The structure and taxonomic position of *Millettia* Schubert, 1911 (Foraminiferida)

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ABSTRACT
The study of opened specimens of *Millettia* species confirms the presence of septula subdividing the individual chambers. Toothplates are present between the individual septular foramina, and the chamber foramen. Polished and etched sections show the test to be bilamellar, but secondary lamination is absent. The toothplates are monolamellar and made up of inner lining, each one continuous with the septula which are formed by doubled-up inner lining. Laterally, the internal chamber walls are covered by a web-like coating of supplementary inner lining, continuous with the septula. X-ray diffraction shows the genus to be calcitic. The genus is revised to include *M. tessellata, M. limbata* and the newly described *M. ipsithillae* and *M. polyxenae.* The monotypic Millettiidae are considered *incertae sedis* within the Rotaliina. *J. micropalaeontol.,* **11** (1): 37-46, June, 1992.

INTRODUCTION.
When Brady, 1884 described *Sagrina* (?) *tessellata*, the seemingly innocuous question mark would prove to be the steady companion of this species for a very long time indeed. The peculiar test morphology and taxonomic confusion concerning the naming of the taxon has continued to be a problem for systematists.

Howchin (1889) reported specimens of *S. limbata* from Tortonian deposits (Miocene) of Muddy Creek, Victoria, Australia

Millett (1903) discussed *Sagrina tessellata* alongside *S. limbata* Brady, 1884 and noted that the chambers are divided by transverse septa. He pointed out that this morphological peculiarity was incompatible with the genus *Sagrina* and that a separate genus might have to be created for them.

In 1911, Schubert proposed the genus *Millettia* to accommodate Brady's *S. tessellata*, having encountered a single specimen in material from the Pliocene of the Bismarck Archipelago. Silvestri (1912) pointed out that the name *Millettia* was preoccupied by Duncan, 1889 and Wright, 1899 and proposed *Schubertia* as a replacement name.

Cushman (1929) presented a detailed discussion of the history and actual morphology of the by now called *Schubertia tessellata*. He demonstrated the presence of a pronounced dimorphism in *Schubertia*. The juvenile chambers in the megalospheric generation are usually biserial and already septate, while the microspheric juvenile chambers are rectilinear and simple. In Cushman's opinion, *Schubertia* was derived from *Siphogenerina* or *Rectobolivina*.

Galloway (1933) classified *Schubertia* in the Uvigerininae.

Hofker (1951) restricted the genus *Sagrina* to include *S. tessellata* only. His thorough study showed for the first time the presence of transverse septa in the rectilinear chambers and of toothplates between the septa. He tried to explain the tessellated nature of the test by describing them as infoldings of the wall at the level of the septa, both horizontallty and vertically (Fig.1).

Loeblich & Tappan (1955) selected a lectotype for *Schubertia tessellata*, and corrected Cushman's description. They described the early stage of *S. tessellata* as being biserial and all the chambers up to the second rectilinear one as non-septate.

Reiss (1963) created the subfamily Schubertiinae to accommodate the genus.

In 1964, Loeblich & Tappan presented evidence to support the reinstatement of the name *Millettia*. The senior homonyms all turned out to be either non-available names or spelled slightly differently, i.e. *Milletia* instead of *Millettia.* Since *Schubertia* was preoccupied as well, *Millettia* was adopted as the correct name. In the description of the genus, the hexagonal pattern which marks the outer walls of the test is said to be caused by the junction of the chamberlet walls with the outer wall, the chambers being divided by horizontal and vertical

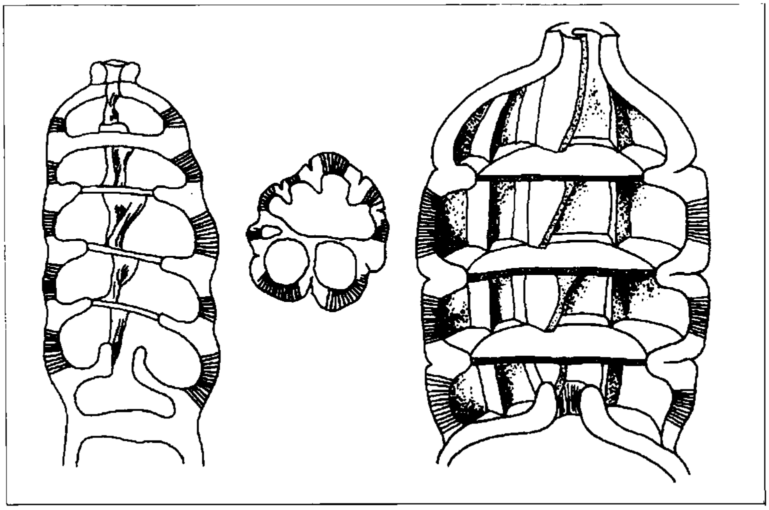


Fig 1. A reproduction of the schematic drawings presented by Hofker (1951).

partitions in a honeycomb-like pattern. *Millettia* was classified in the Eouvigerinidae.

In their latest classification, Loeblich & Tappan (1987) recognise the Millettiidae as a separate family in the Buliminacea.

