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Ultrastructure, morphology, affinities and reclassification of *Cassigerinella* Pokorný (Foraminiferida: Globigerinina)

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ABSTRACT — Re-examination of *Cassigerinella chipolensis* (Cushman & Ponton) and comparison of the ultrastructure of its morphotypes demonstrates that the species should only contain forms with a smooth surface and that those with a pore-cone surface should be distinguished as the type species, *C. boudecensis* Pokorný, a name which is still valid both taxonomically and stratigraphically. Strong resemblance in surface structure, aperture pattern and essential biseriality between many heterohelicids and *Cassigerinella* has been considered to be significant for its reclassification. *Cassigerinella* is, therefore, believed to have originated among the Heterohelicacea rather than in the Globigerinacea or Hantkeninacea as previously proposed by various authors. Morphological features, such as apertural modifications and coiling mode, and the characteristics of several related taxa of the species-group are discussed.

INTRODUCTION

Some thirty years ago, Pokorný (1955) established a new planktonic genus, *Cassigerinella*, to embrace the forms with biserial-enrolled and inflated chambers within the family Orbulinidae (= Globigerinidae, see Pokorný, 1958, p. 346). The type species, *C. boudecensis* Pokorný, 1955, is characterised, according to Pokorný, by an initial planispiral test with a highly arched aperture and a papillose surface, which were believed to be quite distinctive if compared with *Cassidulina chipolensis* Cushman & Ponton, 1932, a species which was also considered to be a *Cassigerinella* by Pokorný *(op. cit.)* in his generic descriptions. Later, basing their interpretation on the planispire in the early stage as described by Pokorný for the type species, Bolli, Loeblich & Tappan (1957, p. 30) believed that *Cassigerinella* should be referred to the Hantkeninidae rather than to the Globigerinidae. They further separated the genus from other hantkeninids by creating for it a separate subfamily – the Cassigerinellinae. In various later biostratigraphic and taxonomic studies the suprageneric position of *Cassigerinella* has never been agreed, and the genus has been placed, mainly, either in the Hantkeninidae (e.g. Loeblich & Tappan, 1964, 1984; Bolli & Saunders, 1985) or among the Globigerinidae (e.g. Banner & Blow, 1959; Blow, 1969, 1979). The main cause of the dispute seems to be belief in the presence or absence of the initial planispiral stage in *Cassigerinella*.

Apart from its type species, *C. boudecensis*, other species which have been referred to the genus under discussion include: *C. globulosa* (= *Cassidulina globulosa* Egger, 1857, from the Miocene of Germany), *C. chipolensis* (= *Cassidulina chipolensis* Cushman & Ponton, 1932, from the Early Miocene of Florida), *C. winniana* (= *Cassidulina winniana* Howe, 1939, from the Eocene of Louisiana), *C. globolocula* Ivanova (1958, from the Late Oligocene of USSR), *C. regularis* Iturralde Vinent (1966, from the Oligocene of Cuba), *C. martinezpicoi* (= *Riveroinella martinezpicoi* Bermudéz & Seiglie, 1967, from the Early Miocene of Puerto Rico) and *C. eocaenica* Cordey (1968, from the Eocene of Florida). All of these, except *C. regularis*, are distinguished by a small test with a diameter of, commonly, 0.1-0.25mm. Among them, the most frequently used species names are *chipolensis* and *winniana*; the former is said to be a subjective senior synonym of both *boudecensis* and *globolocula*, and the latter a senior synonym of *eocaenica* (see Kennett & Srinivasan, 1983, p. 18; Blow, 1979, pp. 1361-1364). In lacking accurate original descriptions and drawings and available topotypes, the oldest name, *globulosa*, had not been used and referred to the genus until Rögl (1985) reused it, even though Pokorný (1955) did mention that Egger's *globulosa* was undoubtedly a *Cassigerinella*. Nevertheless, the criteria for discrimination among these species (excluding *regularis* and *martinezpicoi*) are still so inadequately defined that many workers could often be confused and unable to differentiate them when coming across these tiny planktonic forms in the mid-Tertiary sequences.

Another morphocharacter of *Cassigerinella* to which taxonomic significance has been attached is the tooth-

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plate structure observed by Hofker (1963) and, subsequently, confirmed by Steineck & Darrell (1971). This character, which has been seen in many benthic forms but never in the planktonics, led the authors cited to consider that the genus should belong to neither the Globigerinidae nor the Hantkeninidae but to the Cassidulinidae or Islandiellidae. The presence of a true toothplate and its supposed significance were no longer accepted after Saito & Biscaye (1977) supplied evidence to prove that the alleged toothplate structures of any *Cassigerinella* were merely apertural lips, flanges or other apertural modifications only. However, the relationship between the apertural flanges, protruding teeth and toothplates is a problem which has not yet been satisfactorily interpreted, and one that still needs to be resolved.

Taking into account the enrolled-biserial nature of the tests of *Cassigerinella* and the peculiar aperture pattern, Blow (1979) suggested that a separate and distinct family was warranted for this genus; the presence of only pseudoumbilici, and no true umbilici, in this form also led him to consider it to be, more likely, an enrolled heterohelicid rather than a hantkeninid or globigerinid, and to represent a finally extreme modification of some small tests of the Heterohelicacea known in the later Middle Eocene. Kennett & Srinivasan (1983) paid more attention to the resemblance in the surface ultrastructure of *Cassigerinella* to those of *Chilogeumbelina* and *Streptochilus*, and suggested that a phylogenetic relationship between these forms might once have existed. Unfortunately, little satisfactory information has been supplied, to date, to support these assumptions, possibly because of the relative rarity of some species (not *chipolensis*) and because of the difficulties either in collecting suitable material or in examining the extremely tiny tests possessed by many *Cassigerinella* species.

As an attempt to clarify some of these problems, the present work was carried out with a comparison and re-examination of specimens from the Oligocene of the Cipero Formation (type locality of the *opima opima* Zone, P21) of Trinidad, the Cipero type section, between 20 and 240 feet southwest from the Fixed Point along the Cipero coast (see Bolli, 1957, pp. 100, 103-105, fig. 19). Many specimens of *C. chipolensis* were dissected and observed with the aid of a JEOL-T20 scanning electron microscope in the Micropalaeontology Unit of University College London. Also, the holotype and paratype of *C. eocaenica* Cordey, deposited in the British Museum (Natural History) were re-examined.

RESULTS

Approximately 200 individuals of *Cassigerinella* from Zone P21, Trinidad, were examined; they contained two distinct morphotypes: one is covered with numerous pustule-like cones around the perforations on the wall surface whilst the other possesses a smooth, pustule-less surface structure. Both morphotypes are described and discussed below.

Explanation of Plate 1

Cassigerinella boudecensis Pokorný 1955

(All figures on Pl. 1, as well as other specimens figured on Pls. 2-4, were from *opima opima* Zone(P21) of the Cipero Formation, Trinidad).

Figs. 1, 2, 3. Apertural views of three specimens. Showing sparsely to densely developed pore-cones, asymmetrical apertures and apertural flanges: fig. 1, ×250; fig. 2, ×170; fig. 3, ×170.

Figs. 4-5. A specimen with twisted coiling (see also Fig. 1) and a weak apertural flange: fig. 4, ×170; fig. 5, enlargement of the aperture, ×500.

Figs. 6, 7. Two dissected specimens showing nearly symmetrical apertures and flanges on the penultimate chambers: fig. 6, ×250; fig. 7, ×335.

