

REVIEW ARTICLE

The Foraminiferal Toothplate, A Review

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ABSTRACT

The concept of the foraminiferal toothplate and the way in which this has changed through time is laid out. Historical developments are contrasted with more recent information. Ultrastructure and lamellarity are used to define and differentiate the toothplate from other internal anatomical elements. The function of the toothplate in the test remains an enigma. *J. Micropalaeontol.* **12** (2): 155-168, December 1993.

INTRODUCTION

The context

Recent developments in ultrastructural and morphological studies of smaller benthic foraminifera have caused a watershed in foraminiferal taxonomy. The routine use of the SEM to observe sections, half-sections, etched specimens and casts have substantially increased the amount of available information. Concurrently, a plethora of new names has been proposed to describe the features observed. This has resulted in a bewildering array of terms, the definitions of which are seldom precisely stated and, if they are defined at all then they tend to denote different things to different authors.

Glossaries have been assembled (Loeblich & Tappan, 1964, 1987; Hottinger *et al.*, 1991) in an attempt to unify usage by defining terms unambiguously, but because these glossaries are based on selections lifted from the literature in general rather than on primary observations, their quality and authority is mixed.

The internal structure commonly known as the toothplate is a case in hand. Because of the likely importance of the toothplate in the understanding of the morphology of the foraminiferal test (with all the ramifications this entails), an attempt will be made here to analyse the toothplate historically, morphologically as well as structurally. Because of the changes, subtle or substantial, over the years as to the concept of the toothplate, other structures with which it has been equated will be analysed as well in order to clarify its position.

Historical overview

Internal structures were observed and commented upon in a variety of pleurostomellid taxa, and this from a very early date onwards. Seguenza (1859) described *in extenso* a tube present between foramen and aperture in *Ellipsoidina*. This was later confirmed and expanded upon by Brady (1868; see Fig. 1). Surprisingly, Brady (1884) failed to link

Pleurostomella with *Ellipsoidina* and did not refer again to internal structures. Silvestri (*op. var.* 1900-1904) also painstakingly documented the presence and form of the 'tronchi tubulari' in *Ellipsoglandulina*, *Ellipsopleurostomella* and *Ellipsopolymorphina* (Figs. 2 & 3). In the same vein, the description of *Ellipsoidella pleurostomelloides* by Heron-Allen & Earland (1910) is surprising because it clearly documents the presence of an internal structure, but no attention is really given to it.

Equally surprising, earlier authors failed entirely to report internal structures in what are now commonly known as the buliminids. Williamson (1858) was unaware of any internal structures in the buliminids, despite the trouble he obviously took of embedding specimens in Canada balsam. He did comment on the peculiarity of the aperture, i.e. the fact that one lip disappears behind the other. Although Carpenter (1862), assisted by Parker and Jones, was the first to seriously study the internal structures of an appreciable number of taxa, as far as the buliminids were concerned he only confirmed the statements made earlier by Williamson, and he too apparently did not notice the presence of toothplates. Heron-Allen & Earland in their various publications also never referred to (and hence noticed?) the presence of anything inside the lumen of the buliminids.

This lack of attention then continued for more than half a century. The first mention of the toothplate as a structure by Cushman was when he indicated the presence of an internal tube when describing *Siphogenerina* (Cushman, 1913). Although it was alluded to in passing in his first major classification proposal (1927), Cushman never devoted much attention to this structure. Even in the revisional study of the Virgulinae he paid no particular attention to the possible internal structures of the taxa (Cushman, 1937). Although mentioned, the presence or shape of the internal spiral tube in *Virgulina* and *Bolivina* was not used in the descriptions of the individual species nor were figures provided to illustrate this feature.

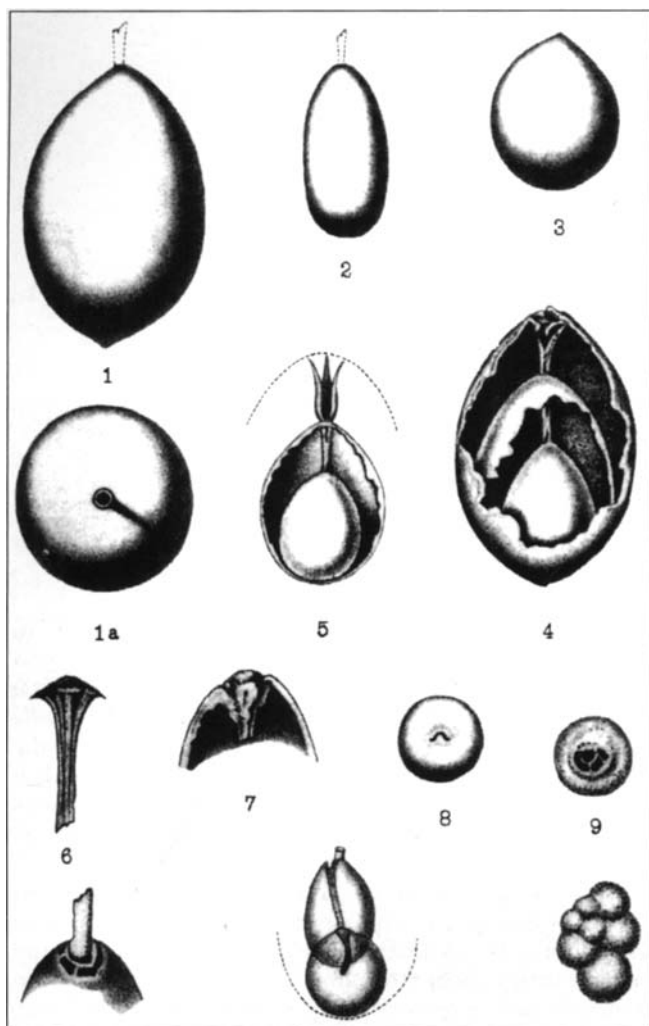


Fig. 1. A reproduction of the drawings by Seguenza (1859) and Brady (1868) of *Ellipsoidina ellipsoidea*. Brady retraced some of Seguenza's original drawings and added his own new observations. The specimens drawn are housed in the BM(NH) and show the great accuracy of Brady's drawings.

The mentioning of the toothplate in passing by Cushman was followed by most researchers following him in time. Galloway (1933) and Glaessner (1945) went barely beyond the remarks made by Cushman although Galloway used "the presence of a tooth in the aperture which extends down onto the preceding chamber as an undulating column" to differentiate the Bulimininae from the Turrilinae. He also implemented the figures of the pleurostomellids, including in the descriptions of the genera the presence of 'a grooved calcareous ribbon' or 'a calcareous column' (Galloway, 1933).

The first serious study of the toothplate is by the hand of Höglund (1947). Through the observation of specimens immersed in clearing oils, he was able to accurately draw what he termed the tongues in *Bulimina*, *Globobulimina* (Fig. 4) and what was to become *Stainforthia* (Fig. 5). However, Höglund did not go beyond the recording of the features of

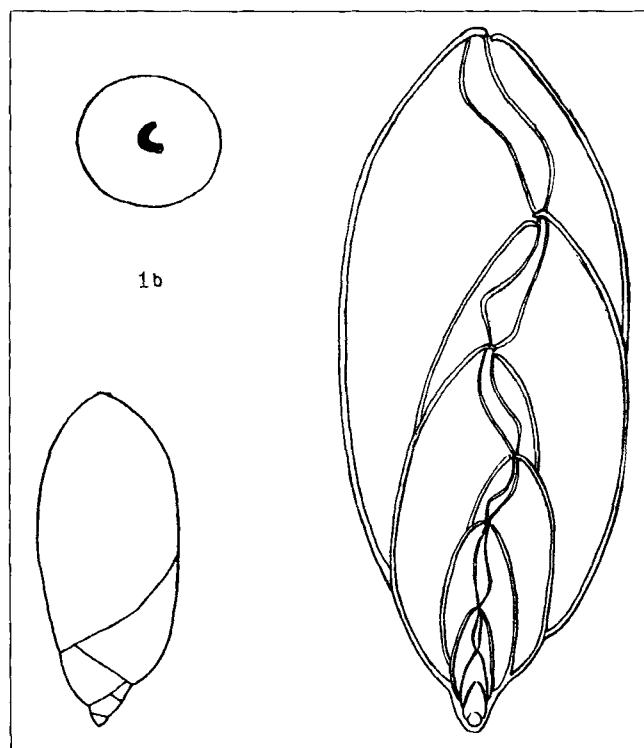


Fig. 2. A reproduction of the type drawings of *Ellipsopolymorphina* by Silvestri (1901), with the very prominent toothplate running between the successive foramina.

the toothplate, he did not venture any suggestions as to its possible function nor did he attempt to use it for taxonomic purposes. Contrary to later authors, he refrained from using terms as toothplate or tongue in the description of *Robertina* and *Robertinoides*, both aragonitic forms (Fig. 6).

