1992, and Olsson and others, 1992), presented a wall texture classification that included a single major category of microperforate wall with various informal subcategories distinguished mainly by the shape and distribution of pustules, pores and pore mounds (see Hemleben and others, 1999:16, fig. 6). Except for *Zeauvigerina*, the Paleocene microperforates were regarded as a natural group descended from the common ancestor *Guembelitra cretacea*. The wall textures of the serial *Chiloguembelina* were compared with modern *Globigerinita glutinata* (Hemleben and others, 1999, pl. 6, figs. 7-18), which was also described as microperforate, although no explicit phylogenetic link was made.

Lee and others (2000) reviewed the taxonomy of the living foraminifera in the context of the Protozoa as a whole. In their scheme, Foraminifera are a class within the Phylum Granuloreticulosa. Non-serial planktonic foraminifera constitute the Order Globigerinida which is divided into two superfamilies, the Candeinacea (microperforates) and Globigerinacea (macroperforates). The Candeinacea are divided into Families Globigerinitidae (including *Globigerinita*, *Tenuitella* and related form-genera) and Candeiinidae (which includes just *Candeina*). This scheme is similar to that of Loeblich and Tappan (1984, 1988) except that the taxa are raised in rank. It also implies that non-serial microperforate planktonic foraminifera constitute a single clade which is a sister group to the macroperforates. Note that fossil groups such as *Cassigerinella* and *Chiloguembelina* are omitted from this classification as were (perhaps inadvertently) modern serial planktonic foraminifera.

In the *Atlas of Eocene Planktonic Foraminifera*, Hemleben and Olsson (2006) included a single category of microperforate wall. Huber and others (2006) divided the Eocene micro- and medioperforates into Families Guembelitriidae (*Jenkinsina* and *Cassigerinelloita*), Chiloguembelinidae (*Chiloguembelina* and *Streptochilus*), Heterohelicidae (*Zeauvigerina*), Cassigerinellidae (*Cassigerinella* and *Tenuitella*) and Problematica (*Dipsidripella*). The relationships between these five groups were left unresolved, allowing for their independent evolutionary origins (see also Pearson and others, 2006, fig. 1.2).

Pearson and Wade (2009) presented new images of the micro- and medioperforate ultrastructure of exceptionally well-preserved uppermost Oligocene taxa from Trinidad and Puerto Rico. They showed that *Cassigerinella* has a different wall texture from the group that comprises *Tenuitella* and *Globigerinita* (and which is also seen in Miocene *Globigerinatella* and *Mutabella*). They separated the Family Cassigerinellidae from Family Globigerinitidae and suggested these two groups had separate origins in the benthos. A distinctive feature of the *Cassigerinella* wall (discussed further below) was the presence of minute internal calcite spikes, called endospikes by Pearson and Wade (2009). Subsequently, D'Haenens and others (2012) illustrated the same feature in the biserial form *Chiloguembelina wilcoxensis*. This strongly suggests a phylogenetic link between biserial *Chiloguembelina* and enrolled-biserial *Cassigerinella*.

MATERIALS AND METHODS

New observations were made on Holocene specimens of the microperforate genera *Candeina*, *Globigerinita*, and *Tenuitella* from the GLOW cruise offshore Tanzania (Kroon and others, unpublished; Station GLOW 19, Latitude 10.000°S, Longitude 40.199°E, box core, top surface). Test dissections of many Oligocene and some lower Miocene forms have also been performed. The best-preserved ('glassy') samples available have been used, except when studying diagenetic effects.

Specimens were mounted on an SEM stub, conductively coated, and imaged, with special attention paid to details of the outer wall texture. They were then crushed using a clean glass plate (microscope slide), re-coated, and the fragments then re-examined. The most representative and clearest views (that is, lacking debris) are presented here.

DESCRIPTION OF WALL TEXTURES

Oligocene micro- and medioperforate taxa exhibit two distinctive wall textures which, it is suggested, represent separate groups of plankton that evolved independently from unknown benthic ancestors. The wall of modern *Candeina* is also considered to be different from the two Oligocene groups, but is not discussed further here as it is only known from the Neogene.