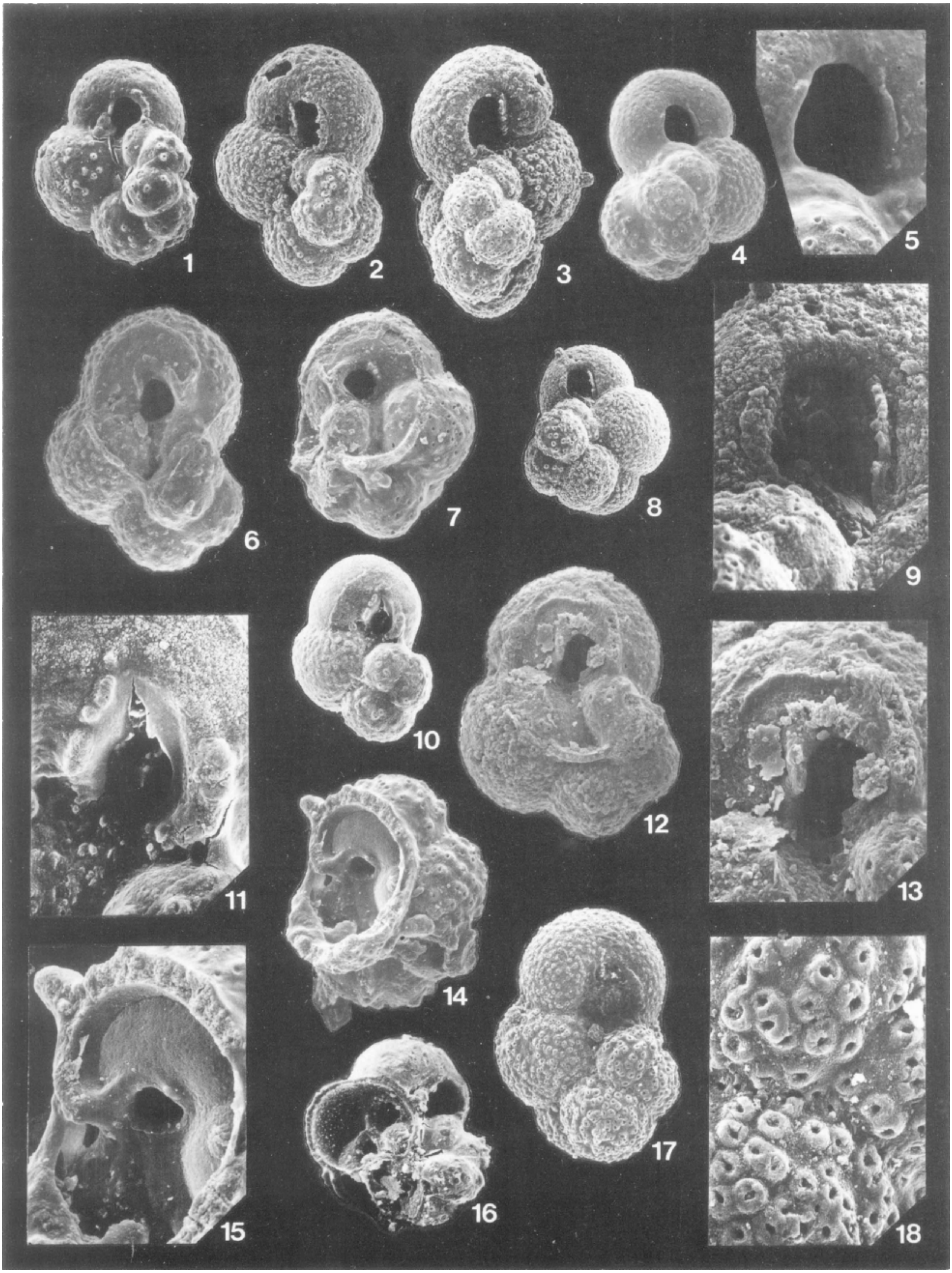
Figs. 8-9. A specimen with symmetrical, highly arched aperture: fig. 8, ×120; fig. 9, enlargement of the aperture, ×500.

Figs. 10-11, 12-13. Two dissected specimens with the aperture and pore-cones developed in various degrees: fig. 10, ×170; fig. 11, enlargement, ×665; fig. 12, ×335; fig. 13, enlargement, ×665.

Figs. 14-15. A heavily walled specimen with dissection to show the low arched aperture without toothplate: fig. 14, ×335; fig. 15, enlargement, ×665.

Fig. 16. A dissected specimen showing absence of the toothplate structure, ×250.

Figs. 17-18. A heavily pore-coned specimen: fig. 17, ×175; fig. 18, enlargement of the pore-cones, ×665.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Coiling mode.

All examined specimens of both morphotypes show, as in benthic *Cassidulina*, a biserially enrolled test throughout ontogeny. No tests with an initially planispiral stage nor globigerine coiling mode have been found, though some specimens had externally the appearance of being planispired initially. In the latter case, however, an alternation of the septal aperture, which indicates their essential biserial coiling, can be traced (Pl. 3, figs. 1, 2). These coiling planes are usually kept ontogenetically unchanged in most individuals, but may be slightly modified in some rare tests with the successive development of more globular chambers in the last whorl (Pl. 1, fig. 4; Pl. 4, fig. 3; Fig. 1).

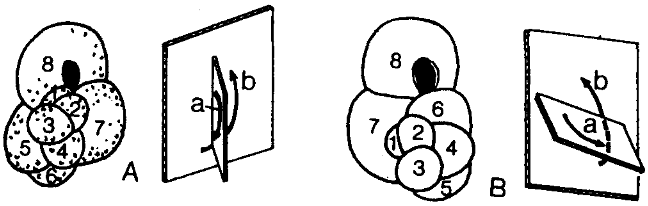

Fig. 1. Modification of the coiling plane from a to b in *C. boudecensis* (A) and *C. chipolensis* (B); compared with Pl. 1, fig. 4 and Pl. 4, fig. 3 respectively. Note the essential biserial coiling still maintained.

Aperture and apertural modifications

In both morphotypes, the geometry (mainly the shape and the size) of the aperture differs in detail from test to test and generally varies in different ontogenetic stages in any particular shell. The aperture in the earlier part is rounded in most cases, and becomes oval, elongate elliptical, subtriangular or even irregular in the final few chambers, in which it is generally asymmetrical (Pl. 1, figs. 1-4; Pl. 4, figs. 1-5) or nearly symmetrical (Pl. 1, figs. 7-10; Pl. 3, figs. 1, 10). It seems that there is no rule for the development and geometric modification of the aperture during ontogeny.

A discontinuously developed apertural rim is always seen in many tests although its growth may be of various degrees. Those which are well developed, protruding rims or flanges, whether blunt or sharp, are much more common and conspicuous (Pl. 1, figs. 1-3, 8, 10; Pl. 4, figs. 1-6, 9-11). Their crenularity and continuity are never consistent, so that most of them appear irregularly beaded and discontinuously arranged around the aperture. In general, the rims in the earlier stages of ontogeny are much weaker but more continuous and lacking beading. No internal structure which extends fully between successive apertures or which is infolded, internally to its aperture of origin (i.e. the toothplate *s.s.*) has been observed. This study has necessitated a brief review of the nature of toothplates, and this is given in the Discussion.

Wall and surface ultrastructure

The wall morpho-structure, of all dissected specimens, is composed of randomly arranged micrograpules (Pl. 2, figs. 8-14; Pl. 3, fig. 9; Pl. 4, fig. 17), which may be of radial optical (crystallographic) structure as described by Hofker (1963), Lipps (1966) and others. It seems to be a general trend that the micrograpules in the thick wall with a pore-cone surface are coarser than those in the thin wall with a smooth surface. Little distinct difference can be seen in the crystalline structure of the outer, inner and septal walls although the last is much the thinnest (Pl. 2, figs. 3, 4).

As noted above, two types of surface ultrastructure were recognised: one is rough, with "pustulate" or

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Explanation of Plate 2

Cassigerinella boudecensis Pokorný 1955

Figs. 1-2. A dissected specimen showing no toothplate: fig. 1, enlargement, ×500; fig. 2, ×250.

Fig. 3. A dissected specimen showing early chambers with thick outer wall and thin septal wall, ×335.

Fig. 4. A specimen with nearly longitudinal dissection to show the inner whorl with low arched aperture, thin septal wall and pore-cones on the earlier chamber surface (pointed by arrow), ×335.

Figs. 5-6. Tilted views of a dissected specimen with an outwardly well-developed apertural flange (fig. 5, ×335) but without any inwardly extending toothplate (fig. 6, ×500).