The major breakthrough as far as the use of the toothplate in foraminiferology is concerned happened when Hofker turned his attention to the internal organisation of foraminifera. In 1951, Hofker defined the toothplate as:

"a peculiar inner structure, a more or less developed, often contorted plate, running from a former, now septal foramen to the next one, through a chamber. This plate is often attached with one of its sides to the axial wall of a chamber, and shows an often folded free border on the opposite side, which in many cases is ornamented by typical denticulations or other structures." (Hofker, 1951a, p. 353).

In a single stroke, he also extended the range of occurrence of the toothplate from the buliminids (Fig. 7) to a very wide spectre of taxa, including amongst others the rotaliids, elphidiids, conorbinids, robertinids, globorotaliids, &c (Fig. 8). With the vast majority of his subsequent publications, Hofker presented a thorough comparative study in which the toothplate played a major role.

Interestingly, Smout (1954, 1955) ignored the occurrence of toothplates in the rotaliids as reported by Hofker to the point of not discussing it. But in a subsequent publication

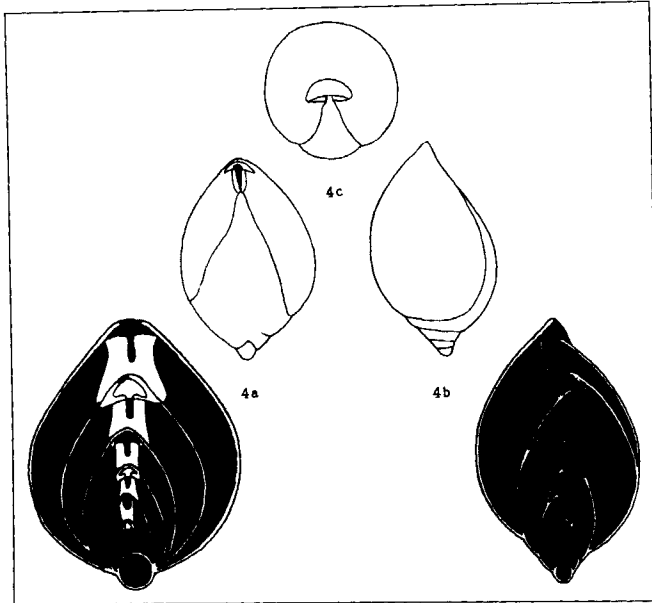


Fig. 3. Another reproduction of type drawings by Silvestri (1904), of *Ellipsopleurostomella pleurostomella*. Note especially the careful analysis of the shape of the toothplate as seen from frontal and lateral viewpoints.

(Smout, 1956), the toothplate as a structure was discussed in the light of Hofker's studies. Nevertheless, the author shied away from fully assessing the relation between toothplate and other internal structures, including canals.

In a letter to L. Hottinger, referred to by Hottinger (1967), Hofker discussed the toothplate as follows:

"Ursprünglich ist eine Zahnplatte anwesend bei den protoforaminates Foraminiferen (*Bolivina*, *Bolivina*, *Præbulimina*, etc). Hier ist es ein, an einer Seite offener Schlauch, der, am Rande eines vorigen Foramens anheftend, durch die Kammer zur Apertur und sich da wieder teilweise anheftet. In den meisten Fällen ein Rand des Schlauches der Kammerwand angeheftet, und zwar in alle den Fällen, wo die Apertur sutural ist. Wird in den Protoforaminata die Apertur areal, dann ist auch dieser Rand frei (*Loxostoma*-Formen von *Bolivina*, *Nodosarella*, etc) und läuft die Zahnplatte frei von Foramen zum nächsten Foramen.

In protoforamen rotaliid gewundenen Schalen ist die Sachlage eigentlich dieselbe. Hier kann aber weitere Drehung den Kammern verwickelte Strukturen liefern. Eine Neubildung kann schon bei mehr rezenten Buliminiden auftreten, indem der festgehaftete Teil der Zahnplatte sich aufrollt und dann, neben

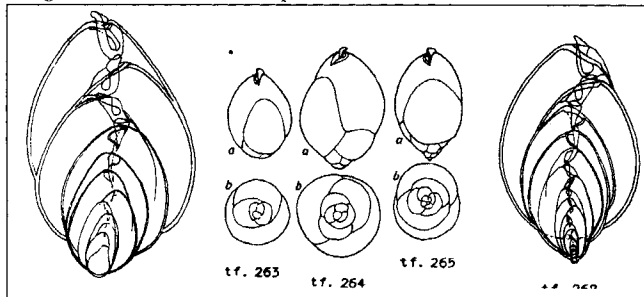


Fig. 4. A reproduction of the drawings by Höglund (1947) of *Globobulimina auriculata* var. *gullmarenensis*.

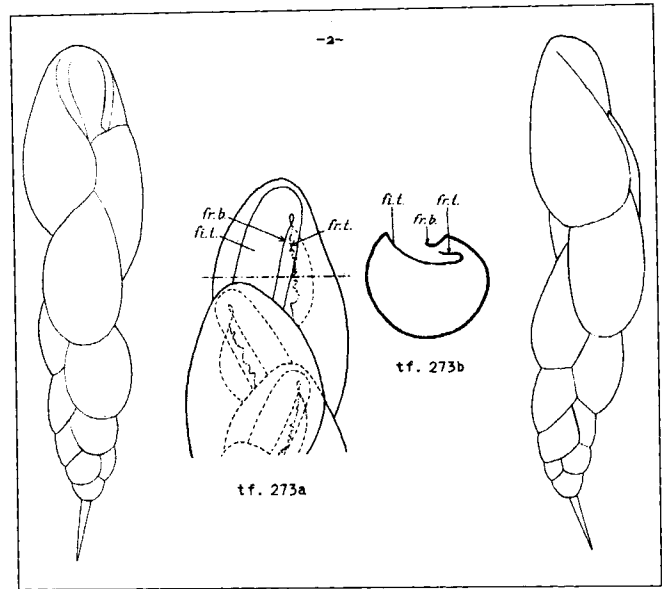


Fig. 5. A reproduction of the type figures of *Stainforthia concava* (Höglund, 1947). Note the high precision in the drawing: the 'toothplates' fuse with the previous chamber well away from the foramen. *fi.t.*: fixed tongue-plate; *fr.b.*: free apertural border; *fr.t.*: free tongue-plate.

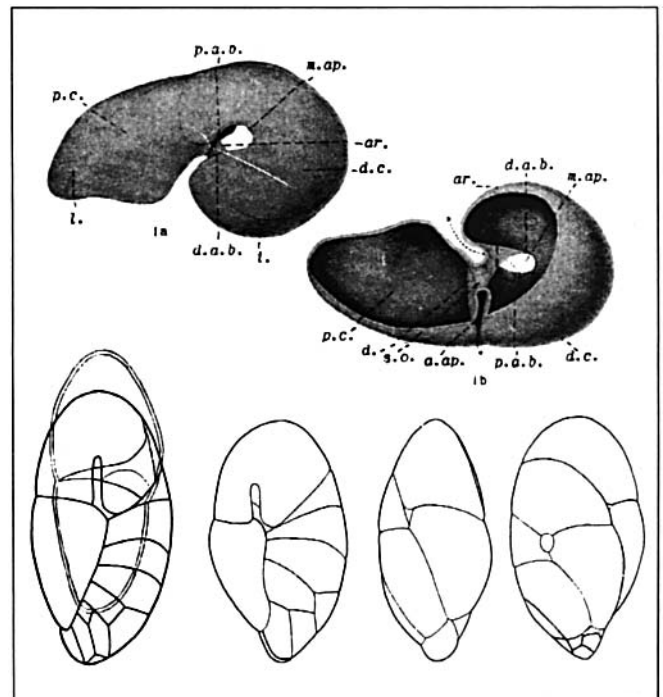


Fig. 6. Höglund's careful and precise analysis of the internal anatomy of *Robertina arctica* d'Orbigny, 1846, in which he avoids equating any of the structural features with the toothplate. *a.ap.*: accessorial aperture; *ar.*: arch; *d.*: diaphragm; *d.a.b.*: distal apertural border; *d.c.*: distal chamber-half; *i.*: insertion line of the next chamber; *m.ap.*: main aperture; *p.a.b.*: proximal apertural border; *p.c.*: proximal chamber-half; *s.o.*: saddle-shaped opening between the two halves of the chamber.