SYSTEMATIC DESCRIPTION

Order **Foraminiferida** Eichwald, 1839
Suborder **Rotaliina** Lankester, 1899
Superfamily ***Incertae Sedis***
Family **Millettiidae** Saidova, 1981
Genus ***Millettia*** Schubert, 1911

non 1848 *Schubertia* Gistl: 169 [Mollusca]
non 1889 *Milletia* Wright: 448, nomen novum
non 1889 *Milletia* Duncan: 191, [Echinoidea]
non 1893 *Millettia* Sherborn: 206, nomen corrigendum pro *Milletia* Wright, sed nomen nudum
1911 *Millettia* Schubert: 90
1912 *Schubertia* Silvestri: 68, nomen novum pro *Millettia* Schubert

Definition. Test free, elongated, sausage-shaped, chambers in rectilinear series, proloculus followed by two biserially arranged chambers, later chambers rectilinear, few chambers making up the test; rectilinear chambers subdivided by septula composed of doubled inner lining, continuous with web-like covering of the internal chamber wall, septula pierced in the centre leaving a small septular foramen, toothplates connecting the septular foramina; aperture terminal, raised on a small neck, upper part phialine, aperture stellate; wall calcitic, bilamellar, no secondary lamination, test ornamented by a superficial network, pores present on top of the network only, internal structures may be resorbed at some stage of the life cycle; dimorphism pronounced.

Type species. *Sagrina* (?) *tessellata* Brady, 1884, subsequent designation by Schubert, 1911.

Millettia tessellata (Brady, 1884)
(Pl. 1, figs 1-13, Pl. 3, figs 1-5, Pl. 4, figs 1-8)

1884 *Sagrina* (?) *tessellata* Brady: 585, Pl. 76, figs 17-19
1903 *Sagrina tessellata* Brady; Millet: 273, Pl. 5, fig. 16
1911 *Millettia tessellata* (Brady); Schubert: 89
1915 *Sagrina tessellata* Brady; Heron-Allen & Earland: 677, pl. 51, fig. 9

Lectotype. ZF2359, British Museum (Natural History), London, designated by Loeblich & Tappan, 1955.

Type locality. Admiralty Islands, —17fms, *Challenger* Station 219A.

Material examined. The lectotype and paralectotype (ZF2359) from the Admiralty Islands, *Challenger* Station 219; 1958:9:15:703 from Raine Island, *Challenger* Station 185; 1955:11:1:4662 from Macassar Strait, —45fms; 1956:6:27:200-205 from the Malay Archipelago; Macassar Strait ex coll. Sidebottom; Raine Island ex coll. Heron-Allen & Earland; and from *Challenger* Type Slide TS C27, square 23; all British Museum (Natural History), London. Phuket, Thailand, Andaman Sea, courtesy H.J. Hansen, University of Copenhagen.

Description. Test free, elongate, cylindrical, coiling axis commonly arcuate, curved nature of the test due to skew joining of the chambers, circular in endview, periphery regularly constricted at the junction of the chambers, first two chambers biserial, later chambers in a rectilinear series; chambers cylindrical, chambers straight, width gradually but only slightly increasing, rapidly increasing in height; sutures circular, not very clear, slightly depressed; aperture terminal, stellate, on a low neck with a somewhat thickened, everted lip, lip marked by grooves; chamber lumen subdivided by septula of doubled inner lining, lateral wall covered by a web-like thin tessellated pattern, made up of inner lining, number of septula per chamber increasing during ontogeny, septula thin, each pierced by a central foramen, successive septular foramina connected by a toothplate originating under the septular foramen, and fusing with the simple septular foramen, at the septal end fusing onto the foraminal everted lip; toothplates almost triangular, slightly curved into a trough, at the bottom rather narrow, commonly both edges free but one edge may fuse with the lateral chamberwall later in ontogeny and form a single vertical partition in the lumen; wall calcitic, hyaline, no secondary lamination, ornamented by a superficial tessellated pattern, only the tesselae perforate.