Figs. 7-9. A dissected specimen with heavily pore-coned surface showing non-lamellar wall with granular structure: fig. 7, ×250; fig. 8, ×665; fig. 9, ×1150.

Figs. 10-11. A piece of wall showing granular structure with a very thin organic lining (pointed by arrow): fig. 10, ×1150; fig. 11, enlargement, ×3400.

Figs. 12-14. A piece of wall showing the randomly arranged micrograpules surrounding the perforations. Note the granules of the pore-cones show no difference from those of the test wall: fig. 12, ×665; fig. 13, ×2500; fig. 14, ×5000.


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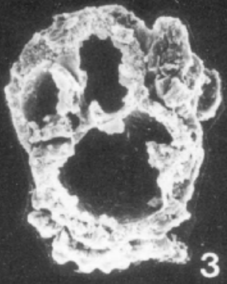
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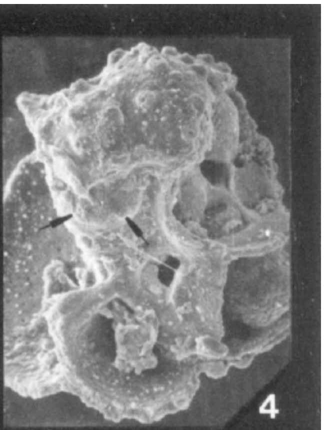
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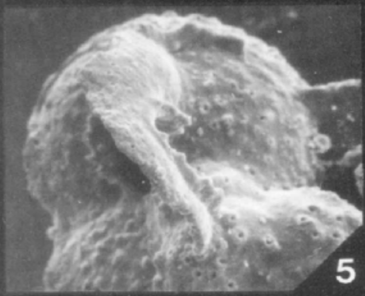
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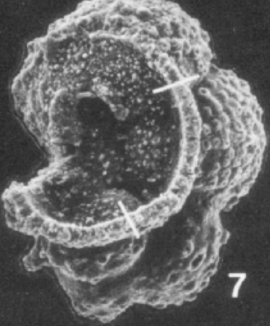
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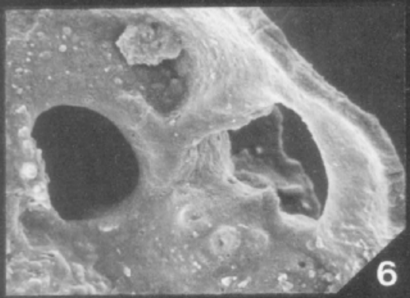
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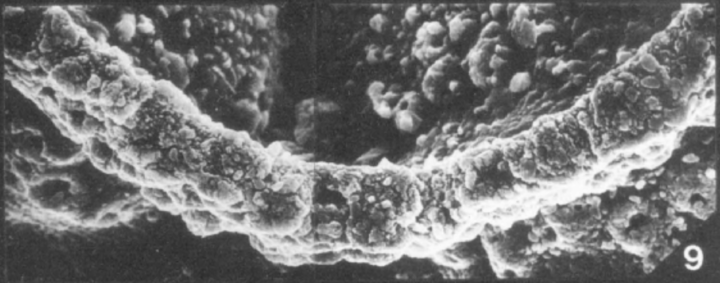
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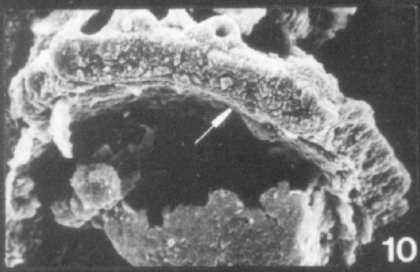
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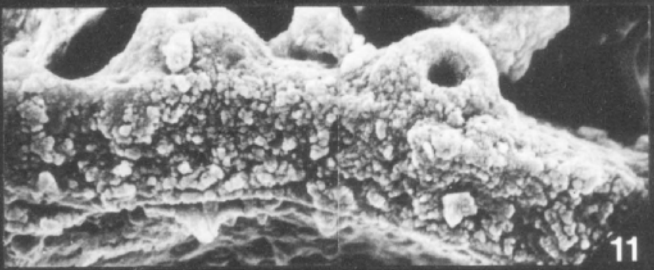
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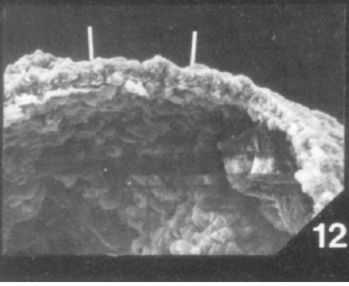
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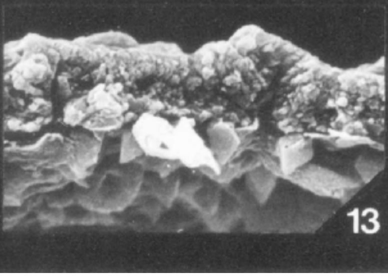
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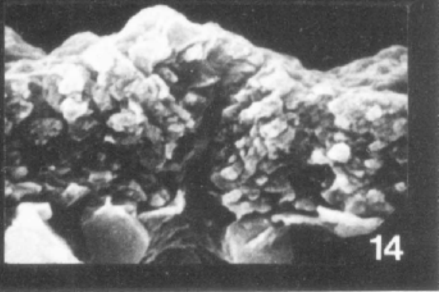
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cone-shaped protuberances (Pls. 1-2; Pl. 3, figs. 1-4), and the other is smooth and pustule-less (Pl. 3, figs. 7-10; Pl. 4). Each pore, in the former case, is surrounded by a projecting, thick, rim-like cone; the adjacent cones may be connected together. The microgranules surrounding the pores are arranged at an angle of about 45° to the axes of the pore tubules (Pl. 2, figs. 12-14). Those tests with a smooth surface show no hint of development of the pore cones.

The morphotype with external pore-cones lacks them on that part of the apertural face which will become the septal face, and the inner surface of the chamber, like the septal face, is covered by a smooth calcareous deposit contrasting sharply with the blocky grains of the rest of the wall; pore-cones on the chamber exteriors, covered by the new chamber, remain open, however (Pl. 1, figs. 6, 7, 10, 12, 14-15). In the smooth morphotype, the inner surface smooth lining seems to be less developed. Either may become covered, scatteredly to densely, with pyramid-shaped calcite crystals (Pl. 2, figs. 11, 12-13; Pl. 3, figs. 8-9); this may be due to diagenetic deposition in optical (crystallographic) continuity with the grains of the wall, and heavily altered specimens (Pl. 4, figs. 12-13) become heavily recrystallised internally even though the exterior appears to be unaltered. A source of internal calcite for redeposition could have been the coccoliths which are sometimes found, relatively unaltered, inside the empty tests (Pl. 2, figs. 7-9).

Perforations and laminations

The morphologically granular wall of *Cassigerinella* is scatteredly perforated by tiny pores which are generally rounded, subrounded and, occasionally, elliptical (Pls. 1-4). Most pore tubules are simply cylindrical and slightly funnel-shaped on both ends; however, they may be obscured or distorted by those irregular microgranules which have been well developed close-by (Pl. 2, figs. 12-14).

Many specimens of both morphotypes of *C. chipolensis* show a non-lamellar wall structure (Pl. 2, figs. 2, 4, 8-14; Pl. 3, fig. 9; Pl. 4, figs. 16-17). On the other hand, some earlier chambers in a few individuals do exhibit a thick outer layer and a few very thin inner "veneers" (Pl. 2, figs. 10-11; Pl. 3, fig. 11) which seem to be some sort of organic linings instead of true lamellae.

