Bicorniferidae: cheilostomatous Bryozoa with articulated colony branches

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Two lineages are distinguished in the Cenozoic anascan family Bicorniferidae, in which groups of zooecia are arranged in internodes, presumably connected by uncalcified joints. The lineage of *Bicornifera* is represented in the Paleocene by a species with internodes composed of four zooecia. During subsequent evolution the number of zooecia per internode was reduced to three, and the shape of the unit became more and more compact. Possibly also the size of the whole zoarium underwent reduction; in the end-member of the lineage, *Bifissurinella*, it was represented by a single triangular unit of three zooecia. In the second lineage of *Voorthuyseniella* connections between zooecia of particular branches were very fragile; consequently only isolated zooecia are found in the fossil record.

Key words: Bryozoa, Cheilostomata, Anasca, Bicorniferidae, microproblematica, biology, evolution, Cenozoic.

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Introduction

Voorthuysen (1949) identified in the Pliocene of the Netherlands *Lagena*-like shells (named *Lagena*-x), described as 'calcareous, milky white, imperforate, with three opening and one fissure' (Voorthuysen 1949: p. 31). They are now known to be more widely distributed and have been found in the Oligocene of Holland (Voorthuysen 1956), Late Miocene of Portugal (Ferriera & Rocha *in* Voorthuysen 1956), Oligocene of Germany (Kummerle 1963, Kummerle & Gunawardena 1967), Eocene of France and Belgium (Bignot 1962), Miocene of Taiwan (Huang 1962), and even in Recent sediments of the South China Sea (Keij 1964). Voorthuysen (1949) referred his *Lagena*-x (*Voorthuyseniella* Szczechura 1969) to the problematica.

Because the basal structures of the test are joint-like, Szczechura (1969) excluded *Voorthuyseniella* from the foraminifers and suggested that it represents a colonial or at least a sedentary form, possibly of protozoan affinity. In 1970 Keij distinguished numerous species of *Voorthuyseniella* (still as a problematicum) from sediments of different ages (Eocene-Recent) and different areas (Western Europe, North America, South China Sea). Finally, in 1977 Keij proposed that *Voorthuyseniella* 'is possibly an aberrant Bryozoa with its articulated zoaria consisting of uniserial, unicamerate internodes attached by an adoral rootlet to the substrate' (Keij 1977: p. 231).

Lindenberg (1965) described a similar microproblematicum, *Bicornifera*, which was supposed to have a calcareous, hyaline test consisting of two chambers of different size separated by a double wall. Keij (1977) studied *Bicornifera* and, partly following the observations of Poignant & Ubaldo (1973) on *Bifissurinella*, (a form supposedly having only two chambers) from the Early Miocene of France, identified simple pores in the walls between chambers as well as pores at the distal ends of some of his specimens. These observations allowed Keij (1977) to suggest that *Bicornifera* possessed uniserial internodes consisting of 3-4 zooecia separated by bilamellar walls perforated by simple septula and with terminal openings which suggest that the internodes were connected by flexible, uncalcified joints. Pores at the distal ends of spindles served as passage ways for parallel rootlets connecting the internodes. Keij distinguished proximal and distal ends in his studied specimens. Both *Bicornifera* and *Bifissurinella* were referred by Keij (1977) to his new family Bicorniferidae, placed within the anascan cheilostomatous Bryozoa.

Keij's view that *Voorthuyseniella* is an aberrant bryozoan close to *Bicornifera* and *Bifissurinella* was accepted by Ruggieri (1978) and Szczechura (1985). Szczechura (1985) pointed out that *Bifissurinella* represents a more integrated colony, with more individualised zooecia than in representatives of the *Bicornifera* group, especially the older ones.

Finger *et al.* (1986) studied the ultrastructure of *B. lagaaiji* and confirmed the observations of Haman *et al.* (1984) that '*Bicornifera lagaaiji* was attached to a substrate at the terminus of its proximal stem' (Finger *et al.* 1986: p. 352). In these authors' opinion in *B. lagaaiji* 'the proximal primary chamber forms prior to the distal primary chamber, as would be expected if the organism lived attached at its proximal stem' (Finger *et al.* 1986: p. 352).