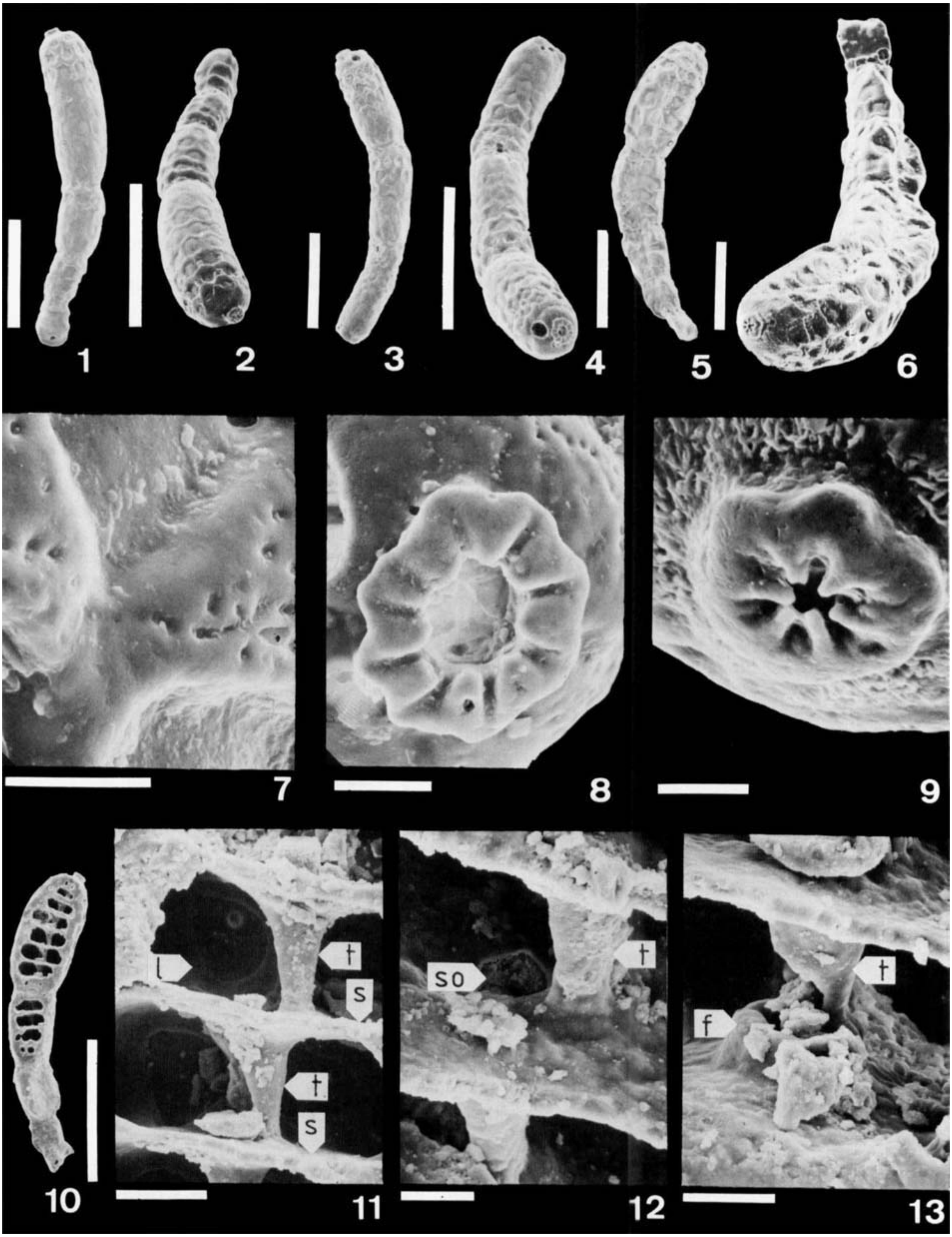
Remarks. A clear dimorphism is present in the species. the microspheric generation differs from the described megalospheric one in the smaller initial part of the test, in possessing an aperture which is present on a much lower neck, and which is obstructed by guttae originating in the thickened lip overhanging the aperture. Furthermore, the test bears a single, conspicuous longitudinal constriction, running continuously over all chambers. This constriction may be reflected in the lumina of the chambers by the presence of a protruding plate, which in the later chambers fuses laterally with the toothplates. Although it is continuous with the inner lining and eventually also with the toothplates, it should be distinguished from the latter.

Millettia ipsithillae sp. nov.
(Pl. 2, figs 1-4)

Holotype. ZF4956, British Museum (Natural History), London

Explanation of Plate 1

Millettia tessellata.
Figs 1, 2, Lectotype, BM(NH) ZF2359; **Fig. 1.** Habitus (200μm); **Fig. 2.** Oblique view, offsetting the superficial hexagonal ornamentation (200μm); **Figs 3, 4**, ZF4953; **Fig. 3.** Habitus (200μm) of a megalospheric individual; **Fig. 4.** Oblique view, showing the ornamentation (200μm); **Figs 5-9**, ZF4953; **Fig. 5.** Habitus of a microspheric individual (200μm); **Fig. 6.** Oblique view (100μm); **Fig. 7.** Close-up of the ornamentation, showing the presence of pores on the ornamented surface only (10μm); **Fig. 8.** Aperture of the megalospheric specimen of Gi. 3. (10μm); **Fig. 9.** Aperture of the microspheric specimen of Fig. 5 (10μm); **Figs 10-13**, ZF4955; **Fig. 10.** Opened specimen, showing the overall internal organisation (200μm); **Fig. 11.** Close-up of the lumen of the final chamber, showing the septula (s), toothplates (t), and the extra internal layer (1) on the test wall (25μm); **Fig. 12.** Close-up of a toothplate and its relation to the septular opening (so) (10μm); **Fig. 13.** Close-up of the toothplate and its attachment to the foramen (f) (10μm). **Figs 3-13** from Port Blair ex. T.S. C27.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Type locality. Macassar Strait, 45fms, ex Earland coll.
Description. Test free, cylindrical, circular in endview, axis of the test arcuate, except for the first few chambers arranged in rectilinear series; chambers cylindrical, with an almost constant diameter, becoming longer throughout ontogeny; sutures circular, depressed, not well defined; aperture terminal, on a slender straight short neck without an everted lip, but clearly grooved; wall calcitic, hyaline, porosity unclear, ornamented partially by an ill-defined hexagonal low network of raised ridges, close to the apex of each chamber becoming scale-like in the form of stacked tiles.
Remarks. Differs from the other species by being very elongated and slender, by possessing proportionally longer chambers, a very fine covering of the test wall, and by possessing scale-like protrusions close to the apex of each individual chamber.