DISCUSSION

i. "Toothplate" and Apertural Modifications

The analogy between the biserial-enrolled *Cassigerinella* and *Cassidulina* extends beyond gross test morphology to the presence in each genus of flange-like skeletal structures associated with septal apertures. Consequently, Banner (1982, p. 196) regarded *Cassigerinella* as a planktonic *Cassidulina*, with the implication (confirmed by Banner, pers. comm.) that the genus had changed the optical characteristics of its wall (from optically "granular" to "radial") and reduced its toothplate during the adoption of a planktonic mode of life in evolution from a benthic cassidulinid ancestor. However, re-examination of *Cassigerinella* from the Cipero Formation of Trinidad fully supports the findings of Saito & Biscaye (1977) that the genus possesses no internal continuously-extending or inwardly infolding, true toothplate. As pointed out by these authors, the alleged toothplate described by Hofker (1963) and Steineck & Darrell (1971) (in specimens of *Cassigerinella* of similar provenance as those used in this study), was really nothing but a variously grown apertural rim or flange, and this is confirmed here. That part of the flange of each septal aperture which is extended and reflected to join the lateral chamber wall (Pl. 1, figs. 6-7, 14-15) is separate

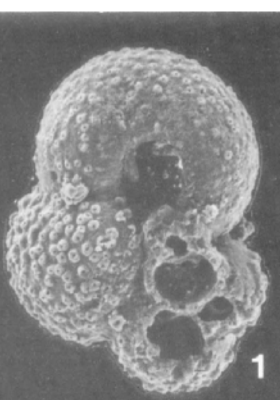
Explanation of Plate 3

Figs. 1-4. *Cassigerinella boudecensis* Pokorný: fig. 1, whole specimen with heavily coned surface; note the earlier chambers, which had been dissected, are planispiral externally, ×250; fig. 2, enlargement showing the alternation of the septal apertures (sa), ×500; fig. 3, pore-cone surface, ×1150; fig. 4, enlargement of fig. 3, ×2500.

Figs. 5-6. *Guembelitria cretacea* Cushman. (reproduced from Smith & Pessagno, 1973, pl. 1, figs. 2-3; for comparison with *Cassigerinella boudecensis*). Note the asymmetrical aperture, well-developed apertural lip/flange and pore-cones, some features which also characterise *C. boudecensis*: fig. 5, ×210; fig. 6, ×2750.

Figs. 7-9. *Cassigerinella chipolensis* (Cushman & Ponton): fig. 7, the whole specimen, after removing half of the final chamber, to show beaded apertural flange, ×250; fig. 8, tilted enlargement, ×335; fig. 9, enlargement of the granular wall, ×2500.

Figs. 10-11. *Cassigerinella chipolensis* (Cushman & Ponton). This atypical specimen possesses a low biserially trochospiral coiling: fig. 10, removal of the final and antepenultimate chambers showing rounded septal aperture and no toothplate structure, ×250; fig. 11, enlargement to show septal apertures (sa) and the organic linings (ol), ×1500.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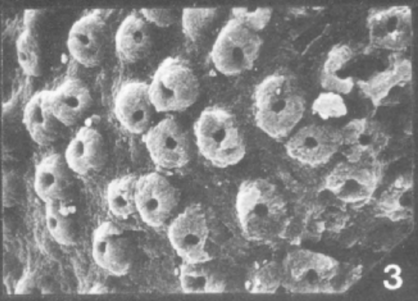
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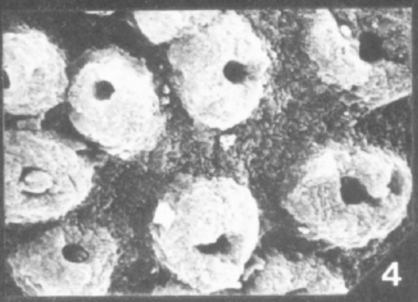
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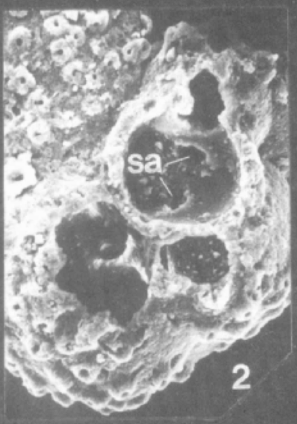

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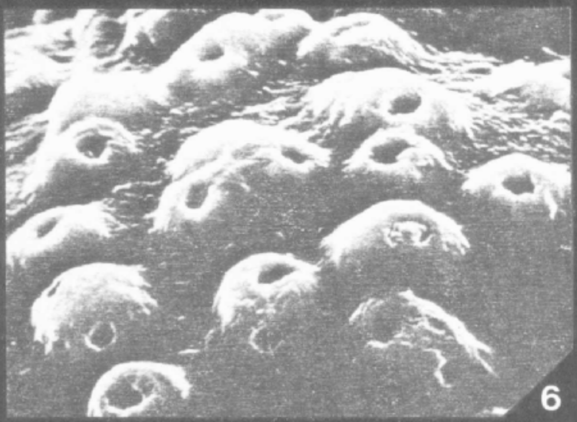
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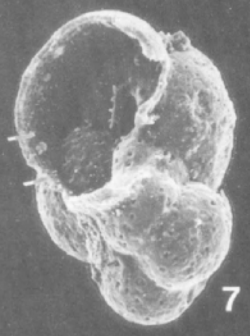
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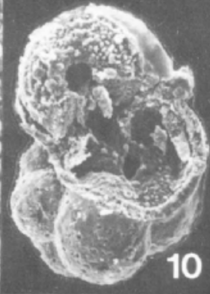
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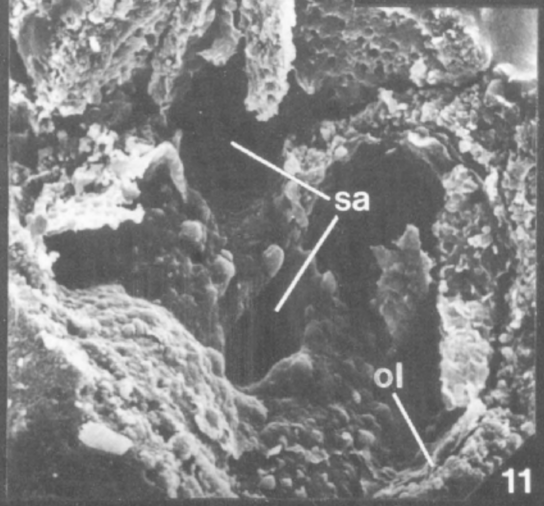

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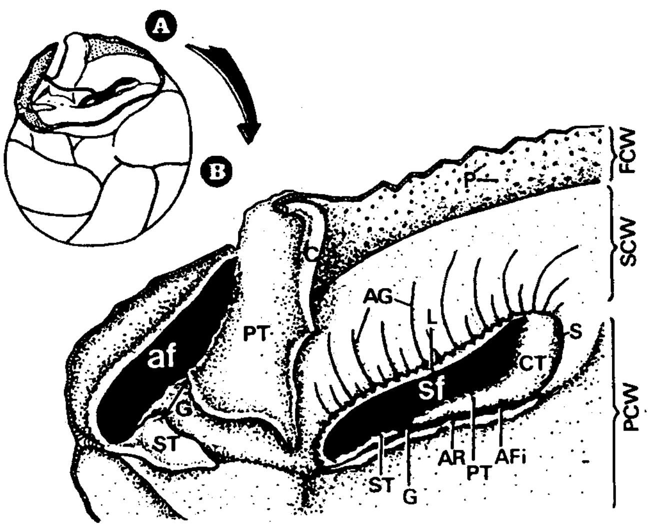
from the flange of the succeeding aperture (Pl. 2, figs. 5-6; Pl. 3, figs. 7-8; Pl. 4, figs. 5, 9) and is neither continuous with it nor inwardly reflected. The term "toothplate" seems to need some redefinition as for many years it has been used overzealously for any type of the modified apertural structure. A toothplate must essentially be an inwardly projecting structure, often developed continuously from one aperture to the next, whereas an apertural lip or flange projects outwardly only.