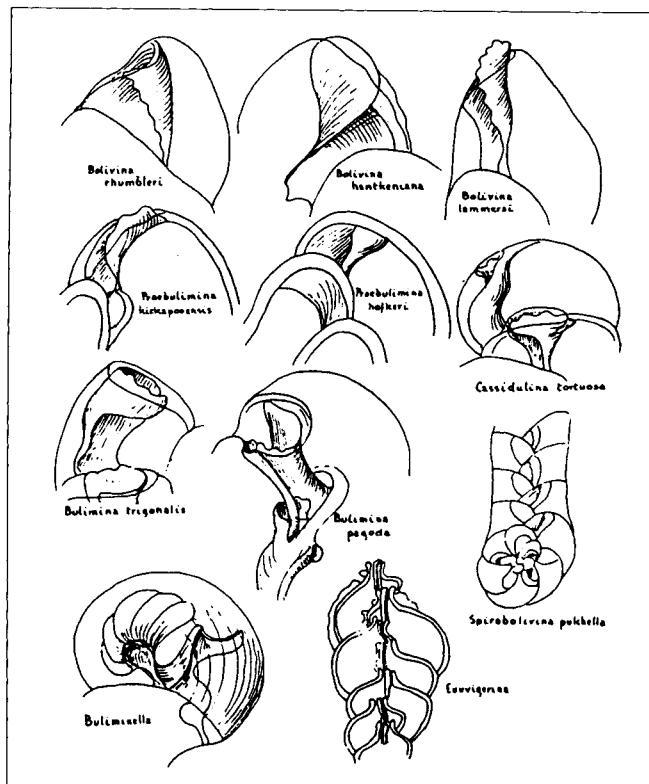


Fig. 7. A selection of drawings of buliminid toothplates by Hofker (1957). Note the rolled up free border in the case of *Bulimina pagoda*, and the external elements of the toothplate in *Buliminella*.

der Apertur, dieser aufgerollte Schlauch apart ausmündet mit einer kleiner Öffnung: Zahnplatten-Foramen. Solche Bildungen treten ebenfalls auf in den Epistomariidae, in *Epistomaria*, in Robertinen. In einigen Fällen werden diese Öffnungen grösser und können in den späteren Kammern von porösen Platten wieder verschlossen werden (z.B. *Robertinoides*). Bei den Deuteroforaminata ist die Zahnplatte immer mit dem Protoforamen verbunden. Auch hier treten oft verwickelte Neubildungen auf, indem die Zahnplatten sehr gross werden können, und Teile der Kammer als Sä..e oder Sekundär-Kammerchen von der Hauptmasse abtrennen können. Wenn dann noch der protoforame Teil nach aussen ein von einer porösen Platte verschlossen wird, treten Bildungen auf wie in den Asterigerinen und in *Amphistegina*. Auch hier ist die Bildes einer Zahnplatte wieder primär.

Dan gibt es noch die Möglichkeit, dass ein Teil der Zahnplatte in der Nähe der Mündung austritt und allehand extra Bildungen liefert, die immer imperforat sind. Solche Bildungen treten schon bei den Protoforaminata auf, z.B. in Globobulimininen (Segelartig) und in *Buliminella* und *Bolivina*, wo sie grosse Teile der Aperturseite der Kammerwand bilden können, welche oft Strahlenartig gestrichelt aussehen. Auch greift in *Lamarckina* ein solcher auswendiger Teil über den Nabel der Schale aus. Reduziert dann auch noch ein grosser Teil der inneren Zahnplatte, dan bleiben nur äussere Lappen, imperforat, übrig, die als Tena u.s.w. bekannt sind und über den Nabel allehand Bildungen formen können, wie die Umbilikallappen von Globigerinen und Globotruncanen. In biforaminaten Foraminiferen tritt dan oft eine Vermischung von Protoforam und

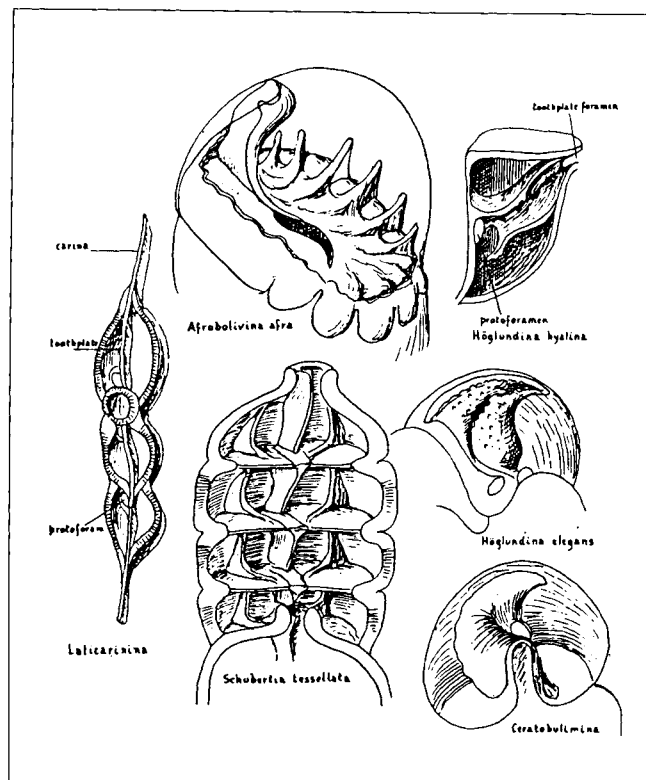


Fig. 8. A reproduction of various drawings by Hofker of non-buliminid taxa in which he recognised the presence of toothplates.

Deuteroforam hinzu (Foramen Compositum).

Bei den an *Rotalia* verwandten Gruppen kann die, noch immer am Rande eines axialen Protoforamen anfangende Zahnplatte sich dicht dem Septum einen Kammer entlang biegen. Ein Teil bildet dann oft ein Zahnplattenforamen dass im Umbilicus ausmündet und daher noch den primitiven Bau der Zahnplatte der höheren Buliminiden verrät, während eine grosse Platte dem Septum und oft anderen inneren Kammerwandteilen entlang die von Wade und Reiss als 'Septal flap' eingeführte Bildung formen. Zwischen Septum und 'Septal flap' können dann Kanäle ausgespart werden, die, zusammen mit dem Umbilicalkanal den Kanalsystem bilden, wie dieser bei reellen Rotaliden und Elphidium ausgebildet wird. Auch hier kann dann dieser Teil der Zahnplatte wieder ander Sutura Zahnplattenforamina bilden, die in diesen Gruppen sehr bekannt sind (*Pseudoeponides*, *Pseudorotalia*, *Elphidium*, etc.). Es kann dann noch die Bildung einer porösen Schliessplatte hinzukommen, wie dies in *Asterorotalia* der Fall ist.

Dies ist, im Kurzen, eine 'Definition' der Zahnplatte. Wie ich schon des öfteren erwähnt habe, ist die Zahnplatte auch schon in vielen agglutinierten Foraminiferen, den Valvulinidae, ausgebildet. Sie findet sich schon in der *Bolivina liassica* vor."

Taking his cue from Hofker, Reiss (1963) re-evaluated the toothplate, differentiating elements of the aperture or the septum from the toothplate proper (*ibid.* p. 28 et seq.). Like Hofker, Reiss was originally of the opinion that the toothplate as a structure occurs in a variety of taxa far extending beyond the buliminids. In the same vein, Reiss linked the occurrence of toothplates with the construction of

canals in low trochospiral forms (Reiss & Merling, 1958; Reiss, 1963).

Restricting the interpretation of the toothplate to the plate encountered in buliminids, Nørvang (1966, 1968) attempted repeatedly to understand the morphology and the function of the toothplate through a refined technique, avoiding some of the difficulties inherent in the preparation and observation of classical thin sections.

In a major overhaul of the classifications, Loeblich & Tappan (1964) restricted the use of the term toothplate to internal apertural modifications applicable to the buliminids only:

"Problematical also is the question as to whether all so-called tooth plate foraminifera are closely related, as postulated by Hofker. If related to a physiologic function of the animal, a toothplate may have developed at more than one time, just as similar test form, chamber arrangement, or apertural character may appear in agglutinated, porcelaneous, or hyaline lineages. In the Treatise classification, apertural tooth plate development is regarded as an advanced apertural feature which developed independently in various lines. Thus, the entosolenian tube in the Glandulinidae, the internal siphon in the Pleurostomellidae, and the tooth plates of the Buliminidae, Bolivinitidae, and Caucasinidae, or the internal partitions of the Ceratobuliminidae and Robertinidae are regarded as convergent rather than divergent features."

A few years later, the SEM became available as an observation tool (Oatley, 1966) allowing for the first time highly detailed observations at high resolutions.

Recent developments

The seminal study of the foraminiferal test wall by Towe & Cifelli (1967) demonstrated the value of the electron microscope for research attempting to analyse morphological elements and their mutual relations. The careful analyses of lamellarity patterns by Hansen and co-workers helped to resolve many standing problems.