Millettia limbata (Brady, 1884)
(Pl. 2, figs 5-9)

1884 *Sagrina limbata* Brady: 586, pl. 113, fig. 14
1889 *Sagrina limbata* Brady; Howchin: 11, pl. 1, fig. 7
1903 *Sagrina limbata* Brady; Millett: 273, pl. 5, figs 17-19
Lectotype. ZF4957, British Museum (Natural History), London, herein designated.
Type locality. Raine Island, Torres Strait, *Challenger* Station 185.
Material examined. ZF 2351, the syntypic series; 1958:9:15:677-680, Raine Island, 1955:11:1:4630-4642, Port Darwin, N Australia; 1956:6:27:209-219, Raine Island; TS C28, square 2, Raine Island. Raine Island, Muddy Creek, Timor; Macassar Strait,—45fms; ex coll. Earland; Torres Strait, ex coll. Millett; Raine Island, 155fms; Torres Strait, ex coll. Heron-Allen & Earland; all British Museum (Natural History), London. Nobori Formation: Pliocene, Japan.
Description. Test free, elongate, laterally compressed, cylindrical, elliptical in endview, a single fold running along the entire test gives it a nicked appearance, periphery flush, axis of the test may occasionally be arcuate, normally straight, earliest part may be biserial but most chambers arranged in a rectilinear series; chambers subcylindrical, straight, slightly if at all inflated, gently increasing in width during ontogeny; sutures circular, depressed, not very clear; aperture terminal, produced on a very low neck with an everted lip, lip marked by irregular grooves; wall calcitic, hyaline, perforate, pores restricted to the low ornamentational ridges, ornamented by annular ridges, annuli connected by a single longitudinal ridge, running in a fold, number of annuli per chamber increases during ontogeny.
Remarks. Differs from *M. tessellata* in the annular ornamentation rather than a tessellated pattern and in being more flaring. The test is generally also more straight rather than arcuate.
As is the case for *M. tessellata*, a clear dimorphism is present in this species and it is identical to that described for *M. tessellata*, except that the longitudinal furrow does not occur in *M. limbata*.

Millettia polyxenae sp. nov.
(Pl. 2, figs 10-15)

Holotype. 1958:8:9:15:677, British Museum (Natural History), London.
Type locality. Raine Island, *Challenger* Station 185.
Material examined. The holotype, also BM(NH) ZF 4956, Timor Sea, off Java
Description. Test free, elongate, elliptical in endview, longitudinal axis arcuate, chambers in rectilinear series except the first ones, periphery clearly lobulate; chambers compressed laterally, broadly ovate, becoming more elongate throughout ontogeny; sutures circular, depressed; aperture terminal, produced on a short thick neck, neck ill delimited, with a broad, slightly everted lip, aperture grooved; wall calcitic, hyaline, pores concentrated along a central band running over the consecutive chambers, ornamented by barely visible annular ridges connected by a longitudinal band.
Remarks. Differs from the other species in possessing large, laterally flattened chambers, and in being distinctly constricted at the sutures. Because of the very low nature of the ornamentation, it is uncharacteristically smooth for the genus.