glutinata-type (Plates 15.1 and 15.2): This wall texture is the original 'microperforate' wall described by Fleisher (1974) in *Globigerinita* and *Tenuitella*. Here it is typified by the modern species *Globigerinita glutinata* (Plate 15.1, Figs. 1a-e). In cross-section the wall is usually between 3 and 6 μm thick and consists of two main layers separated by the primary organic membrane (POM) which can be seen in well-preserved specimens. The inner layer is usually very thin, less than a micron, and typically constitutes about 10-20% of the shell thickness. The thicker outer test wall may be further subdivided into discrete sub-layers although these are often difficult to discern. Distinctively, both inner and outer layers have a prismatic or radially fibrous / crystalline appearance, as opposed to the more isotropic microgranular texture of the other microperforate textures described below (and also all macroperforate planktonic foraminifera). Pore channels are generally straight and have a constant width through the wall, normally about 0.4 μm in width. The pore channels often flare a little on the external and internal surfaces, making the pore openings slightly larger than the channels. The inner surface is very smooth and entirely lacking the 'endospikes' that are characteristic of the *chipolensis* wall subtype (see below). The outer surface is essentially smooth except that it commonly possesses pustules, which may be isolated, fused, or form a distinct surface layer. The pustules can be very dense in some species while in others they are concentrated in particular areas. The pustules are more or less conical or mounded structures formed atop the outer surface. They appear to be superficial, in that they are not rooted in the wall and are not formed by upward bending of the internal wall layers as is the case in the pustules of many macroperforate taxa (e.g., the muricae of the Truncorotaloididae; of Hemleben and Olsson, 2006, plate 4.8). In the modern *Globigerinita* specimens studied, the size distribution of these pustules is distinctly bimodal, with the smaller ones being about 0.5 μm wide and tall and the larger ones 5-8 μm wide and tall. This bimodality is less evident in Oligocene *Globigerinita* and *Tenuitella* but pustules are still quite variable in size. Variations of this wall include species that are almost entirely smooth (modern *Tenuitella anfracta*), species that are covered in very dense pustules so that the smooth surface is barely visible (as in some Oligocene *Tenuitella angustiumbilitata*, for example; see Chapter 16, this volume), and species that have a system of complex arched tunnels within the outer layers

of the wall (as in some Miocene *Globigerinatella*; see Pearson and Chaisson, 1997, plate 1).

The pore channels occasionally bend within the wall below a surface pustule, presumably so as not to be covered up by the pustule, and on the surface the pores often appear to 'erode' into the adjacent pustule. The deflection of pore channels is presumably a late-stage modification so that the pores can stay open, although in some cases pore channels are entirely covered by a surface pustule.

danvillensis-subtype (Plate 15.2, Figs. 3a-4b): In *Dipsidripella danvillensis* the wall has a similar radially crystalline appearance but is typically thinner (just 2-3 μm), pore density is lower and pore diameters typically exceed 1 μm in part or all of the test, making the texture technically medioperforate. Large areas of the chambers can be effectively non-porous. Pore channels may be straight or may expand upwards in distinct terraces at each internal layer. Pustules also tend to be larger and more sparsely distributed than in most *Tenuitella* and *Globigerinita*.

ototara-type (Plate 15.3): This wall texture is typified by *Chiloguembelina ototara*. In cross-section the wall is thin, usually between 2-5 μm thick and consists of two main layers. The inner layer is typically just 0.3-0.5 μm in thickness. It seems likely that this was the site of the POM, and the pores typically constrict markedly at this point. The thicker outer layer may be further subdivided into discrete layers, although they are often difficult to observe, and they do not usually correspond to distinct constrictions in the pore channels. The wall as a whole has a distinctly microgranular texture, with granules having an irregular shape and a typical diameter of 0.1 μm . In this respect, the wall is similar to that seen in macroperforate planktonic foraminifera and quite unlike the *glutinata*-type 'radially crystalline' wall described above. Pores are usually about 0.50-0.75 μm in diameter but can exceed 1 μm in part of the test. Pore channels are straight. In most cases the inner surface is very smooth, entirely lacking the endospikes that are typical of the *chipolensis*-subtype wall. In some specimens the pore channels flare into the interior (Plate 15.3, Fig. 2b). The outer surface is smooth or pustulose to various degrees. Pustules are conical or mounded. As in the *glutinata*-type wall, pores frequently 'erode' into the sides of pustules, suggesting late-stage modifications to keep them open.

In some instances the pustulose wall is modified to form prominent costae (ridges) along part or the entire length of the test (as is diagnostic of *Chiloguembelina cubensis*, for example). Individual costae terminate in rounded endings and pores are frequently set into the sides of the costae. This appears to be a superficial modification and is not considered here as a materially distinct wall texture. The term ‘costae’ is preferred in this work to ‘striae’ as the ridges are raised rather than grooves cut out of the wall, although both terms are acceptable.

chipolensis-subtype (Plates 15.4 and 15.5): This wall texture, typified by *Cassigerinella chipolensis*, was illustrated by Pearson and Wade (2009:198-200). In cross-section the wall is usually between 3-5 μm thick and consists of two main layers which, presumably, were separated by a POM in life. As in the *glutinata*-type wall, the inner primary layer is usually very thin, about 0.5 μm or less, typically constituting less than 15% of the shell thickness. Unlike that texture, both inner and outer layers have a microgranular texture (see also Li, 1986) with no clear radial structure, and pore channels generally widen through the wall, being normally about 0.5 μm in width on the inner surface and sometimes over a micron on the outer surface. The outer surface is fairly smooth but may show local thickenings, especially around the pores. In some specimens these thickenings are very pronounced and constitute pore mounds. In cross-section the pore mounds appear to be an integral part of the wall texture as opposed to the superficial pustules described in the *glutinata*-type wall. The thickening of the wall and development of pore mounds tends to be more pronounced on the earlier-formed chambers and progressively less so on the later ones suggesting that they thicken through ontogeny as successive chambers are added. The extent of development of the pore mounds in *Cassigerinella* varies substantially between sites and within populations, with some specimens essentially smooth throughout the test, others with very well developed pore mounds, and still others in an intermediate state.