The study by Hansen & Reiss (1971) of the rotalian wall structures gave up the use of the term toothplate in a non-bulimine context, referring to plate-like structures in i.a. *Animonia*, *Pseudorotalia*, *Pararotalia* as foraminal plates and coverplates. In this, they supported the proposals by Loeblich & Tappan (1964):

"At the umbilical border of the partly resorbed foramen, near the axial chamber wall (previous coil), the inner lining forms a plate-like extension, folded along an axis running towards the spiral side. This plate is glued to the umbilical wall of the adjacent coil at its end near the spiral wall and appears in section as a hook-like structure. This plate is referred to here as the 'foraminal plate' and is present in all chambers, including the last formed one. It is in fact part of the 'toothplate' of Hofker (1951), Reiss & Merling (1958), Reiss (1963), and of Ujié (1965), as well as part of the 'axial plate' as well as the 'apertural lip' as shown on Pl. 21 in Cifelli (1962). In addition to forming the septal flap and the foraminal plate, the inner lining extends from the foraminal plate into the previous chamber where it forms an umbilical

'coverplate', glued to the axial wall (previous coil), to the lip, as well as to the foraminal plate -below the fold- of that chamber. The coverplate leaves a communication open to the chamber interior corresponding to part of the posterior labial aperture. ... The coverplate is in fact part of the 'toothplate' of Hofker; Reiss & Merling; Reiss; and Ujié (op.cit.), and corresponds to part of the 'axial plate' of Cifelli (1962). Chamber wall, septal flap, foraminal plate, and coverplate in a previous chamber, are formed by the inner lining as one continuous structure." (p. 332)

"Whether or not the folded foraminal plate of the rotaliaceans is homologous with a true toothplate, like in the Buliminacea, remains questionable. It is certainly not characteristic of all rotaliaceans." (Hansen & Reiss, 1971, p. 342).

Buliminid toothplates were for the first time observed in the SEM by Glaçon & Sigal (1974), confirming the diversity in shape shown earlier by Höglund and Hofker. Scott (1977, 1978) reported on the toothplates in *Bolivinita*, extending the preliminaries by Glaçon & Sigal and confirming some of their reserves as to the interpretations made by Hofker.

Haynes (1981) apparently restricted the use of the term toothplate also to a buliminid context, but the structure is mentioned as occurring in larger rotaliids where they would form the secondary chambers. For example:

"Similar arcuate equatorial chambers occur in the complex rotaliaceans such as the Miogypsinidae and Lepidocyclinidae but appear to be modifications of the toothplate".

Here, Haynes echoes to some extent the terminology used by Hansen & Reiss (1972) when they described the formation of chamberlets in the asterigerinids as being the result of a toothplate cutting across the main lumen.

In a study of the toothplate of *Bulimina*, Verhallen (1986) attempted to resurrect the ideas of Hofker and surmised that the toothplate in *Bulimina* is folded onto itself so as to form a kind of axial canal

"If we assume that all successive central pillars are interconnected by bridge structures, they form a compound internal canal, which apparently runs throughout the entire test, more or less along the test axis, but in a complex, staggered spatial pattern" (Verhallen, 1986, p. 375).

He further postulates that this canal contains ectoplasm, assisting in the uptake of oxygen.

Using the techniques first developed by Hansen, Revets (1989) analysed the lamellarity of the buliminid toothplate, reporting it to be made up of inner lining only. He defined the toothplate as "a piece of inner lining (is) drawn out from under the axial-most part of the aperture into the chamber lumen and attached to the septum, close to the foramen. At least one edge of this plate leaves the chamber wall, becoming the free border."

In various subsequent publications, Revets applied the diversity in toothplate morphology within the Buliminacea for taxonomic purposes.

Müller-Merz (1980), Billman, Hottinger & Oesterle (1980) and Hottinger & Leutenegger (1980) in an in-depth study of

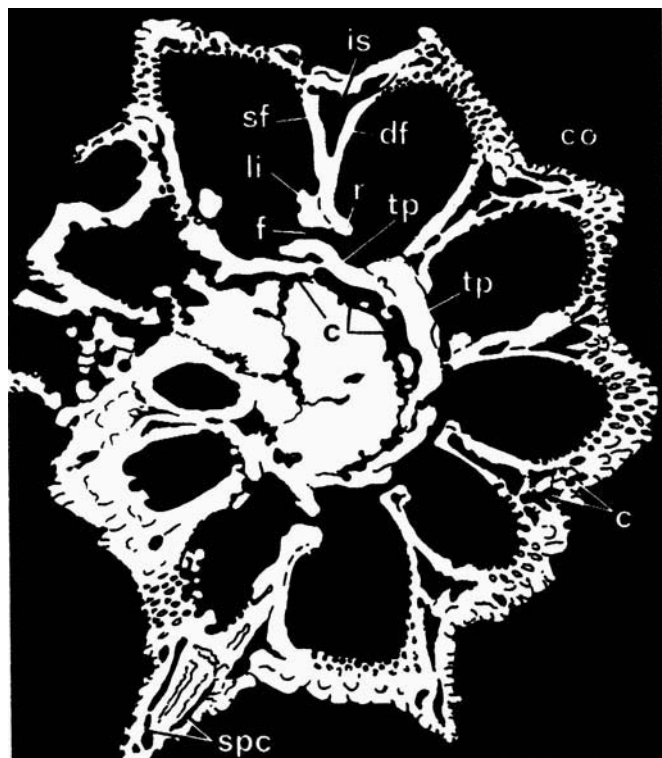


Fig. 9. The reinterpretation by Hottinger *et al.* (1991) of the horizontal section through *Neorotalia calcar* (d'Orbigny, 1826) by Hansen & Reiss (1971).

rotaliid foraminifera essentially adopted the position of Hansen & Reiss (1971), rejecting the term toothplate and using umbilical-, foraminal- and coverplate to denote structures in the taxa investigated. Contrary to the studies by Hansen & Reiss, no etched sections were prepared but broken specimens and Araldite casts for SEM observation and thin sections for light microscopy were used. Müller-Merz (1980) distinguished an umbilical flap from a coverplate by pointing out that the former is a primary closure of the umbilical-most part of a chamber, while the latter is its secondary analogue, i.e. not present in the final chamber.

Dealing with *Pararotalia*, *Neorotalia* and *Calcarina*, Hottinger *et al.* (1991) returned to the position held by Hofker and the early Reiss and reinstated the term

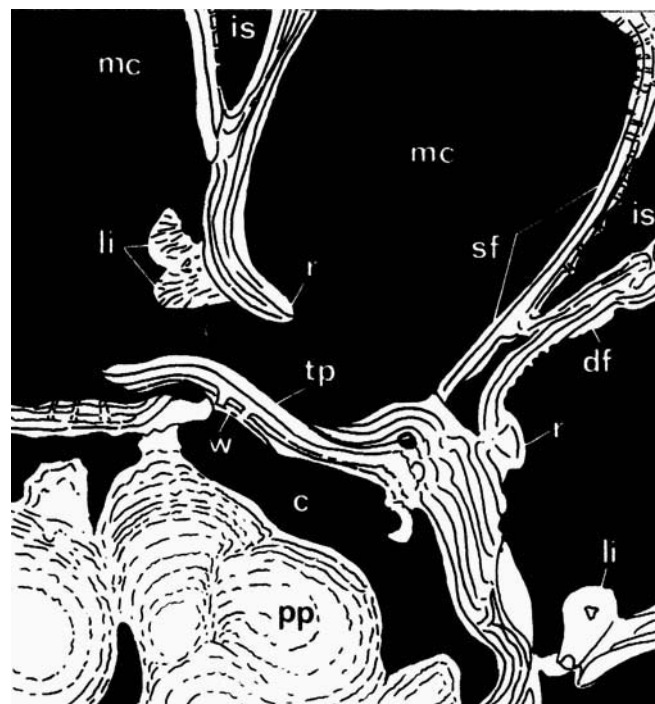
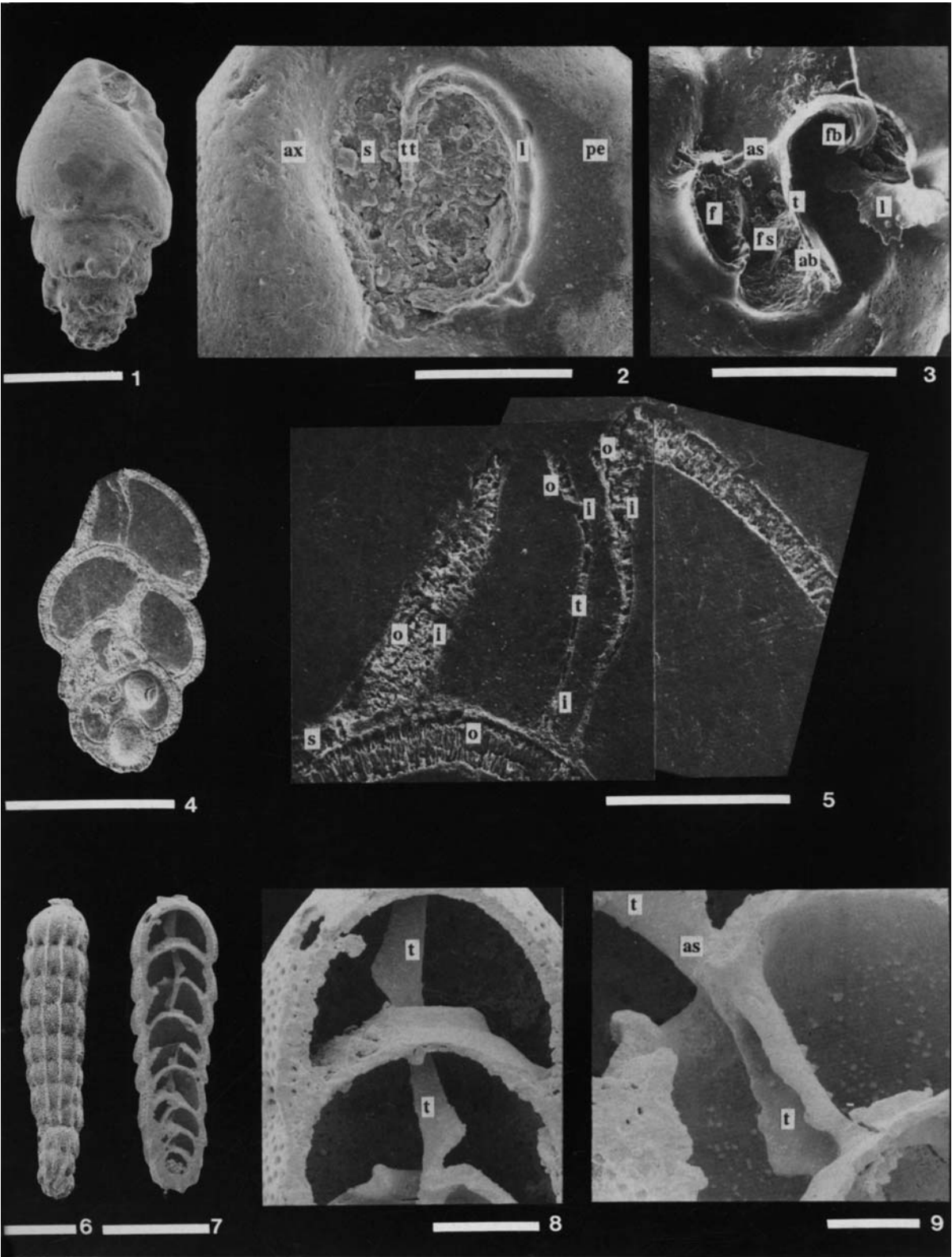