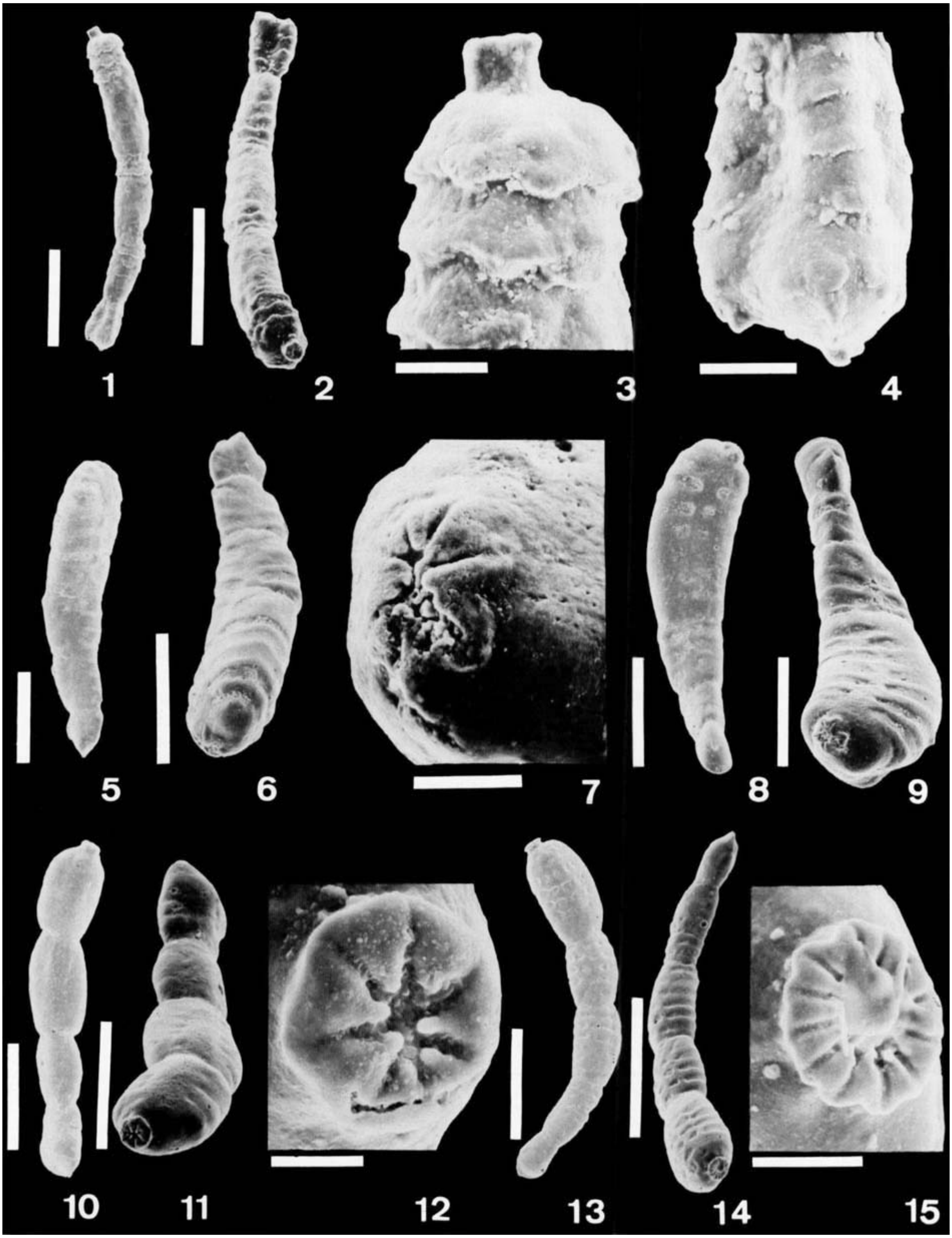
DISCUSSION

Despite recurrent attempts to understand the genus *Millettia*, it has been eluding systematists ever since its original description. The vacillations of the genus in the different classifications proposed over the years clearly indicate the difficulties it has been causing. The observations reported here on the ultrastructure underlying the complex internal morphology only confirm earlier experienced ungainliness and do little to alleviate the problematic status of the taxon.

Morphologically speaking, *Millettia* shows some affinities to buliminid genera such as *Siphogenerinoides*. The elongated

Explanation of Plate 2

Figs 1-4, *Millettia ipsithillae.*
Holotype, BM(NH) ZF4956. **Fig.1.** Habitus (150µm); **Fig. 2.** Oblique view, offsetting the scale-like nature of the ornamentation (150µm); **Fig. 3.** Close-up of the apertural end, with the pronounced stacked ornamentation (25µm); **Fig. 4.** Close-up of the prolocular end, again with the scale-like ornamentation and showing the comparatively small proloculus (25µm).
Figs 5-9, *Millettia limbata.*
Lectotype, BM(NH) ZF 4957. **Fig. 5.**Habitus (150µm); **Fig. 6.** Oblique view, showing the annular ornamentation (150µm); **Fig.7.** Close-up of the aperture. Note its irregular nature and the absence of a clearly defined neck (25µm). Topotype, BM(NH) ZF 4958; **Fig. 8.** Habitus (150µm); **Fig. 9.** Oblique view, stressing the annular ornamentation (100µm).
Figs 10-15, *Millettia polyxenae.*
Holotype, BM(NH) 1958: 9: 15: 677 . **Fig. 10.** Habitus (150µm); **Fig. 11.** Oblique view, showing the low and unpronounced ornamentation (100µm); **Fig. 12.** The aperture (10µm). Timor Sea, off Java BM(NH) ZF XXXX; **Fig. 13.** Habitus (250µm); **Fig. 14.** Oblique view, showing the ornamentation as intermediate between annular and hexagonal (250µm); **Fig. 15.** Aperture (25µm).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test, the rectilinear arrangement of the chambers, the aperture produced on a neck and the presence of toothplate-like structures in *Millettia* does point to a buliminid parentage. However, the subdivision of the individual chambers by septula, the presence of septular foramina linked to the toothplates and the extension of the septula onto the lateral chamber wall in a web-like fashion are without counterpart in the buliminids (Pl. 1, figs 10-13).

The use of etched sections results in even more surprises. Although the test wall is basically bilamellar, secondary lamination is absent (Pl. 4, figs 7, 8). An important part of the test is actually trilamellar due to the deposition of an extra layer of inner lining inside the chamber lumen (Pl. 4, figs 2, 4, 8). The construction of the septula leads to a partial doubling of the inner lining on the lateral chamber walls, and to a doubled inner lining which form the actual septula (Pl. 4, figs 2, 4). Doubled-up inner linings are known only in *Elphidiella* and *Asterigerina* (see Hansen & Reiss, 1972 and Hansen & Lykke Andersen, 1976). Contrary to these genera, the features in *Millettia* linked to the double inner lining do not serve to isolate part of the chamber lumen: there is no analogy to the morphological elements in either *Elphidiella* (i.e. subsutural canal) or *Asterigerina* (stellare chamberlets). The ultrastructure of the wall is also highly unusual. *Millettia* appears optically radial under polarised light, and this observation is confirmed by the actual disposition of the individual crystal elements. What is unusual is the apparent inability of the organism to bend round corners when depositing chamber wall: the elongated crystals either form twins or leave a discontinuity which shows up prominently in the etched sections. This is very well illustrated in the construction of the aperture and the test wall in the immediate surroundings. This peculiar feature enhances the unusual construction pattern of the successive 'chamberlets' (Pl. 4, figs 2, 3, 4, 8).

The detailed mapping of etched specimens gives some indication as to the order in which the test may be built. Apparently, a chamber is constructed a 'chamberlet' at a time. Tracing the different layers, it appears that a break is present in the outer lamella as well as in the inner lining between each 'chamberlet': younger 'chamberlets' seem to rest on top of the previous one (see Pl. 4).