Nomura (1983) both reviewed the historical development of the term "toothplate" and described the toothplate development of many genera of the Cassidulinidae. Nomura stated that the toothplate in the cassidulinid group should be composed of three distinct constituents (see Fig. 2): *Primary tongue* (a free internal folding plate), *Cristate tooth* (externally projecting part of the tongue), and *Copula* (a conjugating structure of the cristate tooth and infolding chamber wall). He also found that these three components were never consistent in cassidulinids as they might be well developed or partially or wholly reduced. Those without a free-folding tongue were regarded (Nomura, *op. cit.*) as having been reduced during evolutionary process, and their phylogeny might have been once closely related. Some questions may arise from this suggestion: does the various degree of development of the toothplate on different taxa really represent a true phylogenetic relationship between them? If this is true, why did some of them reduce this structure, uniformly developed in all individuals of any one species, which must have been meaningfully functional in bio-ecology or environmental adaptation or both? The contrary



af – aperture foramen
AFi – apertural fissure
AG – apertural groove
AR – apertural ridge
C – copula
CT – cristate tooth
FCW – final chamber wall
G – gap
L – lip
P – pore
PCW – previous chamber wall
PT – primary tongue
ST – secondary tongue
SCW – septal chamber wall
sf – septal foramen
S – sulcus

Fig. 2. Toothplate and other apertural modifications in the Cassidulinidae (simplified from Nomura, 1983, fig. 13). See text for explanation. Note the reflexed primary and secondary "tongues" (PT and ST) of a true toothplate have no equivalent in *Cassigerinella*.

Explanation of Plate 4

Cassigerinella chipolensis (Cushman & Ponton)

Figs. 1, 2. Two specimens with asymmetrical, highly arched apertures and apertural flanges: fig. 1, ×335; fig. 2, ×250.

Fig. 3. A specimen with twisted, low trochospire-like coiling (see also Fig. 1), ×250.

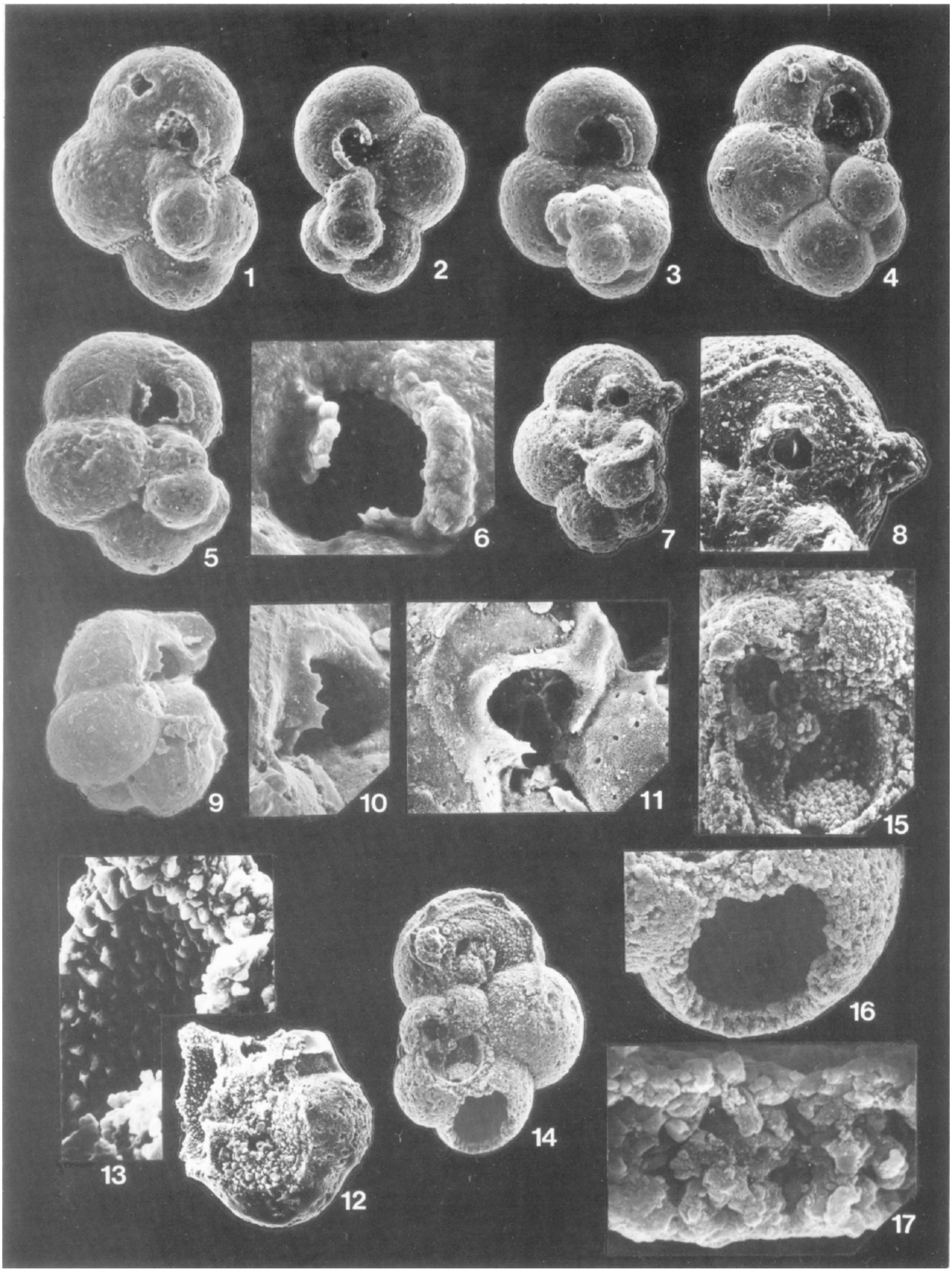
Figs. 4, 5-6. Two specimens with compact, weakly inflated chambers and well-developed apertural flanges. They are referable to Rögl's (1985) *C. globulosa* (Egger) – see text for explanation: fig. 4, ×250; fig. 5, ×335; fig. 6, enlargement of fig. 5, ×1160.

Figs. 7-8. This is an atypical specimen dissected to show the rounded penultimate aperture: fig. 7, ×250; fig. 8, enlargement, ×500.

Figs. 9-11. A low trochospirally biserial-enrolled specimen with a well-developed apertural flange: fig. 9, ×250; figs. 10, 11, enlargement, ×665.

Figs. 12-13. A dissected specimen showing the interior surface with well-developed pyramid-shaped calcite crystals: fig. 12, ×335; fig. 13, enlargement, ×1700.

Figs. 14-17. A specimen dissected to show the flange-less aperture (fig. 14, ×250), rough interior surface with calcite crystals (fig. 15, ×665) and non-lamellar, granular wall (fig. 16, ×665; fig. 17, enlargement, ×5000).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view, that the species without internal folding toothplates are possibly the primitive types (rather than merely descendants from certain taxa by reduction of the toothplates) is equally tenable. This assumption, of course, does not exclude any possibility of reversible or irreversible transformations or transfigurations (see Fig. 3). It is theoretically more likely that the direct lineal relationships of Fig. 3 would be more successful under ideal conditions. The possible development or reduction of certain morphological structures should therefore be given equal attention in order to avoid overlooking any kind of phylogenetically sensitive characters. It would be wise neither to over-emphasise certain merely possible relationships, nor to consider some of them much more important than others, as their transitional stages are in many cases still missing or unrecognised. This is the reason why we prefer standing by its original definition by Hofker (1951) and refer "toothplate" to the internal, inwardly and continuously free-extending structure only. Other characters of the apertural modification, as in the case of *Cassigerinella*, are accordingly considered to be no more than apertural rims, lips, flanges, etc., some structures found commonly in both benthic and, significantly, planktonic foraminifera. It is among the latter that apertural flanges (more readily comparable to the *Cassigerinella*-structures than are the toothplates of *Cassidulina*) particularly may be found (as described further below).