Fig. 10. A close-up of the reinterpretation shown in fig. 9. c: canal; co: cover on intraseptal interocular space; df: distal chamber wall; f: intercameral foramen; is: intraseptal interocular space; li: apertural lip; mc: main chamber lumen; pp: multiple piles; r: retal bend; sf: septal flap; spc: canaliculate spines and canal; tp: toothplate; w: inner ventral perforate chamber wall coating toothplate at their junction.

toothplate in a rotaliid context, rejecting the terms and analyses by Hansen & Reiss (1971) of the foraminal- and coverplate. As before, the results were obtained on dissected specimens and Araldite casts. The illustrations by Hansen & Reiss of *Neorotalia* and *Calcarina* were reinterpreted on the basis of the new position reached on this issue (Figs. 9 & 10). They concluded that notwithstanding the obvious differences in test geometry, there are important similarities in the toothplates of Buliminidae and Neorotaliinae, especially in the light of the ideas put forward by Verhallen. Hottinger *et al.* (1991) define the toothplate as "a contorted plate running from an intercameral foramen to an aperture, attached to both; folded in a single, double, or spiral fold; folds or tongues

Explanation of Plate 1

Fig. 1, 2, 4, 5. *Bulimina marginata* d'Orbigny, 1826, topotypes. Fig. 3. *Bulimina biserialis* Millett, 1900, Gulf of Elat. 1. Habitus (200 µm). 2. Close-up of the aperture. ax: axial side, pe: peripheral side, l: lip, tt: top of the toothplate, s: sulcus, a: aperture. (50 µm). 3. View of a dissected specimen. l: lip, t: toothplate, fb: free border of the toothplate, ab: attached border of the toothplate, as: attachment site, f: foramen, fs: foraminal sulcus covered by the toothplate. Note that the lip, although large, does not merge into the toothplate at the bottom-most portion of the aperture (100 µm). 4. Overview of etched section. (200 µm). 5. Close-up of the section through the final toothplate. Note the thick upper part of the toothplate, rapidly thinning out. t: toothplate, i: inner lining, o: outer lamella, s: secondary lamella. (50 µm) Figs. 6-9. *Siphogenerinoides plummerae* (Cushman, 1926), topotypes. 6. Habitus, showing the early coiled chambers, with most later chambers in rectilinear arrangement (200 µm). 7. Section overview, with the toothplates arranged in opposition, demonstrating the biserial coiling (200 µm). 8. Close-up of two successive toothplates (t) (50 µm). 9. Close-up of the attachment site (as) of the toothplate (t). Note also the peculiar shape of the toothplate (20 µm).



with free, often serrated distal ends and distally protruding into the aperture; a toothplate separates partly or entirely the main chamber lumen from an axial space (adapertural depression) in post-embryonic stages; interconnected toothplates produce a primary canal; in contrast to an umbilical plate, the toothplate is never associated with a foliar or stellar chamberlet and it does protrude with a free edge distally and adaxially to the aperture".

As a result, Hottinger *et al.* (1991) recognise a toothplate in *Pararotalia* and *Neorotalia* but deem it absent in *Rotalia*, *Ammonia*, *Cuvillierina* and *Calcarina*.

Current state-of-the-art

The knowledge of the toothplate is at present disparate and its status equivocal. The opinions of the different authors are at variance with each other, some of them to the point of being mutually incompatible. The changes in position over the years by some authors further cloud the issue. Essentially three points of view can be discerned. The Hofker position, shared by Hottinger *et al.* and Verhallen, is that the toothplate is a part of the chamber wall running from foramen to aperture, folded onto itself so that it forms a primary canal. But according to Hottinger *et al.* (1991) the canal may remain open in the direction of the lumen of the adjacent chamber, while Verhallen (1986) claimed that the tube formed in the buliminids is isolated from the chamber lumina. The toothplate always protrudes in the aperture. The Hansen position is less clear-cut. His apparent rejection of the toothplate as occurring in the rotaliaceans did not restrict its possible presence to the buliminids. It is explicitly mentioned in the context of the robertinids, where the feature identified as the toothplate is bilamellar (Hansen, 1979) while in the asterigerinids, the toothplate is identified as doubled-up inner lining (Hansen & Reiss, 1972). The Revets position is the most restrictive of the three. Confining the toothplate to a plate of inner lining running from aperture to foramen, it is effectively limited to the buliminids *sensu lato*. The photographs provided by Hansen & Reiss of etched sections of rotaliids confirm this point of view: the so-called toothplates (according to the re-interpretation of Hottinger *et al.*, 1991) are at least bilamellar, and they seem to receive secondary lamination (see Fig. 10, feature w).

Resolving the problem of the nature of the toothplate can only be achieved through the combination of morphological and structural observations. The lamellar nature of the different internal elements allows the recognition of their

mutual relationships, while morphology can be used to trace developments of the structures in the different taxa.

MORPHOLOGY

Position and shape of the toothplate

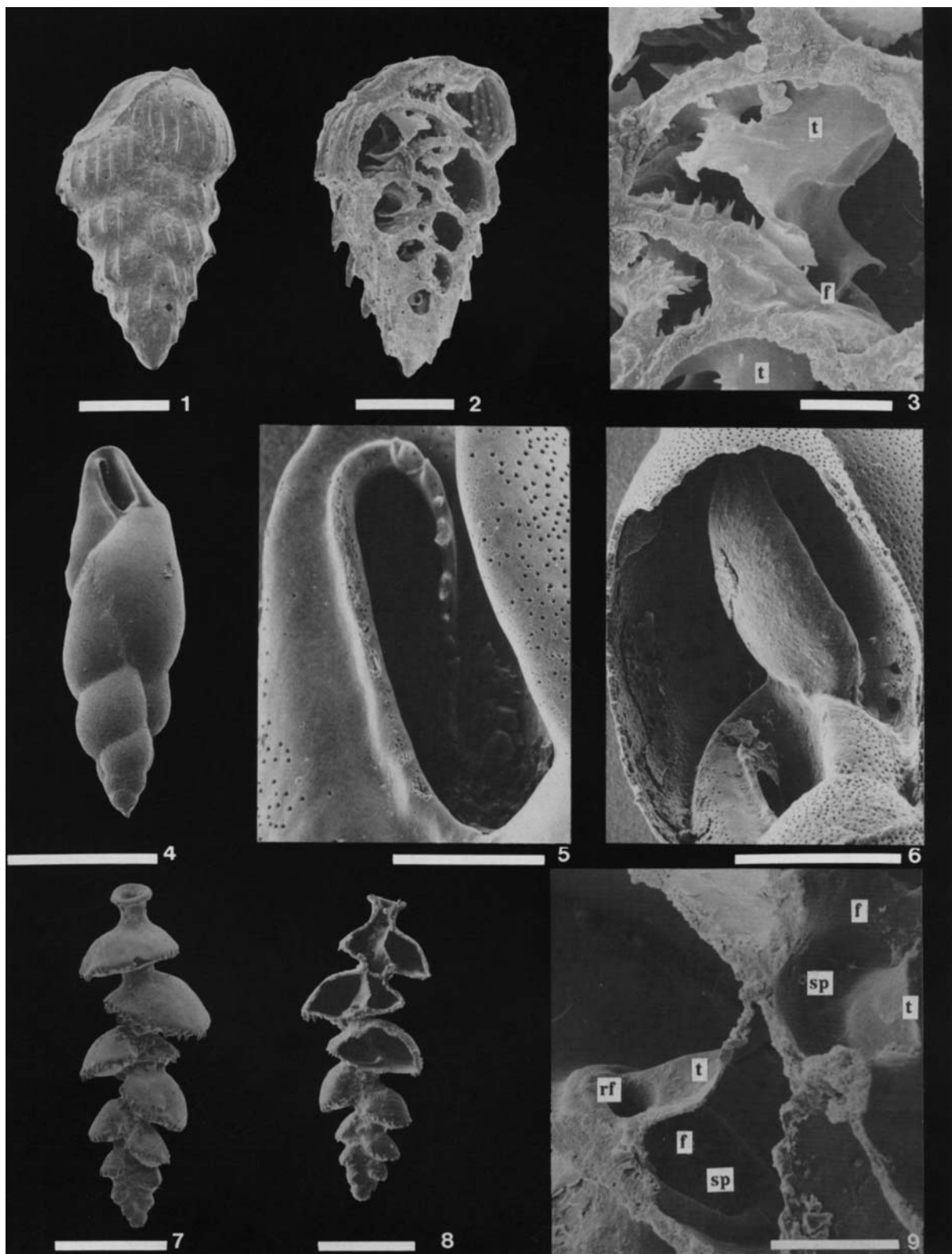
A characteristic feature of the toothplate, and recognised as such from early on, is the fact that it is partly visible from outside the test as a protrusion into the aperture. However, this in itself is not sufficient to indicate the presence of a toothplate. The most obvious examples are of course the various kinds of "teeth" found in the aperture of many miliolids. It is well established that these protrusions are indeed protrusions, without any progression into the chamber lumen, let alone coming near the foramen. There are very good reasons to believe that the miliolid "teeth" are constructed by the organism after the building of the chamber to which they belong (Arnold, 1964; Angell, 1980). In the case of the larger, complex miliolids, structures do occur which run along the entire chamber length, but there is no relation with apertural modifications along the lines seen in the classical toothplate-bearing forms (see e.g. Hamaoui & Fourcade, 1973 on *Rhapydionina*).