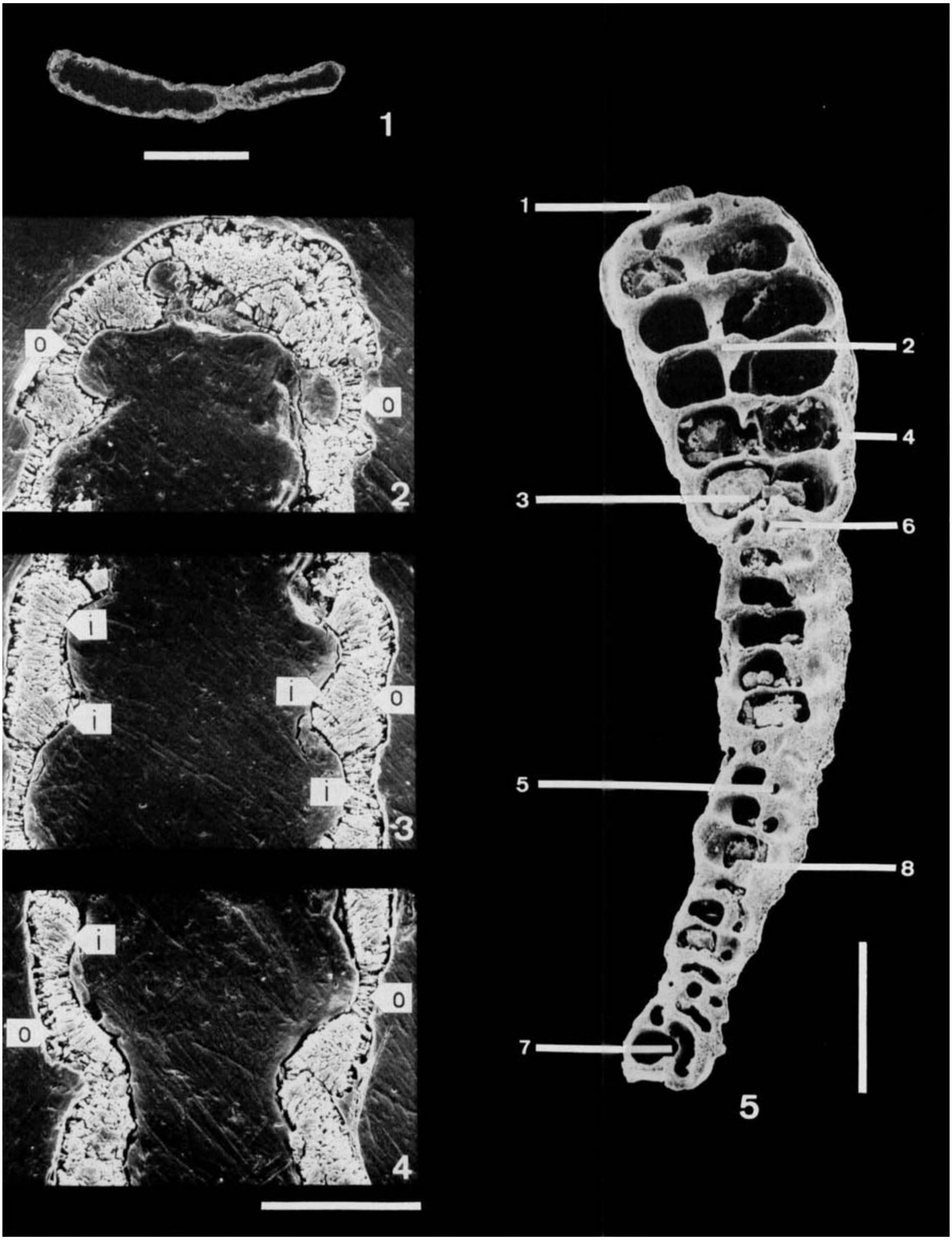
Also, resorption of the internal partitions seems to occur quite often, leaving the lumina completely empty (Pl. 3 fig. 1). The stripping away of inner lining seems to extend even to the inner lining belonging to the lateral chamber wall, leaving only outer lamella in some places (Pl. 3, fig. 2, 4). Contrary to *Buliminoides*, in which considerable resorption takes place as well, the aperture in *Millettia* is not modified in the process (compare Pl. 1, figs 8 & 9 with Revets, 1989, Pl. 5, fig. 5). As is the case for the former, resorption may be linked to reproduction, but at the present time not enough information nor specimens are available to substantiate this hypothesis. Extensive resorption, together with the occurrence of porefields, (i.e. the pores are clustered on the raised anastomosing network overlying the outer test wall and absent from the 'windows' in between) immediately suggests an affinity to aragonitic taxa (see Hansen, Reiss & Schneidermann, 1969 and Hansen, 1979). However, X-ray diffraction shows beyond doubt the calcitic nature of *Millettia*.

As a result, *Millettia* shows some similarities with respectively Robertinid (porefields, resorption, peculiar deposition of $CaC0_3$), Buliminid (Seriality, aperture and presence of toothplates) and Nodosariid (Absence of secondary lamination) taxa. Because of this unique combination of characteristics, *Millettia* cannot be placed in any of these. I therefore propose to retain the genus in its own family and to consider the Millettiidae *incertae sedis* within the Rotaliina. Because of the current ongoing revisions of the toothplate-bearing taxa, it is deemed premature to recognise a separate superfamily for this enigmatic genus.