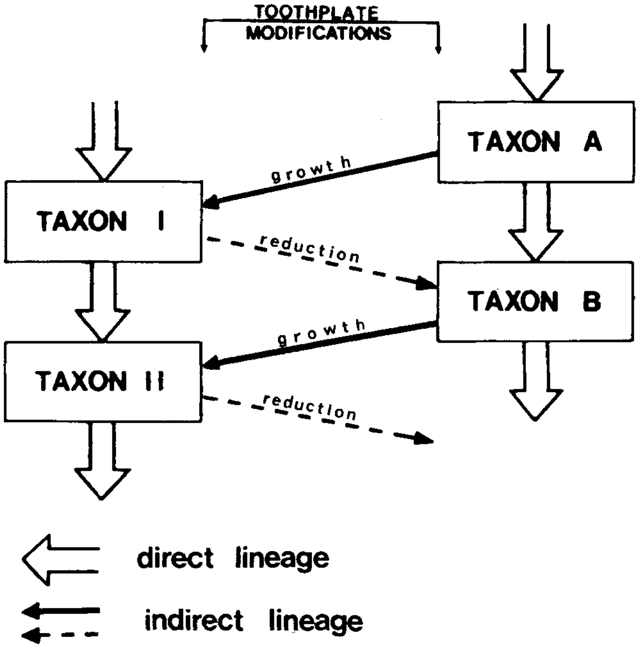

Fig. 3. Idealised diagram showing possible relationships between taxa with or without toothplates.

ii. **Planktonic Features in Cassigerinella**

Unlike many planktonic species, *Cassigerinella* possesses neither spines nor keels. The only morphological character suggesting its planktonic mode of life is the inflated test with the globular chambers which are very common in the planktonic globigerinids. Some authors, e.g. Hughes & Jenkins (1981), regarded *C. chipolensis* as a planktonic taxon mainly because of its widespread geographical distribution. Also, it has been widely reported to occur commonly in deposits rich in other, unequivocally planktonic foraminifera (e.g. Bolli, 1957; Blow, 1979).

Boersma & Shackleton (1978) discovered that the oxygen and carbon isotopes of *Cassigerinella* indicated that the genus maintained a planktonic mode of life by living near the ocean surface; unfortunately, they gave no detailed analytical results. Nevertheless, this has become the only convincing direct evidence to prove *Cassigerinella* a planktonic rather than a benthic genus (Saito & Biscaye, 1977). It is clearly in agreement with the evidence for planktonic habitat indicated by its inflated tests and wide, apparently pelagic distribution pattern (recorded mainly for specimens usually referred to *C. chipolensis* and *C. winniana*).

iii. **The Coiling Mode of *Cassigerinella***

The initial stage in *Cassigerinella* was first suggested to be planispiral by Pokorný (1955) in his original generic description. In order to support his idea the author supplied two schematic drawings, as reproduced here in Fig. 4a-b, of the first whorl in *C. boudecensis*. However, his drawings do not agree with the assumption that *Cassigerinella* is merely planispiral initially and essentially, but supply evidence to prove the validity of his statement: "In some specimens the chambers of the first stage are not quite regularly arranged."

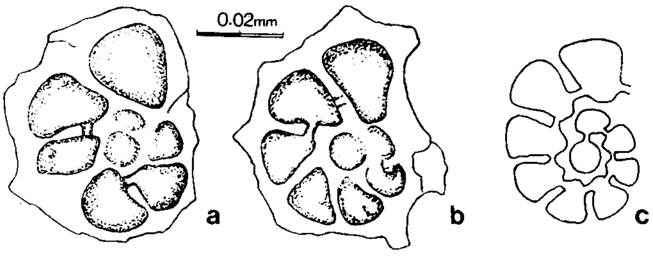

Fig. 4. Comparison of the early chambers arranged in *Cassigerinella boudecensis* (a and b, after Pokorny, 1955, tables 2, 3) and in a genuinely planispiral test (c, schematic drawing). Note the foramen tubules in *boudecensis* tend to be alternating.

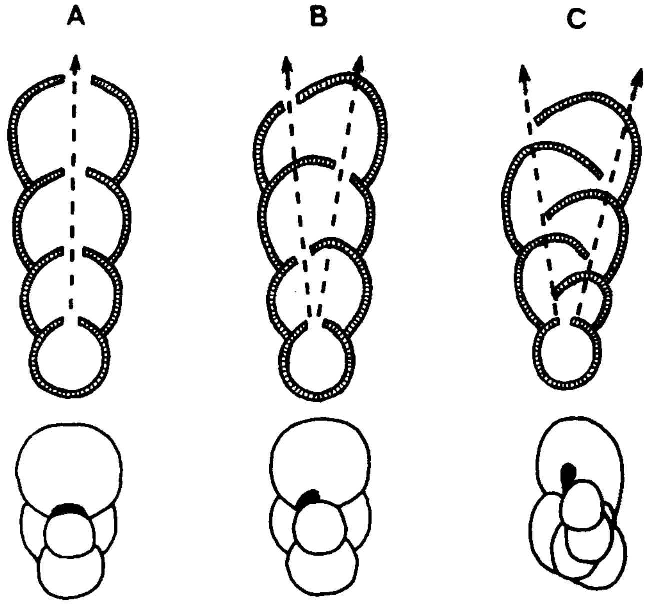

Fig. 5. Schematic figures showing the chamber arrangement in different coiling modes from A, uniserial planispiral to C, biserial enrolled. Note the morphologically transitional form B, or pseudo-planispiral, produces an appearance of planispiral coiling with alternating apertures (arrows indicating the growing orientation of the apertures).

In analysis of the coiling mode adopted by *Cassigerinella* species, it is essential to (a) distinguish between possible uniserial and biserial chamber arrangements and (b) recognise the planispirality or trochospirality of the chamber series (be it uniserial or biserial). Until now, neither has this been adequately done, nor have the two distinct elements of the coiling mode been adequately discriminated. In a truly uniserial planispire, successive septal apertures must lie in the (single) plane of the spire (Fig. 5A); in a biserial planispire, the septal apertures will alternate from one side to the other of the plane of the spire (Fig. 5B). In perfect equatorial section (i.e. in the plane of the spire), all successive septal apertures will be recognised if the test is uniserial (Fig. 4c), but, in the plane of section, only alternate septal apertures will be observed if the test is essentially biserial (Fig. 4a). The "not quite regularly arranged" chambers and septal apertures of the early stage of *C. boudecensis* Figs. 4a, b) alternate and are, therefore, a biseries (in a planispire or a very low trochospire). This is confirmed here by SEM (e.g. Pl. 3, fig. 2; compare the "adult" of Pl. 2, figs. 1-2).

With some schematic drawings, Cordey (1968) differentiated his new species, *C. eocaenica*, from *C. chipolensis* by its supposedly distinct initial, planispiral stage, to be seen even in the early portion of the last whorl, where the chamber sequence is indicated as a uniseries. This would seem to have confirmed the belief that the genus had evolved from a planispiral, uniserial ancestor. On the other hand, Banner & Blow (1959) and Blow (1979) apparently doubted the initial planispiral stage in *Cassigerinella* as described by Pokorný (1955) and Cordey *(op. cit.)*, and suggested that it may be a low trochospire instead. After re-examining the holotype and paratype specimens of *eocaenica* deposited in the British Museum (Nat. Hist.), the present writer has found that the type specimens, in fact, are not simply planispiral as shown in Cordey's drawings. The planispiral, uniserial character illustrated by him is an error for a compact arrangement of chambers which alternate within a planispire (see Fig. 6).

It is likely that the initial planispire in the specimens of *Cassigerinella* described by various authors, e.g. Egger (1857, pl. 11, figs. 4-7), Pokorný (1955, figs. 2-3, see above), Ivanova (1958, pl. 11, figs. 3a-c) and Cordey (1968, figs. 1e-h), was due to the misunderstanding of a series of chambers in compactly biserial coiling and to the externally small difference between that and a uniserial planispire when the apertural position is difficult to recognise. This is why the specimens of *Cassigerinella* figured by various authors including Blow (1969, 1979), Saito & Biscaye (1977) and Bolli & Saunders (1985) did not show any characters which can be related to a true uniserial planispiral coiling mode in the early stage of the ontogeny.

In view of the fact that neither satisfactory information from other studies nor evidence from our own observations on *Cassigerinella* can confirm any species of the genus being uniserially planispiral initially, it is now suggested that *Cassigerinella* is compactly biserial in the early growth stage (in a planispire or low trochospire) before leading to a typical biserial-enrolled low trochospire in the adult.