A necessary condition for a structure to be a toothplate is that it must progress through the chamber lumen towards the foramen. This effectively rules out the miliolid "tooth" but does not dispose of the structure present in a number of agglutinated foraminifera. A toothplate-like structure has been recognised in *Tritaxia*, *Martinottiella* and in *Clavulina* where it forms a fairly massive plate, but clearly trough-shaped. The apparent 'toothplate' in *Eggerelloides scaber* is apparently agglutinated throughout (Haynes, 1973). Interestingly, an in-depth analysis by Coleman (1980) showed the plates in *Clavulina* to be made up of calcite alone, without allochthonous particles embedded, while the tooth visible in the aperture is clearly agglutinated. At the septum, it fuses on the top of the foraminal tooth. Strikingly, the plate is continuous with a calcareous non-perforate layer coating the septum (Coleman, 1980). Technically speaking, the structure can be seen as homologous to the toothplate and continuous with a septal flap. However, it seems inappropriate to borrow terminology used to describe features occurring in a different suborder, and, as stated by Loeblich & Tappan (*vide supra*), convergence and analogy are rife within the foraminifera, a fact to which toothplate-like structures are apparently no exception.

In fully spiral, high trochospiral taxa (i.e. with chambers

Explanation of Plate 2

Fig. 1-3. *Sagrina pulchella* d'Orbigny, 1839, topotypes. 1. Habitus (100 µm). 2. Overview of an opened specimen, already showing the complex nature of the toothplates (100 µm). 3. Close-up of a toothplate (t) in an earlier chamber, illustrating the complex folding of the plate, the presence of internal spines and the positioning in the foramen (f) (20 µm). **Fig. 4-6.** *Stainforthia concava* (Höglund, 1947), Laesø, Kattegat, Denmark. 4. Habitus (200 µm). 5. Close-up of the aperture, apparently very bulimine in outline (25 µm). 6. View of a dissected specimen, with the very prominent 'toothplate'. Note however the attachment site is well clear from the foramen (50 µm). **Fig. 7-9.** *Siphouvigerina fimbriata* (Sidebottom, 1918), Gulf of Elat. 7. Habitus, illustrating the very 'open' structure of the test (100 µm). 8. Opened specimen, with prominent toothplates (100 µm). 9. Close-up of the foraminal complex. Note especially the peculiar sealing off of most of the foramen and the small relict opening. f: foramen, t: toothplate, sp: sealing plate, continuous with the toothplate, rf: relict foramen (20 µm).



in a non-rectilinear arrangement), the asymmetry of the test allows the unambiguous localisation of the toothplate. The upper part of the toothplate is located at the axial side in the asymmetric aperture (Pl. 1, fig. 2). It thereby defines a sulcus, a depression present between itself and the axial apertural border. This sulcus is in fact the internal surface of the trough which is the toothplate proper. The attached border of the toothplate is continuous with the axial border of the aperture and, lower down, with the lateral axial chamber wall. The upper part of the free border is very often capped by the apertural lip which has turned into the apertural opening, and it is this upper part which is visible in the aperture. The trough, that is, the toothplate, is contained between the free and attached border (Pl. 1, fig. 3). As the toothplate descends through the lumen towards the foramen, the free border nears the attached border, mainly because the plate as a whole narrows. The precise mode of attachment is quite diverse, sufficiently so to warrant separate treatment.

The description just given is the basic architecture of the toothplate encountered in the buliminids. As far as the majority of buliminid taxa are concerned, differences in shape are due to the varying proportions of the elements making up the structure. For example, the toothplate in *Uvigerina* is at its top clearly curved, as can be ascertained by looking into the aperture, but while it descends through the apertural neck, the free border stretches out to stand almost perpendicular and straight on the lateral chamber wall just before it fuses with the foraminal phialine lip, while in most bolivinitids the free border flares out into the lumen (Revets, in press).

Those taxa with at least some chambers in rectilinear series show a different toothplate shape, which can nevertheless be traced back to the basic model. The toothplate has become entirely free to the point where it is bilaterally symmetric and is present in the centre of the chamber. The plate is 'buckled' somewhat above the foramen, where it flexes from concave to convex just before it fuses with the foramen opposite the site from where it originates under the aperture (Pl. 1, figs. 7-9). There are taxa intermediate between the basic model and the just described one, so there can be little doubt that the structure is a real toothplate. Note incidentally that this is basically the same architecture as the one encountered in *Clavulina* (ut supra).

However, in a not to be neglected number of buliminid taxa, the toothplate has become a highly convoluted structure. From the relatively intricate toothplate in *Fijiella* and *Mimosina*, the pinnacle of complexity has been reached

in *Sagrina*, where the plate, contorted in various directions, even bears long, fine spines (Pl. 2, figs. 2, 3). These morphologies do not support the proposal of a single possible function for the toothplate at all, but rather intimate that a uniform explanation might well be impossible.

In low trochospiral taxa (the rotaliids) the toothplate, as recognised by Hottinger *et al.* (1991) and thereby echoing Hofker (*op.var.*) and Reiss (*op. var.*), rises up from the septal flap, attached with one border to the umbilical chamber wall and butts into the inner-most corner of the aperture, where it protrudes its free, serrated edge. While traversing the lumen it is folded along two axes: parallel and normal to the coiling axis. Thus it partially delimits an intra-toothplate space, presumably the equivalent of the sulcus in the buliminid toothplate. Because successive toothplates attach to each other in an adaxial position, a continuous spiral canal is formed which in the taxa investigated remains open to the adjacent chambers.