Despite the fact that relatively few specimens were available for study, an evolutionary scheme within the genus can tentatively be put forward (Fig. 2). The morphological features of *M. ipsithillae* clearly indicate it as being further removed from the other species. Its very slender nature and quite deviating ornamentation support this claim. Nevertheless, the aperture and the partial occurrence of the hexagonal sculpturing shows its relation to *M. tessellata*. *M. limbata* stands also a bit apart, mainly because of its rather dumpy nature and the different aperture. Contrary to other species, *M. limbata* has a non-hexagonal ornamentation pattern and an aperture that is not really clearly produced on a neck. Also, the delimitation of the apertural opening is much more irregular. As a result, it is an unlikely ancestor for the genus. Since only *M. tessellata* and *M. limbata* have a fossil record, the most likely candidate for stem species of the genus seems to be *M. tessellata*. The real difficult resides with the position of *M. polyxenae*. Because it combines features of the three other species, it may well be a case of parallelism or the beginning of iterative evolution. The finding of a specimen of *M. limbata* from Pliocene deposits of Japan seems to point to a geological history of unsuspected interest and diversity. Unfortunately, not enough sightings of these species have occurred to resolve the many tantalising questions.

Explanation of Plate 3

Millettia tessellata.
BM(NH) ZF4960, Port Blair. Polished and etched section through a specimen that has undergone resorption.
Fig. 1. Overview, showing the emptied lumina (200μm).
Figs 2-4. Close-ups of different parts of the final chamber, showing the various degrees of removal of lamellae [(i): inner lining; (o): outer lamella] (25μm).
Fig. 5. BM(NH) ZF 4961, Sulu. Polished and etched section, dissolved out of the Lakeside Cement. Overall organisation of the test (the numerals refer to the close-ups depicted in Pl. 4 (the outermost layer, peeling off in some palces is the remnant of a prior coating with Au and should not be mistaken for an organic outer layer) (100μm).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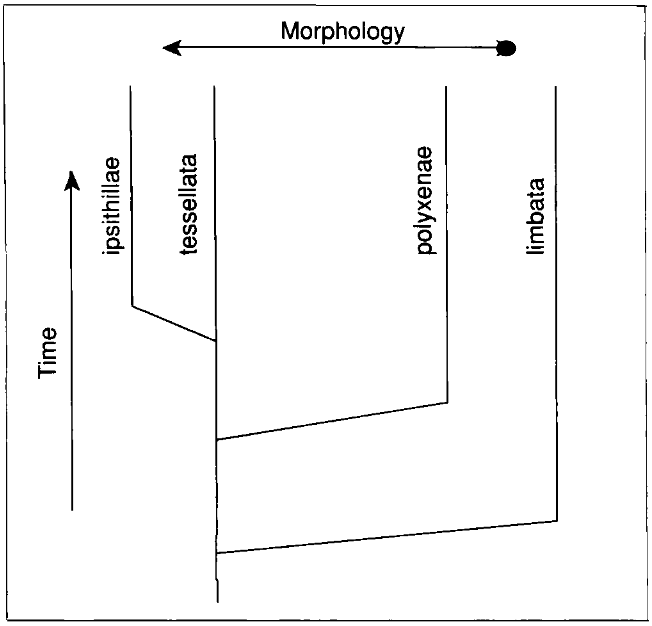

Fig. 2. A likely phylogeny of the different *Millettia* species.