Uniquely for foraminifera (as far as is known) the inner surface is strewn with minute sharp projections called ‘endospikes’ by Pearson and Wade (2009:200). These are typically less than a micron across at their base, which are longer than broad, and 1-2 μm tall, shaped like miniature sharks’ teeth. There is approximately the same number of endospikes as there are mural pores. The early

SEMs of *Cassigerinella* by Saito and Biscaye (1977) were of relatively poorly preserved material hence such structures are not visible; however similar spikes can be observed in some of Li’s (1986) images (especially his pl. 3, fig. 9). Li noted their presence, but suggested that they may be due to diagenetic deposition on the interior surfaces (Li, 1986:54). Many of Li’s specimens do indeed contain diagenetic precipitates as well as endospikes, but our material is much cleaner. The nature of the endospikes has been a matter of debate within the Working Group. There are strong arguments against a diagenetic explanation. They do not have the habit of inorganic calcite crystals and their spaced distribution is more typical of biogenic structures (diagenetic crystals tend to nucleate in clusters in particular areas). Pearson and Wade (2009) illustrated specimens from both Trinidad (see Plate 15.5, Fig. 1a-c) and Puerto Rico (Plate 15.5, Fig. 2a-c). Further dissections have been conducted and the same inner surface texture has now been found in well-preserved Oligocene cassigerinellids from the western North Atlantic Slope (samples courtesy of C. Liu and R.K. Olsson; Plate 15.5, Fig. 3a-c), the Coatzintla Fm. in Mexico (also courtesy of R.K. Olsson; not shown), the Pausramer marl of the Czech Republic (courtesy of M. Kučera; Plate 15.5, Fig. 4a-c), and the Pande Fm. of Tanzania (not shown). Together these localities constitute the Working Group’s best ‘glassy’ material. Very similar endospikes have been found in every specimen dissected, but never in specimens of other small taxa from the same samples. Very similar endospikes were illustrated in a single dissected specimen of *Chiloguembelina wilcoxensis* by D’Haenens and others (2012, pl. 4, fig. 6). This is a significant observation because it suggests a phylogenetic link between *Chiloguembelina* and *Cassigerinella*, and that the *chipolensis* wall is best regarded as a subtype of the *ototara*-type wall.

DIAGENESIS

Most of the specimens illustrated here are from clay-rich facies and are exceptionally well-preserved. In contrast, foraminifera from Oligocene deep-sea carbonates tend to be almost wholly recrystallized, a process that destroys fine test features such as the endospikes in the *chipolensis*-subtype wall and can make the pores and pore channels difficult to discern. Even so, the general nature of wall texture can usually be identified. Pustules and costae on the test surface tend to

survive, albeit replaced by diagenetic crystallites which are commonly overgrown (see for example, Plate 15.2, Fig. 2a-b and Plate 15.3, Fig. 6a-b).

HIGHER TAXONOMY

Parker (1962) suggested that modern species of *Globigerinita* (along with forms that were later included in *Tenuitella*) evolved independently from the rest of the planktonic foraminifera. Based solely on observations with the light microscope, she described their wall as “smooth or finely hispid and non spinose” (Parker 1962:252) and assigned them to ‘Incertae Familiae’ (see the discussion under *Globigerinita* in Chapter 16, this volume). At the time this was a radical proposal but genetic evidence from ribosomal DNA gene sequences has subsequently proved her case. Stewart and others (2001) showed that two modern species of *Globigerinita* cluster together in their gene sequences but fall far outside the clade of macroperforate forms (that is, the Globigerinidae, Globorotaliidae, etc.). Ujiie and others (2008) and Darling and others (2009) provided similar evidence for the serial microperforate genera *Gallitellia* and *Streptochilus* respectively. Combining these results with observations from the fossil record, Leckie (2009) suggested that a number of microperforate groups may have had separate benthic origins, including the Paleogene groups *Dipsidripella*, *Tenuitella*, *Cassigerinella*, and *Streptochilus*.

The two Oligocene microperforate wall types described here are sufficiently different from one another and from the macroperforate wall texture of the Globigerinoidea to suppose that they evolved separately from different (as yet unidentified) benthic groups. This is supported by gross shell morphology. The *glutinata*-type wall is found only in trochospiral forms, the *ototara*-type in serial forms or enrolled-serial forms. For this reason two groups are recognized in respective chapters of this work at the superfamily level as Globigerinitoidea and Guembelitrioidea. The placement of these superfamilies relative to others in the foraminifera is undetermined. If a benthic ancestor can be determined, then it may be that these superfamilies can be subsumed into benthic groups, just as *Streptochilus* is included in the Bolivinoidea (see Chapter 19, this volume).