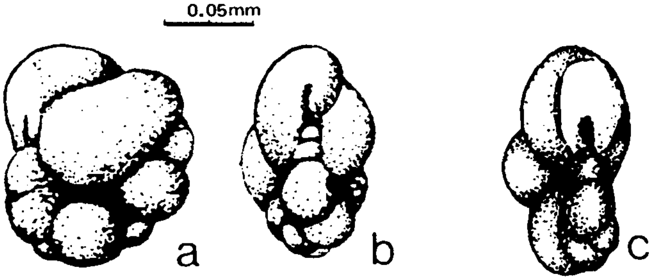

Fig. 6. *Cassigerinella eocaenica* Cordey, 1968 – a paratype: a and b, after Cordey (*op. cit.*, figs. d-e); c, a re-drawing based on the same specimen deposited in the B.M. (N.H.), no. P46839. This specimen is, in fact, an imperfect test with the last chamber missing. The planispiral coiling in the early portion of the last whorl indicated in fig. b is not accurate because the specimen shows compactly biserially coiling as in fig. c.

iv. **Emendation and Reclassification of *Cassigerinella***

Three characteristics of *Cassigerinella* revealed by this study, i.e. (a) pore-cone surface structure, (b) asymmetrical, alternating apertures and flanges, without a toothplate and (c) lack of a uniserial planispiral stage (i.e. biseriality is established throughout growth), can easily rule out any possibility that the genus should belong to the Globigerinidae as described by Pokorný (1958), Banner & Blow (1959) and Blow (1969, 1979), or to the Hantkeninidae as designated by Bolli, Loeblich & Tappan (1957) and Loeblich & Tappan (1964, 1984). On the other hand, strong resemblances do exist in the apertural characters and surface structure of *Cassigerinella* and of some heterohelicids.

The distinct pore-cone surface developed in one morphotype of *Cassigerinella chipolensis* has no parallel in any known Globigerinacean or Cassidulinacean, but is indistinguishable from that well known to be characteristic of certain Heterohelicaceans, e.g. *Guembelitria cretacea* Cushman (Maastrichtian) and *G. cenomana* (Keller) (Cenomanian-earliest Turonian) (e.g. Smith & Pessagno, 1973, pls. 1 and 2). Even though the Heterohelicacea have been extensively studied by many authors, there is no known stratigraphic or phyletic link between these two species of *Guembelitria* (e.g. Caron, 1985, pp. 40-41, 57), so it is not impossible that they, with their distinct pore-cone surface, arose independently from some *Globoconusa*-like ancestor; if so, then pore-cone structures could evolve iteratively in the Heterohelicacea during the Cretaceous and it is not impossible that they could do so again in that superfamily in the Palaeogene (the ultrastructure of the surface of *Guembelitria (Jenkinsina) stavensis* Bandy, of the Eocene, is not well known).

Biseriality has been shown in this paper to be a fundamental character of the coiling mode of *Cassigerinella*. Biseriality is also the dominant construction of most Heterohelicaceans, including all species of the Palaeocene – Oligocene genus *Chiloguembelina*. Significantly, the interiomarginal aperture of many species of *Chiloguembelina* (including the Palaeocene type species, *C. midwayensis* (Cushman) and the Early to Late Eocene *C. martini* (Pijpers), among others, is a high, narrow arch, asymmetrically placed laterally to the equatorial plane of the biseries, furnished with an equally asymmetrically developed apertural flange-like lip, and in a position "which alternates regularly within one specimen as a result of the biserial arrangement of the chambers" (Beckman, 1957, p. 86). This is an almost exact parallel to the apertural system of *Cassigerinella s.s.* (Fig. 7). In fact, if *Chiloguembelina* sp., similar to *C. martini* (see Fig. 7Ib) were to become enrolled in a planispire or low trochospire, it would become *Cassigerinella* like *C. winniana* or the smooth morphotype of *C. chipolensis*. It is suggested here that this evolution occurred abruptly in the Late Eocene to produce *winniana*, which, with further chamber inflation and trochospirality, became *chipolensis*, a species which iteratively developed pore-cones in one morphotype during the Oligocene. Lateral compression and increased narrowing and heightening of the aperture in the smooth morphotype could then evolve *C. (Riveroinella)* in the Early Miocene (but see further discussion below).

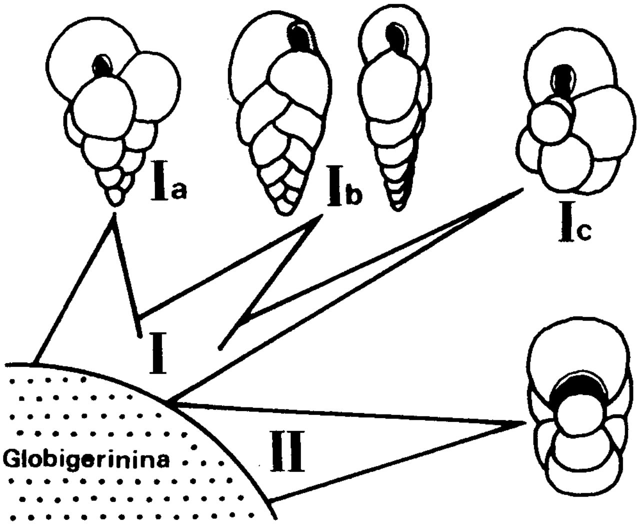

Fig. 7. Comparision of the coiling modes and modifications of the apertural position in the Heterohelicacea (I) and the Hantkeninidae (II).
Ia – triserial Guembelitriidae;
Ib – biserial Chiloguembelinidae;
Ic – biserial-enrolled Cassigerinellidae.

This confirms the conclusion originally reached by Blow (1979), because of the absence of a true umbilicus in *Cassigerinella*, and maintained by Kennett & Srinivasan (1983), that *Cassigerinella* should be placed in the Heterohelicacea; in order to exclude it from the rectilinear heterohelicids, an independent monogeneric family seems to be necessary. The emended description of the genus and the discussions on species which belong to (or have been assigned to, or considered to be related to) *Cassigerinella* are given below.

SYSTEMATICS

Order Foraminiferida Eichwald, 1830
Suborder Globigerinina Delage & Hérouard, 1896
Superfamily Heterohelicacea Cushman, 1927
Family Cassigerinellidae Bolli, Loeblich & Tappan, 1957
Genus *Cassigerinella* Pokorný, 1955

Type species. *C. boudecensis* Pokorný, 1955.
Emended Description. Test small, nearly planispiral or irregularly coiled in the first few chambers, becoming

low trochospiral in adult; always biserial-enrolled with the chambers alternating in arrangement in the coiling plane (as in *Cassidulina*); chambers 6-8 per whorl, relatively compressed and compactly together in early ontogeny but usually becoming strongly inflated, ovate to semiglobular in last whorl; wall calcareous, optically radial but granular in structure, sparsely pierced by small perforations; pores simple or surrounded by protruding rim-like pore-cones; aperture interiomarginally alternating, asymmetrical, highly arched to virguline in shape, without toothplate structure, but often with apertural rims or laterally asymmetrical flanges more-or-less developed (Late Eocene to Middle Miocene).

1. *Cassigerinella boudecensis* Pokorný 1955, and *C. chipolensis* Cushman & Ponton, 1932.