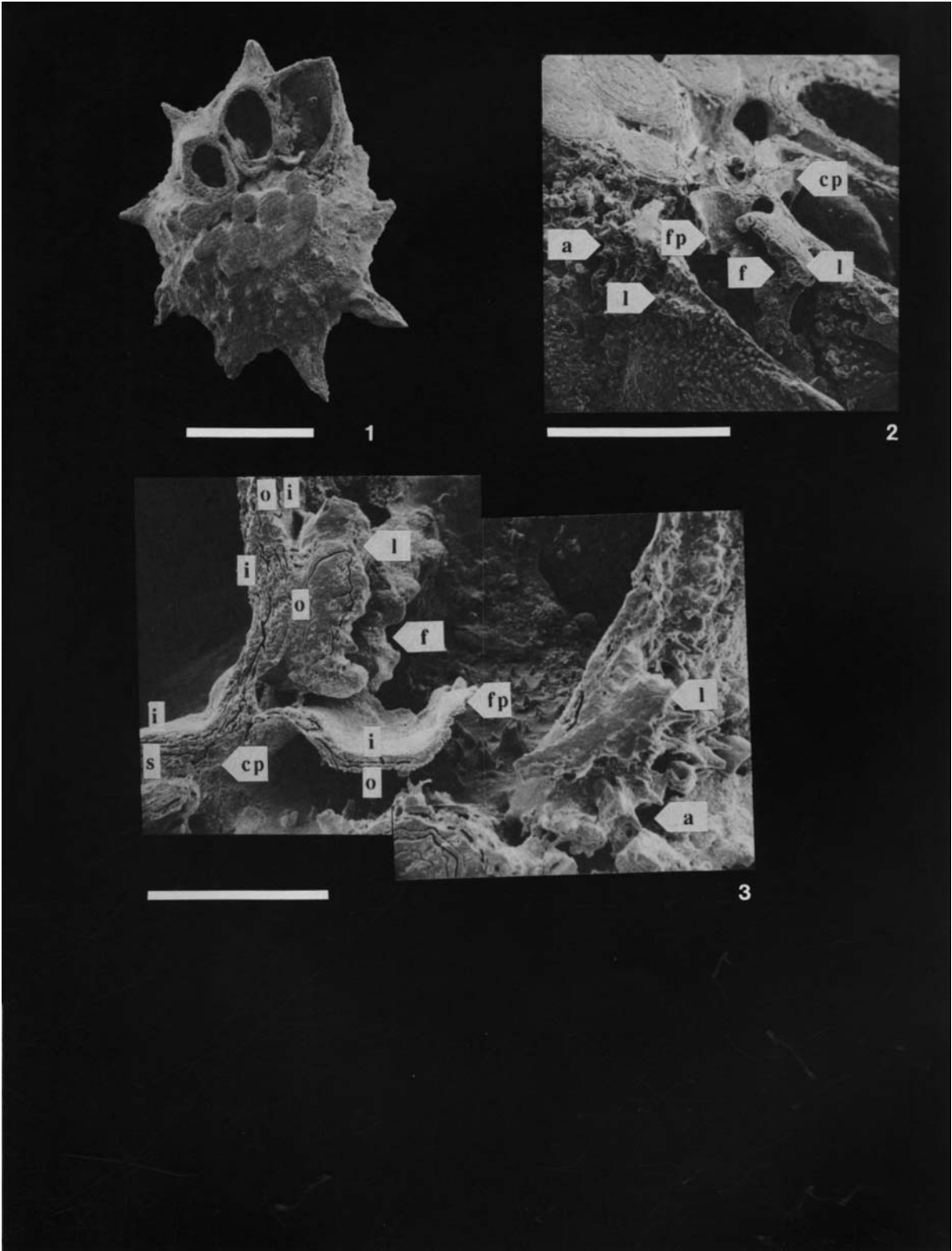
The attachment site

Regardless of whether the toothplate runs up or down the chamber lumen, it has to make contact with either the inside of the apertural wall or the outside of the foraminal wall. Because the toothplate as a structure belongs to a chamber, i.e. it is constructed within a chamber and thus occurs in every single one (contrary to a coverplate), Revets (1989) claimed that the toothplate descends into the lumen towards the foramen. It is thus a structure belonging to the apertural complex, an essentially internal feature underhanging the aperture. The precise mode of attachment in the foraminal region is quite variable, and obviously a function of the complexity of the foraminal morphology. The toothplate may fuse with the upper edge of the toothplate protruding in the foramen without any further developments. It may however also spill over onto the lateral part of the foramen, constructing something akin to a bridge between foraminal toothplate and foraminal border. Depending on the taxon, the emphasis of attachment may shift from foraminal toothplate to lateral foraminal wall attachment (Fig. 11). In case of the latter, the attachment always seems to be on the axial side of the foramen. Another kind of attachment is where the toothplate fuses with the foraminal lip. In some taxa, the toothplate is reported to attach to the septum without contacting the foramen at all; the cassidulinids (Fig. 12) being the best example (Nomura, 1983a & b).

The relation to other structures

Explanation of Plate 3

Fig. 1-3. *Neorotalia calcar* (d'Orbigny, 1826), Gulf of Elat. 1. Overview of an partially sectioned specimen, polished and etched. Note that the final chamber is intact (200 µm). 2. Oblique close-up of the last chambers. Note the open umbilical-most part in the final chamber, and the closed equivalent in the previous chamber (100 µm). 3. Detailed view of the umbilical-most part of the final and part of the penultimate chamber. The foraminal plate (fp) is present in the final chamber and continues into the previous chamber to form there the coverplate (cp) by fusing with the previous foraminal plate and thus sealing off the umbilical cameral opening. The canal thus formed receives extra lamellae, as it is topologically outside (s). Note also the changes in lamellarity due to this deposition (50 µm) a: aperture, f: foramen, l: lip, fp: foraminal plate, cp: coverplate, i: inner lining, o: outer lamella, s: secondary lamination.



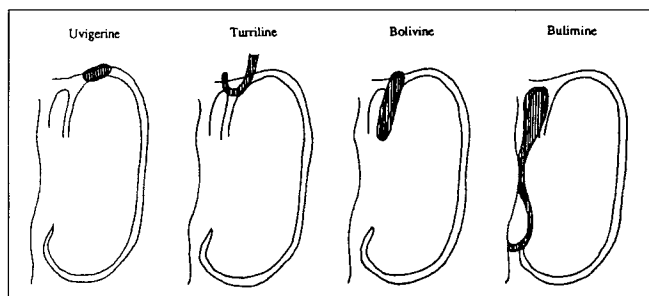


Fig. 11. The various types of attachment encountered in the buliminid taxa. The shaded area represents the actual attachment of the toothplate.

In the Buliminacea the situation is simple to the extent that no other internal structures are present: there can be no confusion between toothplate and, say coverplate, foraminal plate &c. It is therefore pointless to use a different term to denote the toothplate: 'central pillar', 'tongue', or 'siphon' are superfluous and serve only to obscure its true nature from the student.

Unfortunately, the situation is not as simple in the Rotaliacea. Hottinger *et al.* (1991) equate the toothplate in *Pararotalia* and *Neorotalia* with the foraminal plate and coverplate as understood by Hansen & Reiss (1971). But the observation of a foraminal plate and coverplate in the earlier stages of *Calcarina spengleri* by Hansen & Reiss (1971) is rejected by Hottinger *et al.* (1991): the genus is described as lacking toothplates, coverplates and foraminal plates altogether. The latter authors do distinguish the toothplate from coverplates in *Ammonia* while *Rotalia* and *Cuvillierina* are deemed to possess umbilical plates but no toothplates. They consider these genera do not possess a spiral umbilical canal (but see Haynes & Whittaker, 1990), while this canal has been shown in *Pararotalia* and *Neorotalia*. It seems thus that the toothplate in low trochospiral forms is linked to the presence of a canal. The question this raises is: do toothplates occur in *Challengerella*, *Asterorotalia*, *Cavarotalia* and *Pseudorotalia*? According to Müller-Merz (1980), they do not. The internal structures delimiting the canals are the perfect homologues of the foraminal- and coverplate of *Ammonia*, except that the sealing off by the coverplate is incomplete, allowing access from the chamber to the partly sealed-off umbilical end of the chamber, those lumina forming the canal.

Limitations of morphology

Except for the contributions by Hansen & Reiss (1971) and Revets (1989), all discussions and changes have been based on morphological interpretations only. Most authors have attempted to come to grips with the different anatomical elements by studying their relative positions and occurrences within the tests. This necessarily results in a restricted view of the structures because a good deal of knowledge has to be inferred. By observing only shape and superficial relations inside chambers, it is not possible to decide how a structure is built, i.e. is it drawn up from the septum, does it descends into the lumen, is it glued against

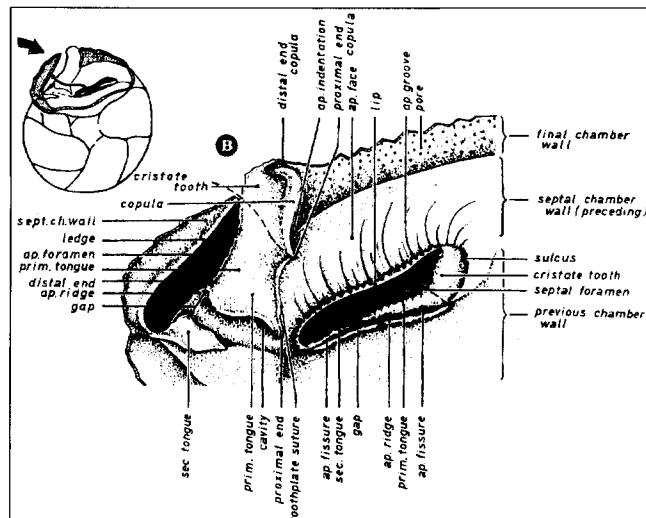


Fig. 12. A reproduction of the analysis of the cassidulinid apertural complex by Nomura (1983a).

the lateral wall or is it continuous with it? These are questions beyond the reach of resolving if only morphological observations are performed. It is necessary to elucidate the exact structural relations, because only through those structural relations are the morphological constructions seen in opened specimens defined.