We note that genetic evidence (Ujiie and Lipps, 2009) indicates a close relationship between modern *Candeina* and *Globigerinita* as has also been proposed

on paleontological grounds (Blow 1969, 1979) but this conflicts with personal observation (unpublished) that *Candeina* has a rather different wall texture. Resolving this issue is outside the scope of the present study, hence the question as to whether *Candeina* belongs in the Globigerinitoidea remains unresolved. As yet, no gene sequences exist for modern *Tenuitella* (Aurahs and others, 2009). The clear prediction from morphology is that *Tenuitella* will group genetically with modern *Globigerinita* (although perhaps with significant sequence differences given the relatively deep early Oligocene divergence between the lineages). *Candeina*, on the other hand, has a very different wall structure from *Tenuitella* or the serial genera, and when sequenced may represent a separate group again. Because *Cassigerinella* and *Chiloguembelina* are both extinct, genetic evidence can not help resolve the question of their relationships except by establishing the general rule that very different wall structures define distantly related groups.

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Plate 15.1 The *glutinata*-type wall, Holocene

1, *Globigerinita glutinata*, Holocene, Station GLOW-19 box core-top (**a**, whole specimen; **b**, detail of wall showing smooth microperforate surface with pustules of varying size; **c**, detail of broken wall showing radially crystalline texture and pore channels of constant thickness; arrow highlights the primary organic membrane; **d**, detail of broken wall illustrating superficial nature of surface pustules, arrow as in **c**; **e**, detail of broken wall illustrating pores of constant thickness; arrow highlights pore deflecting under surface pustule); **2**, *Tenuitella* sp., Holocene, Station GLOW-19 box core-top (**a**, whole specimen; **b**, detail of broken wall showing radially crystalline texture, arrow highlights the primary layer). Scale bars: **1a**, 50 μm , **2a**, 20 μm , all close-ups, 2 μm .

Plate 15.2 The *glutinata*-type and *danvillensis*-subtype walls, Oligocene, with diagenetic modification

1, *Tenuitella munda*, Zone O2, Ottenthal Fm., Austria (**a**, whole specimen; **b**, detail of broken wall showing radially crystalline texture and superficial pustules; **c**, surface texture); **2**, *Tenuitella munda*, Zone AO1, ODP Site 1137, Elan Bank, Kerguelen Plateau (**a**, surface texture showing diagenetic recrystallization of wall and obliteration of pores; **b**, whole specimen); **3**, *Dipsidripella danvillensis*, ODP Hole 647A/28R/3, 44.5-46.0 cm, Labrador Sea (**a**, whole specimen; **b**, **c**, details of broken wall showing multiple internal layers; **d**, surface texture showing large pores and conical pustules); **4**, *Dipsidripella danvillensis*, Zone O2, Ottenthal Fm., Austria (**a**, whole specimen; **b**, detail of wall showing peripheral area lacking in pores). Scale bars: whole specimens, 50 μm , all close-ups, 5 μm .

Plate 15.3 The *ototara*-type wall, Oligocene, and diagenetic modification

1, *Chiloguembelina ototara*, Zone O1, ODP Hole 647A/28R/7, 103-104 cm, Labrador Sea (**a**, whole specimen, **b**, detail of broken wall showing microgranular texture); **2**, *Chiloguembelina ototara*, Zone O1, ODP Hole 647A/28R/3, 44.5-46.0 cm, Labrador Sea (**a**, whole specimen, **b**, detail of broken wall showing depressed pores on interior surface); **3**, *Chiloguembelina ototara*, ODP Hole 647A/19/4, 89 cm, North Atlantic Ocean (**a**, whole specimen, **b**, detail of surface with conical pustules and pores); **4**, **5**, *Chiloguembelina adriatica*, Adriatic Sea, lower Oligocene, Istra More-3 well, 968-974 ft (**4a**, **5a**, whole specimens, **4b**, **5b**, details of costae on test surfaces); **6**, *Chiloguembelina adriatica*, Zone O4-O6 undifferentiated, ODP Hole 872C/16H/1, 20-22 cm, tropical North Pacific Ocean (**a**, whole specimen, **b**, detail of costae on test surface showing diagenetic modification). Scale bars: whole specimens, 50 μm , all close-ups, 5 μm .

Plate 15.4 The *chipolensis*-subtype wall, Oligocene and Miocene

1a-2b, *Cassigerinella chipolensis*, Zone O7, Cipero Fm., Trinidad (Pearson and Wade, 2009, pl. 1, fig. 1; **1a**, whole specimen, showing pore mounds on earlier chambers, **1b**, **1c**, details of broken wall showing raised pore mounds and flaring pore channels and endospikes within; **2a**, whole specimen, **2b** detail of wall surface showing slightly raised pore surrounds); **3**, Subzone M1b, Sample LC09T71, Tanzania (**a**, whole specimen, **b**, detail of wall surface showing essentially smooth texture); **4a-5b**, Oligocene, Pausramer marl, Czech Republic (specimens showing smooth to weakly pustulose wall textures with pore mounds). Scale bars: whole specimens, 50 μm , all close-ups, 5 μm .