Remarks. Pokorný (1962, *in* Blow & Banner, 1962, p. 83) regarded his type species *boudecensis* as a synonym of *chipolensis* regardless of their different surface structures and the aperture pattern. From then on, many authors have grouped these forms, found in the Oligocene and the Early to Middle Miocene sequences, under the name *chipolensis* so that their combined, wide distribution pattern has become entrenched in the literature. However, according to the original descriptions, *boudecensis* is characterised by a papillose surface (= pore-cone structure here), usually with a highly arched aperture (e.g. Pl. 1) whilst *chipolensis* is distinguished by a smooth test, often with an elongate, narrowly-arched aperture (e.g. Pl. 4). The differentiation among these tiny forms with the aid of only a light microscope is often difficult, especially when the surface structure of the specimens has been degraded by poor preservation. However, our observations indicate that, as mentioned above, the smooth tests are essentially different from those with a pore-cone surface structure, though the sparsity and formation structure of the perforations seem to be consistent. In view of this, we would separate these two taxa by retaining the (type) species name *C. boudecensis* for forms with pore-cones, and to refer to *C. chipolensis* only those with smooth tests and with a high narrow aperture, as already done by Rögl (1985). It is difficult for us to accept the suggestion of Saito & Biscaye (1977) that *chipolensis* should include both those smooth and pore-cone morphotypes, when small differences of surface texture are often considered to be generic criteria (e.g. in the Globigerinacea by Kennett & Srinivasan, 1983). The forms with smooth tests might possibly have developed a secondary, crustal thickening as found in other planktonic species (see Bé & Lott, 1963) as pore-cones, but there is no other evidence for such crustal thickening in *Cassigerinella*. In contrast, there is the finding by Hofker (1963) that specimens with pore-cones (so-called 'pustules") were more common at stratigraphically lower levels (*opima opima* Zone) while the large, smooth tests dominated a higher horizon (*dissimilis dissimilis* Zone) in the Cipero sequences of Trinidad. Our view seems also adequate to explain why Blow (1969, 1979) did not mention any forms of *Cassigerinella* with a pore-cone surface structure, i.e. *C. boudecensis*.

2. *C. winniana* (Howe, 1939), *C. eocaenica* Cordey, 1968, and *C. globolocula* Ivanova, 1958.

Remarks. Blow (1979) discussed in considerable detail the relationship between *C. chipolensis* and *C. winniana* (a senior synonym of *eocaenica*), and suggested that they are undoubtedly closely related to each other or, possibly, represent a single evolving biological species. He separated these two taxa mainly according to the aperture character: long virguline-shaped in *chipolensis* and conversed triangular in *winniana* (which was also thought, incorrectly, to possess a longer uniserial-coiling in the early stage). This seems reasonable, as most *C. chipolensis* observed in this study do show a large, high aperture tending to be areal but rarely possess either narrowly elongate or rounded apertures. If this can become practicable, the USSR form *C. globolocula* should not be considered to be a synonym of *C. chipolensis* but rather of *C. winniana*. However, the variations of the aperture are so great that we would not like to recommend this as the only criterion for species differentiation. It is still uncertain to which taxon we should place those smooth tests with a somewhat rounded to areal aperture (Pl. 3, figs. 10-11; Pl. 4, fig. 8), but it is possible that they may be regarded merely as variants of *C. chipolensis*.

3 *C. globulosa* (Egger, 1857)

Remarks. Rögl (1985) referred those early Miocene *Cassigerinella* with smooth, compressed and ovate chambers to Egger's *C. globulosa*. However, the specimens figured by him are quite similar to some forms illustrated here (see Pl. 4, figs. 4, 5), which are also superficially identical to *C. winniana* of other authors (e.g. Blow, 1979; Bolli & Saunders, 1985), in spite of the fact that the latter taxon is from stratigraphically older sediments. We are sceptical about the validity of Rögl's suggestion but, on the other hand, we have not yet found any convincing evidence to prove it for the lack of available study material. The species *globulosa* might prove to be a juvenile of *chipolensis* or a stratigraphically younger variant of *winniana*, or it may even simply represent a senior synonym of the last of these. Its taxonomic status remains uncertain until the type specimens are adequately revised.

4. *"C." regularis* Iturralde Vinent, 1966

This species, so far reported only from its type locality (the Late Oligocene of Cuba) is remarkable not only for its very thick, finely perforate, smooth wall, many-chambered and peculiar coiling ("8 to 9 chambers visible in the central coil . . . 4 to 5 chambers in the lateral coils . . .") but also for its alleged alternation of microspheric and megalospheric generations. The last is not certainly known in either the Heterohelicacea or the Globigerinacea. The generic (and superfamily) assignment of this species is very doubtful, and is unlikely to be referable to *Cassigerinella*.

5. *Riveroinella martinezpicoi* Bermudéz & Seiglie, 1967

Remarks. The differences from *Cassigerinella* in the denser perforation pattern, the compressed chambers and apertural shape of *R. martinezpicoi* are still the main reason why we are unwilling to accept that *Riveroinella* should be considered to be a full synonym of *Cassigerinella s.s.* as suggested by Saito & Biscaye (1977); unfortunately, they paid little attention to its wall and surface structure, a key criterion for the discrimination of planktonic foraminifera. The species is not, as yet, known from areas other than within the Caribbean, an endemism which contrasts strongly with the cosmopolitan distribution of *Cassigerinella s.s.* It is possible that *martinezpicoi* was a late Oligocene-Early Miocene descendant of *C. chipolensis*, phylogenetically terminal and both morphologically and phylogenetically specialised for a particular proto-Caribbean palaeoenvironment (as yet unrecognised). Further study of the morphology and ultrastructure of these forms is necessary.

6. *Cassigerinelloita amekiensis* Stolk, 1963

Remarks. This species, described by Stolk (1963) from the Middle Eocene of West Africa (Nigeria), has been suggested by some authors (e.g. El-Naggar, 1971) to be a possible ancestor of *Cassigerinella*. Unlike the latter, it possesses a much inflated to globular test with several supplementary sutural apertures. The possible relationship between these two taxa has been questioned by Blow (1979), who suggested that *amekiensis* has been based on teratoid forms probably referable to a *Globigerinita* or to a small globigerinid morphotype. Some characters of this species as figured by Stolk (*op. cit.*), such as the low-arched aperture without rims or flanges and having a pore-pit surface structure, clearly indicate that it can not be considered to be ancestral to *Cassigerinella* (which, instead, is probably phylogenetically related to the Heterohelicacea as described above).

CONCLUSIONS

The characteristics of the principal species of *Cassigerinella* are summarised in Table 1. The evolutionary trends in this group seem to be: (1) coiling mode – biserially enrolled from nearly planispiral to low trochospiral, (2) test chambers – from compact, closely coiling to inflated and globular, (3) aperture – from rounded (symmetrical) to highly arched, virguline and narrowly elongate (assymmetrical) and (4) surface structure – from smooth to pore-coned, pustulate.

The results of a re-examination of *Cassigerinella* show that no specimens which are related to the genus possess an internal extending toothplate. The initial planispiral stage as described in earlier publications seems to be of no more than a pseudo-planispire of chambers compactly arranged biserially with an alteration of the apertural position in each pair of the biseries. The characters of these unique biserial-enrolled, pseudoumbilicate tests, sometimes with the unusual pore-cone surface, and almost always with asymmetrical flanges and high apertures suggest that the genus cannot be placed in the Globigerinacea or the Hantkeninacea, but has origin and place within the Heterohelicacea. Because of that, an independent, though monogeneric, family (the Cassigerinellidae) is necessary to achieve separation from other biserially built heterohelicids. It is probable that *Cassigerinella* (*C. winniana* or its as yet unknown ancestor) was derived from a tiny biserial chiloguembelinid ancestor in the Eocene and subsequently evolved through the Oligocene and Lower to Middle Miocene (*C. boudecensis, C. chipolensis, "C."(R.) martinezpicoi*).

Comparison of the different surface structures in the specimens from the Cipero Formation (and descriptions of previous studies) has led the present author to believe that they may be of supraspecific value. Therefore, the type species, *C. boudecensis* Pokorńy, is believed to be still valid and to include the forms with pore-cone surface structure.

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Table 1. Characteristics of the principal species of *Cassigerinella*

Species and Authors	Synonymy	Test/Chambers	Surface	Aperture	Stratigraphic Range
winniana (Howe, 1939)	*eocaenica* Cordey, 1968; ?*Cassidulina globulosa* Egger, 1857	compactly coiling	smooth	conversed triangular, rounded to areal	P14-P20 (Blow, 1979)
chipolensis (Cushman & Ponton, 1932)	*globolocula* Ivanova, 1958;	more inflated	smooth	highly arched to narrowly virguline	P18-N14 (Blow, 1979)
boudecensis Pokorny, 1955		inflated	with pore-cones	highly arched, asymmetrical	P18-?N14

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