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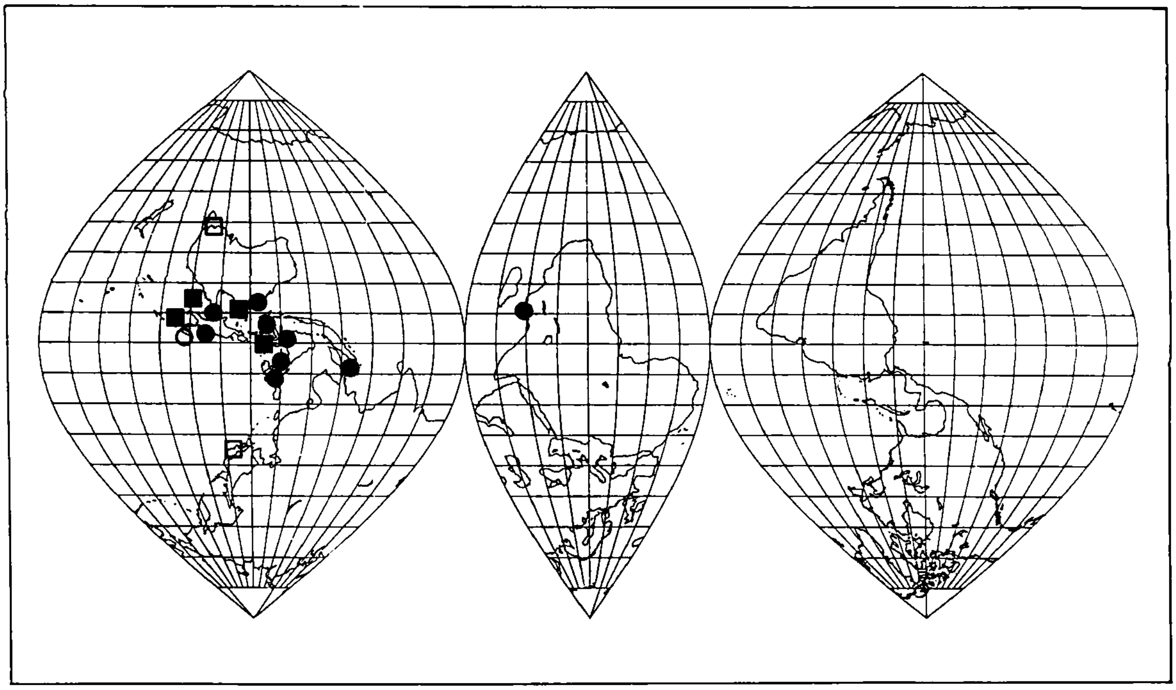
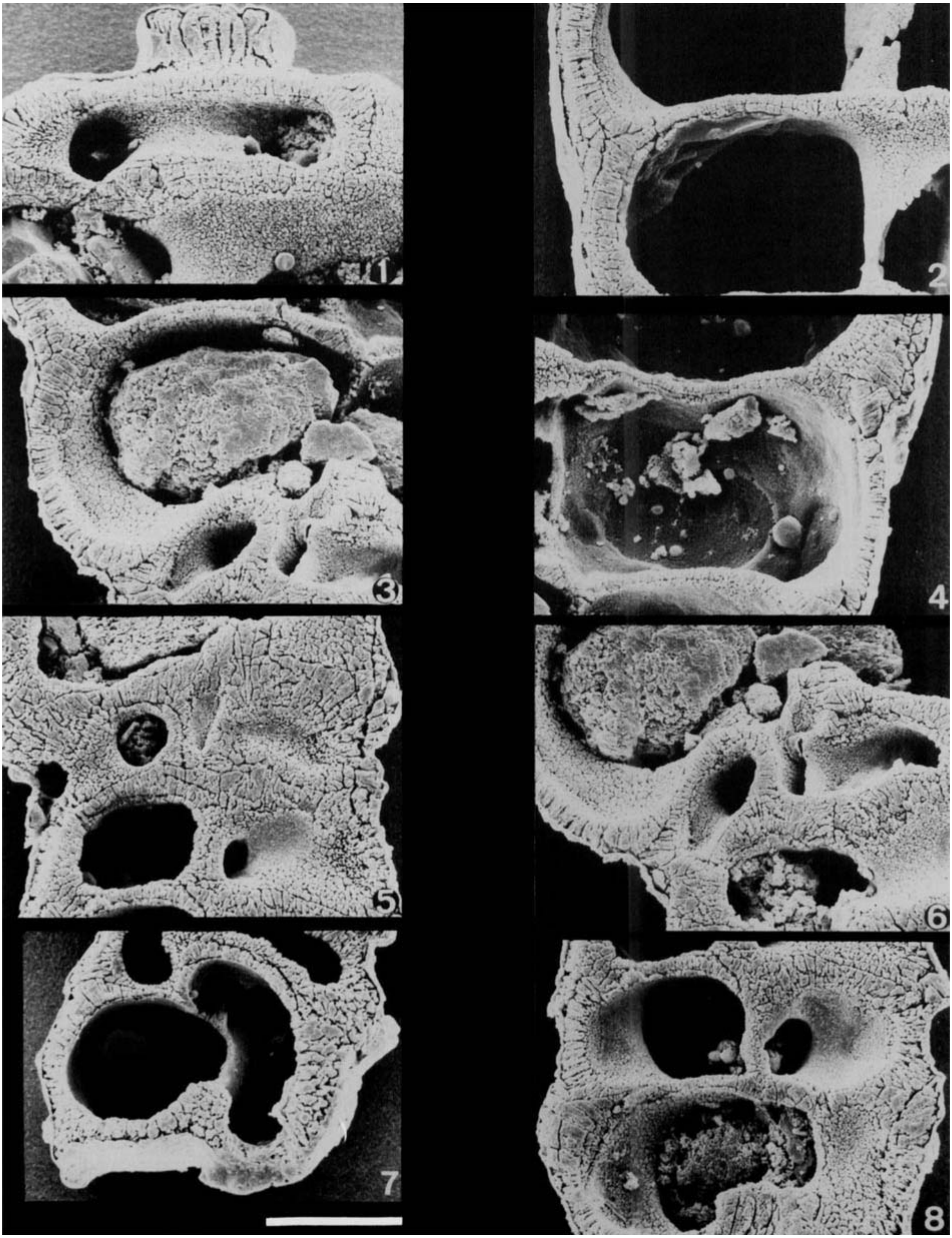


Fig. 3. The biogeography of *M. tessellata* (fossil O, Recent ●) and *M. limbata* (Fossil □, Recent ■)

Explanation of Plate 4

Millettia tessellata.

Close-ups of section BM(NH) ZF4961 (25μm). **Fig. 1.** Apertural region. The etching shows the peculiar organisation of the crystal elements making up the apertural neck; **Fig. 2.** The succession of septula dividing the chamber. Note the bilamellar outer wall, and continuation of the inner lining into the septulum and toothplate; **Fig. 3.** The region of a foramen. The crystal elements of the side wall tend to form twins, rather than bend along the jointure; **Fig. 4.** Part of the chamber lumen, with the internal coating clearly shown. Note also how this extra layer is painted onto the normal inner lining and shows up at the edge as a third layer. Note also the continuity between this layer and the septula and toothplates; **Fig. 5.** The region of an earlier foramen, showing very clearly the disposition of the individual crystal elements making up the wall; **Fig. 6.** Foraminal region, showing the peculiar relation of the spaces made by the septula and the final space giving access to the aperture; **Fig. 7.** Proloculus. Note the well defined deuteroconch. This photograph also clearly demonstrates the absence of secondary lamination; **Fig. 8.** Section through the fourth chamber, with at the bottom the foramen. Note the twinning of crystals ocurring at the left hand side. Note also the absence of secondary lamination.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