Plate 15.5 The *chipolensis*-subtype wall, Oligocene

Cassigerinella chipolensis, test dissections from various localities to illustrate commonalities in microstructure (microgranular texture and endospikes on internal surfaces); **1a-c**, Zone O7, Cipero Fm., Trinidad (Pearson and Wade, 2009, pl. 1, fig. 2); **2a-c**, Zone O5, Juana Diaz Fm., Puerto Rico (Pearson and Wade, 2009, pl. 1, fig. 3); **3a-c**, Oligocene, Atlantic Slope Project corehole 5B, western North Atlantic Slope; **4a-c**, Oligocene, Pausramer marl, Czech Republic. Scale bars: whole specimens, 50 μm , all close-ups, 5 μm .

Note: Post production Plate 15.5 was replaced with a higher resolution version and specimen 2a rotated, thus the PDF differs from the printed volume.

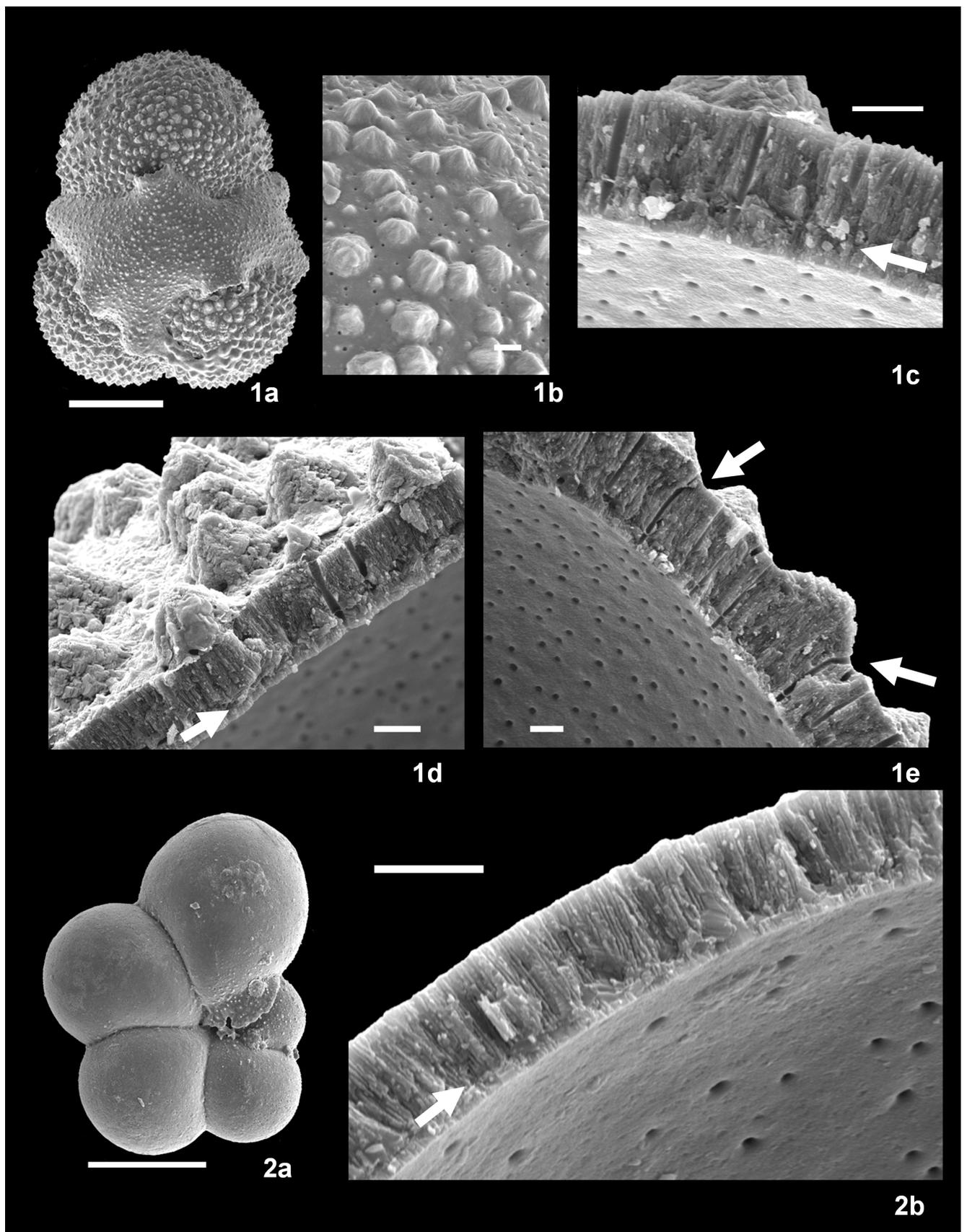


PLATE 15.1 *glutinata*-type wall, Holocene

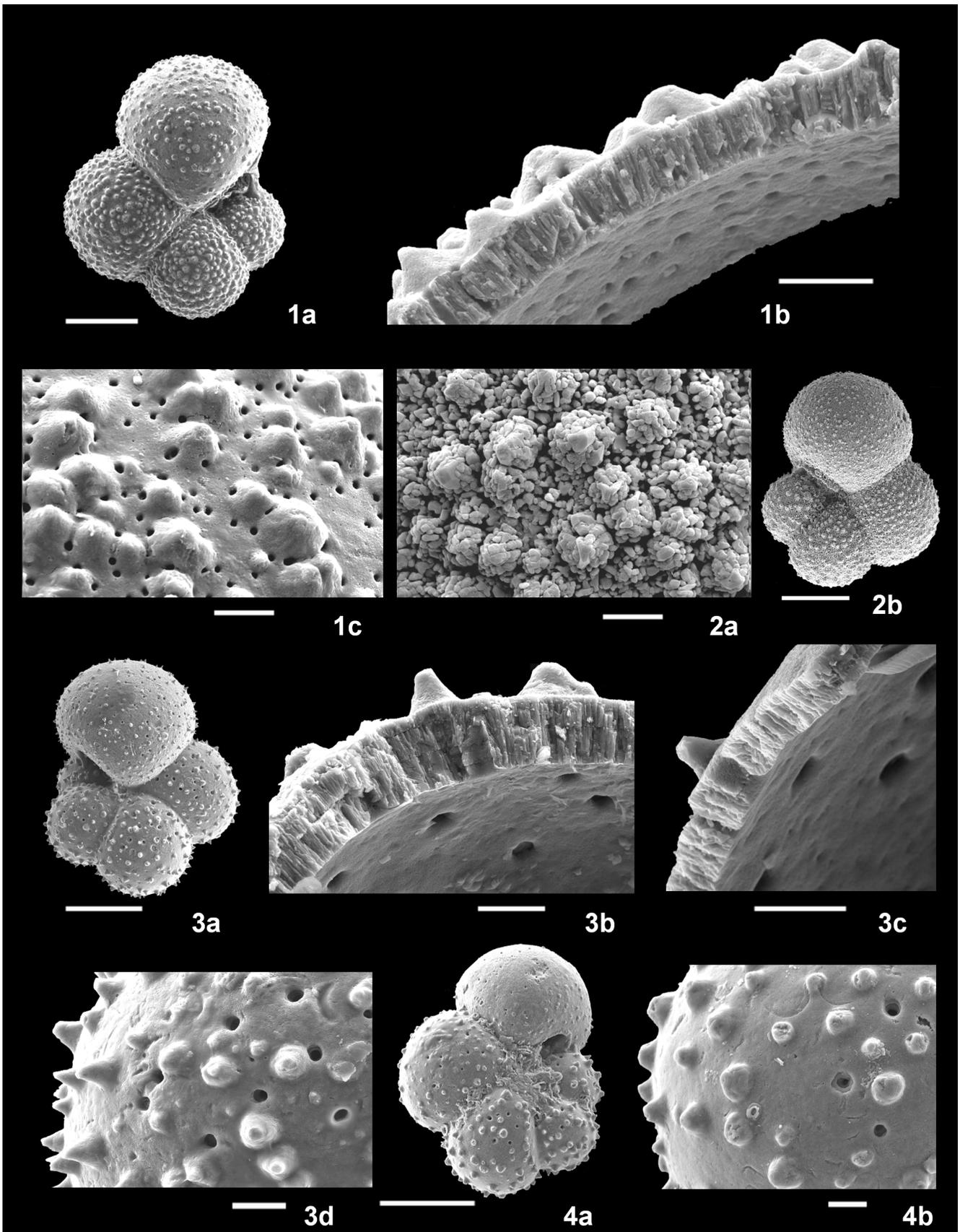


PLATE 15.2 *glutinata*-type and *danvillensis*-subtype walls, Oligocene, with diagenetic modification