STRUCTURE

The use of ultrastructure

Etched sections allow the recognition of the different lamellae, so that these can be traced in the different morphological elements. By tracing the lamellae and recognising them for what they are, i.e. inner lining, outer lamella or secondary outer lamellae, the mutual relations between the internal structures and to the remainder of the test can be resolved. As a result, some conclusions can also be drawn as to the role or function of these features (i.e. functional surface of Hansen shown by the deposition of secondary lamination, thus proving the feature to remain in contact with the outside world, topologically speaking; pure inner lining, indicating the strictly internal nature of the structure). A good example is the recognition of a septal flap. According to the precise definition (Hansen & Lykke Andersen, 1976), a septal flap is formed when the inner lining of the chamber wall continues inside the chamber to cover its septum, i.e. the wall of the previous chamber forming the floor of the current chamber. It is thus defined as that part of the septum that exhibits an ultrastructural pattern of inner lining, outer lamella, inner lining. Obviously, the chamberwall at the back of a chamber forming the limit of an interocular space cannot be denoted as a septal flap, since it is bilamellar, or, later in ontogeny, will bear more outer lamellae due to secondary lamination being deposited. These distinctions can only be made properly through the preparation of adequately positioned etched sections.

More importantly, it allows a much more precise

dissecting of the apertural complex, and a proper assessment of the various anatomical features recognised by different authors over the years. Etched sections should reveal, for example, what the precise nature of the umbilical flap (Müller-Merz, 1980) or umbilical plate (Hottinger *et al.*, 1991) is with respect to the other chamber elements. It is virtually certain that the umbilical flap is bilamellar and perfectly continuous with the remainder of the chamber wall. If this is indeed the case, then there is every reason to demote the term in the sense of a discrete structural element, since it would denote nothing more but the chamber wall at the umbilical-most part of the chamber. The term would be misleading since it purports to define something which is in fact nothing but a direction or position, not a distinct anatomical feature.

The apertural complex

In the Buliminacea, etched sections show that the toothplate is made from inner lining (Pl. 1, figs. 4, 5). The Buliminacea do not possess a septal flap, hence the toothplate is necessarily drawn from the wall underlying the aperture and progresses through the chamber lumen towards the foramen. The apertural lip is no more than a continuation of the chamber wall and thus bilamellar. Consequently, the foraminal region is trilamellar at the attachment site of the toothplate. It is thus also very likely that the toothplate is constructed contemporaneously with the remainder of the chamber. The toothplate is attached to the lateral wall deeper down in the chamber by 'gluing' the free border against the wall, but it does not extend into the previous chamber at all. Inside earlier chambers the lamellarity remains as it was. This observation proves that a closed tube is indeed absent, as the inside of such a tube would be topologically outside world, and should thus receive secondary lamination.

Preliminary observations on *Ammonia* show that the foraminal plate and the coverplate are originally bilamellar (Hansen & Reiss, 1971, pl. 3, fig. 4) composed of inner lining covered by outer lamella and that the outer lamella receives secondary lamination for as long as it remains accessible from the umbilicus (*ibid.*, p. 333, pl. 4, fig. 3-4). This seemed to be the case in *Pseudorotalia* (*ibid.*, pl. 7, figs. 2, 3, 5) as well as in *Neorotalia* (*ibid.*, pl. 9, figs. 3-5. See also fig. 10).

New etched sections vindicate this interpretation. In *Neorotalia calcar*, the final chamber is partially open on the umbilical side, allowing free access to the chamber lumen. However, in the penultimate chamber, this access is closed off by a true bilamellar coverplate with at its beginning a foraminal plate which is rather prominent. As the coverplate butts into the foraminal plate of the prepenultimate chamber, it covers its outside by a secondary lamella, so that this foraminal plate cum coverplate is trilamellar. Thus, purely structurally, *Neorotalia calcar* is the equivalent of *Ammonia*. The only structural difference is the presence of a canal in *Neorotalia calcar*, absent in *Ammonia*. Interestingly, the canal in *Neorotalia* receives secondary lamination in its inside (Pl. 3, fig. 3), thus supporting the hypothesised scenario of Revets

(1989) as to the structural changes during ontogeny in tubes or canals. These observations contradict the analysis put forward by Hottinger *et al.* (1991) and confirm the interpretations of Hansen & Reiss (1971).

The internal structures in rotaliids are not equivalent to toothplates, rather they all seem to conform to the foraminal plate coverplate concept. Clearly, a major divide exists between the buliminid toothplate and what is referred to as toothplate in the rotaliids.

THE TOOTHPLATE REASSESSED

A definition

As the concept of the toothplate was originally created for the internal structure encountered in buliminids and its description consequently limited to what one encounters in these taxa it seems to be nothing but good practice to adhere to the original intentions, but further clarified by the newly obtained information. The case to do so is particularly strong since more than sufficient grounds have been found to prove that subsequent extensions of the concept are incorrect and thus unwarranted.

The toothplate is a wholly internal structure without direct contact to the outside world. The upper part of the toothplate is capped by the apertural lip, effectively shielding it from the outside. Interestingly, this recalls the situation encountered in *Clavulina*, where the upper part of the "toothplate" is clearly agglutinated, but the internal part is wholly calcitic. Structurally, it is composed of a single piece of inner lining and remains so throughout ontogeny. The attempt to reinstate the ideas of Hofker by Verhallen (*op. cit.*) cannot be supported. Careful reading of the proposal furthermore reveals that the ideas put forward are hypothetical, and not based on actual observation of the closed tube. It is basically a curved plate, trough-like, which runs from aperture to foramen. In principle it has one so-called attached border, which is the lateral contact with the chamber wall. In forms where chambers become arranged in rectilinear series, this attached border becomes free as well. The toothplate attaches to the foramen itself, depending on the taxon, with the foraminal lip, foraminal toothplate top or both, without progressing into the foramen or spreading over the septum. It remains an open trough, except perhaps at the bottom, where it ends blindly where the curving free border reaches the lateral chamber wall.

A reappraisal of previous points of view

Restricting the definition of the toothplate (*ut supra*) effectively enforces the reappraisal of the structures that have previously been called 'toothplate' but do not conform any longer. Lamellarity patterns show that there are essentially no differences between the rotaliid 'toothplates' and the foraminal plates and coverplates as defined by Hansen & Reiss (1971). As mentioned above, in many of the forms with 'toothplates' these structures are connected to the presence of a spiral-umbilical canal. It is of more than passing interest to pause at the illustration of a rudimentary spiral canal in *Ammonia* provided by Billmann *et al.* (1980,

pl. 2, fig. 4), especially since the internal structures of *Ammonia* continue to be regarded explicitly as foraminal and coverplates. As shown, the similarities between *Ammonia* and neorotalian structures are such that no reasons remain to denote these structures by different names. The only possible way forward is to apply the terms foraminal plates and coverplates to the internal structures in rotaliids. The term toothplate should be allowed to lapse in the rotalian context and be reserved for exclusive use in the buliminids.

Outstanding problems

Despite the definitions given and the distinctions drawn, a large number of difficult and potentially serious problems remain, both within the buliminids as within the rotaliids.

Because of the form of the toothplate, especially the formation of a dead-end, the function or role remains as enigmatic as ever. The restrictive definition of the toothplate and its consequent limitation to buliminids effectively removes as well the temptation to link its presence to canals &c.

In a variety of taxa, the nature of the toothplate is either unclear or else highly unusual. Paradoxically, in view of the extensive early attention devoted to them, the toothplate structure in the Pleurostomellidae is not clear, especially its relation to the foramen. Nevertheless, preliminary results do show that the plates are monolamellar inner lining, and hence fall within the definition of the toothplate. The internal structures in *Tubulogenerina* are highly variable in shape and the relation to classical buliminid structures is at present utterly unclear. From the excellent illustrations given by Gibson (1987, especially pl. 4, figs. 3-5, pl. 5, figs. 2, 5, 6: 1989, pl. 1, figs. 1-2) and Gibson & al. (1991) some indications may be gleaned for a different interpretation altogether. The often complex and multiple structures appear to be bilamellar and it seems that a septal flap is present. If these potentially controversial interpretations were to be confirmed through closer scrutiny, *Tubulogenerina* may well have to be moved to the edges of the buliminid taxa. The observation of the internal structures in *Stainforthia* (Pl. 2, figs. 4-6) and *Francesita* show these taxa to be closer to cassidulinids, structurally speaking (Revets, in press).

The internal organisation of *Siphovigerina* (Pl. 2, figs. 7-9) is highly unusual and presents serious problems especially because of the similarities with *Stilostomella*, another very peculiar taxon.

CONCLUSIONS

Progress in the debate surrounding the toothplate has only been possible through the use of a variety of different techniques, allowing the gathering of as much primary information as possible. The supplementing of purely morphological observations by lamellarity proved to have made a crucial impact in the elucidation of the nature of the structures supposed to be toothplates. By involving lamellarity it has become possible to dissect the various plates and reveal their true nature. This resulted in an

unambiguous definition of the toothplate, considerably restricting its taxal distribution. Unfortunately, the results obtained effectively refute all currently existing hypotheses as to the function of the toothplate.

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