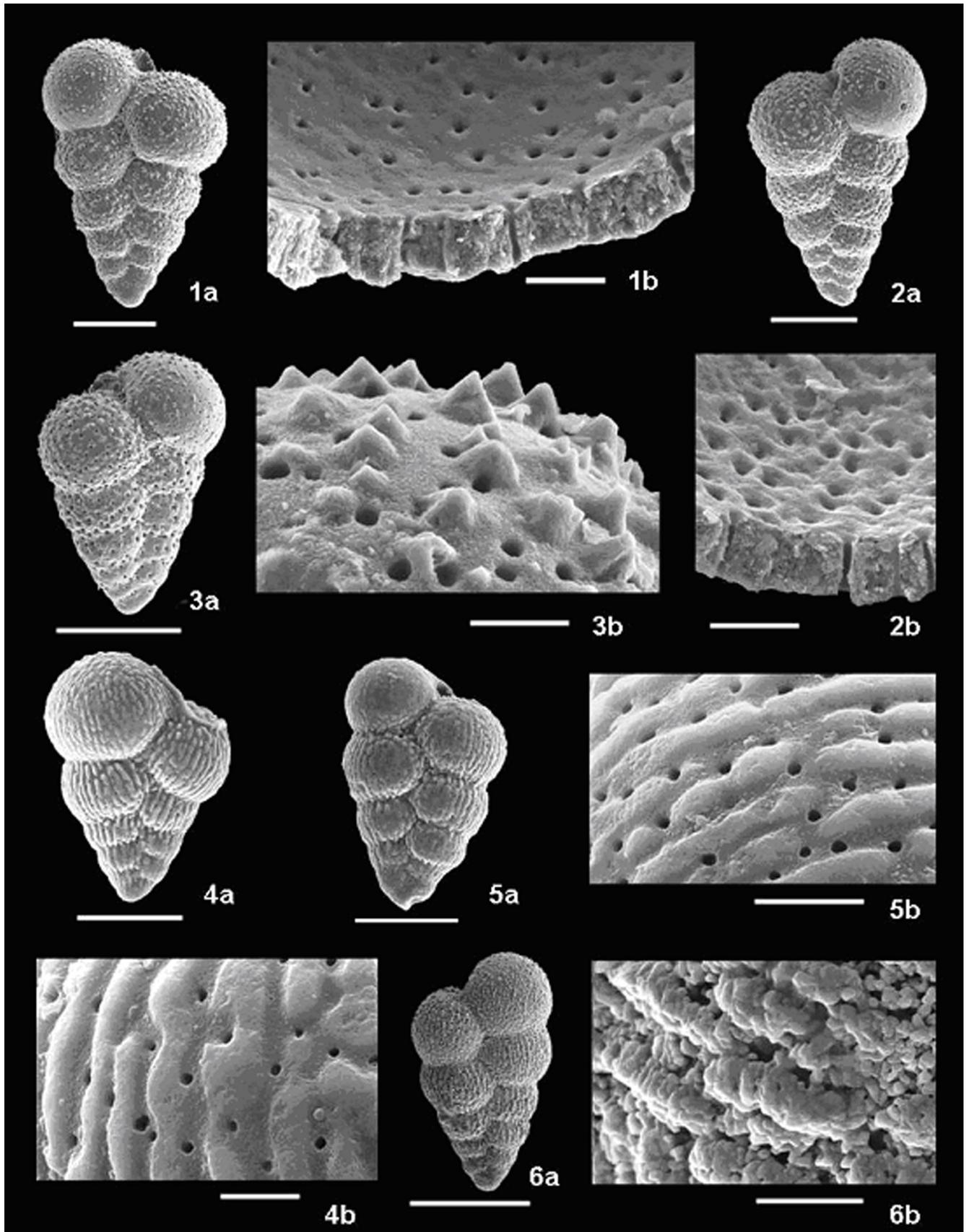
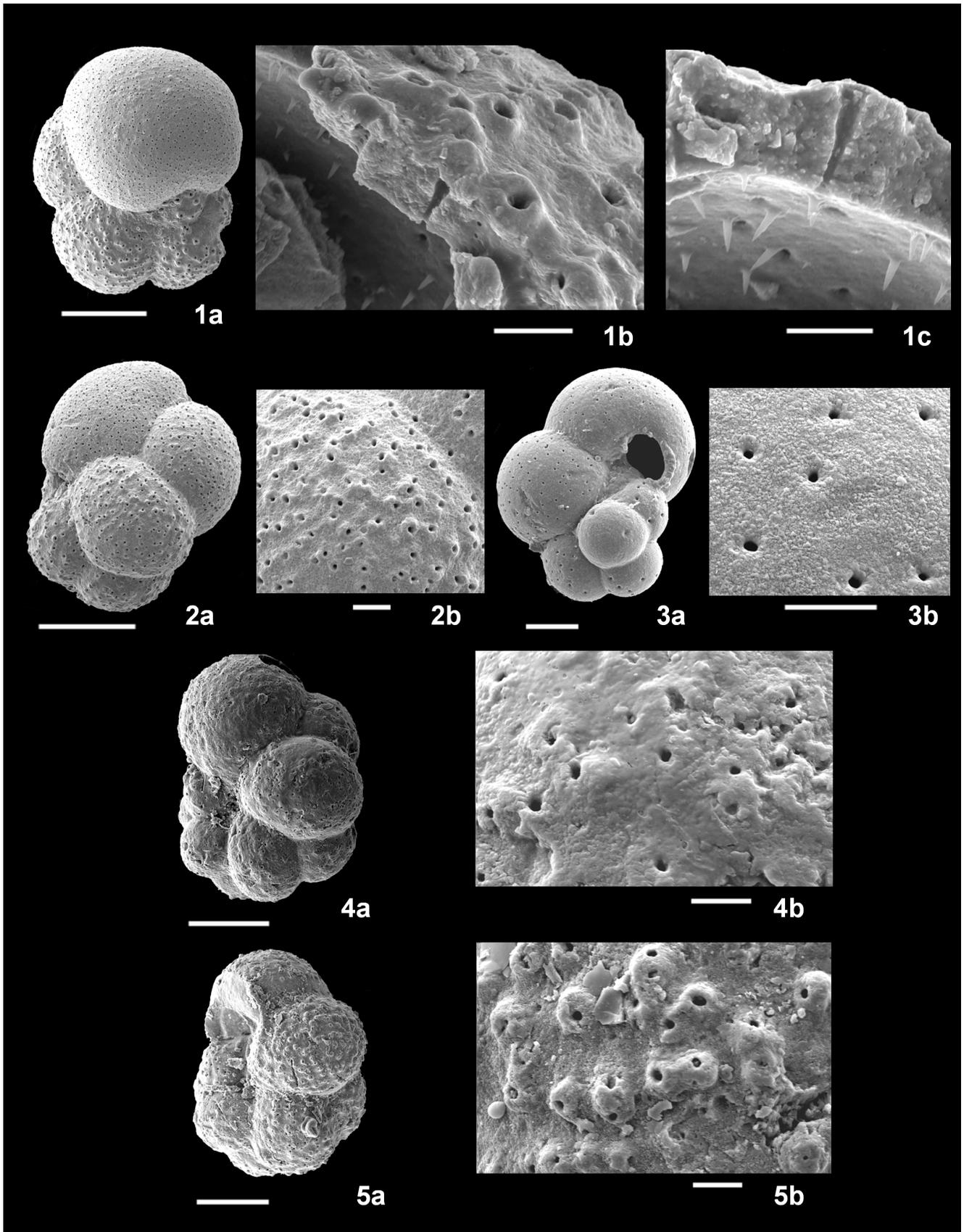


PLATE 15.3 *ototara*-type wall, Oligocene



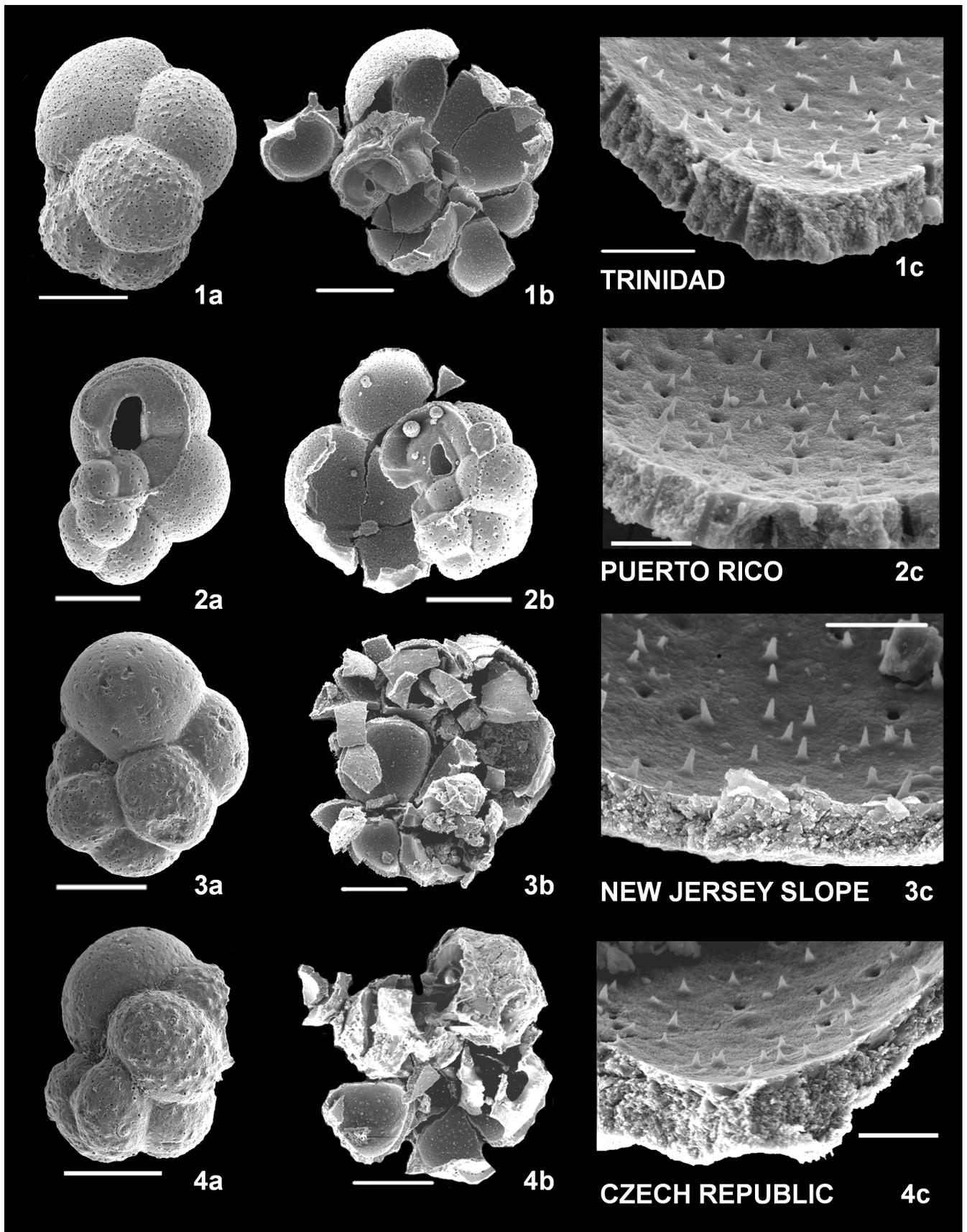


PLATE 15.5 *chipolensis*-subtype wall, Oligocene

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