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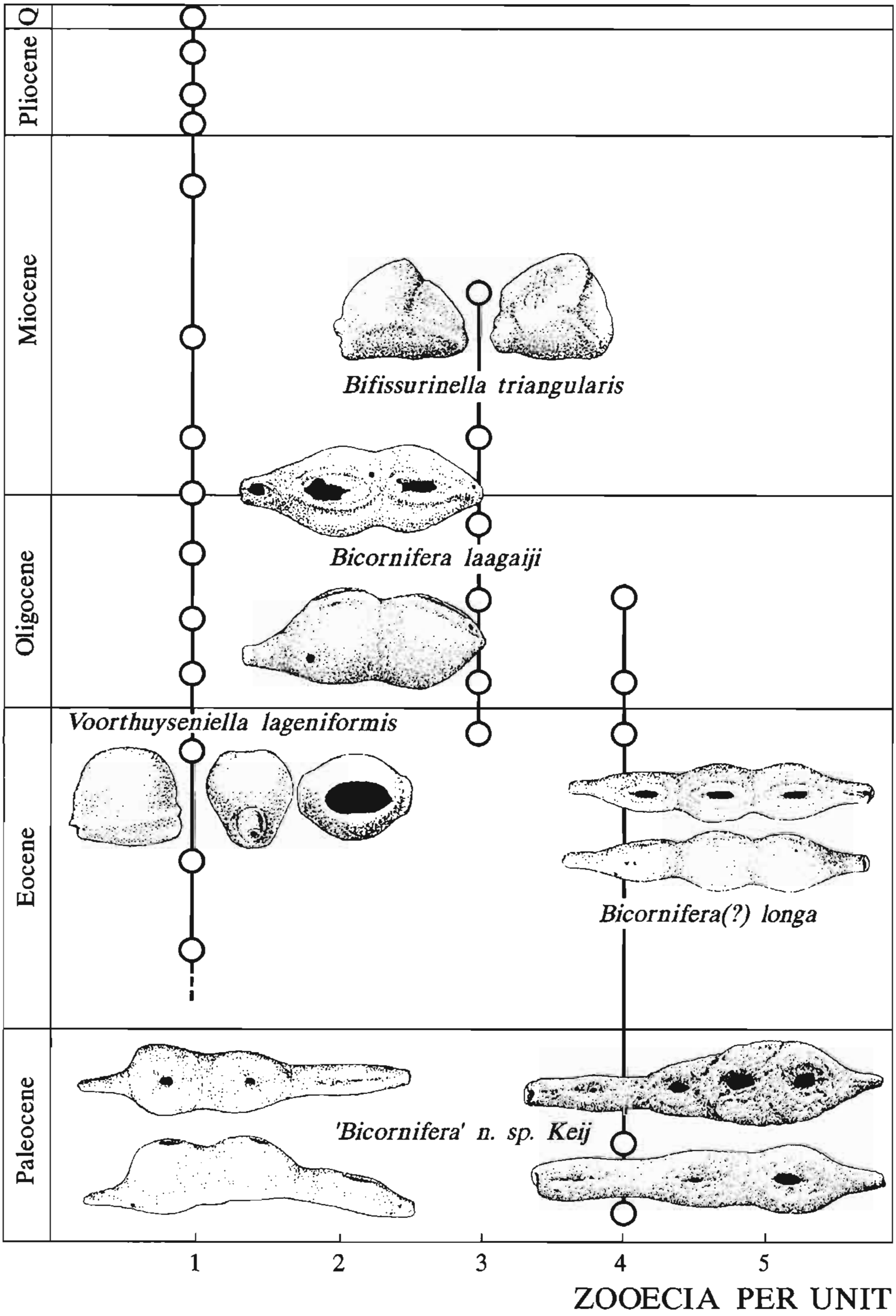
Fig. 1. Stratigraphic distribution and evolution of the Bicorniferidae. '*Bicornifera*' n. sp. Keij 1977 from the Early Paleocene of the Netherlands after Keij 1977, Pl. 1: 1, 2, *Bicornifera(?) longa* Lindenberg 1965 from the Late Eocene of NE Spain after Keij 1977, Pl. 1: 9, *Voorthuyseniella lageniformis* Szczechura 1969 from the Late Eocene of SE Poland after Keij 1970, Pl. 1: 9, *Bicornifera lagaaiji* Keij 1977 from the Late Oligocene of Alabama after Keij 1977, Pl. 1: 4, *Bifissurinella triangularis* Poignant & Ubaldo 1973 from the Early Miocene of SW France after Keij 1977, Pl. 2: 1, 2.


Q
Pliocene
Miocene
Oligocene
Eocene
Paleocene
Bifissurinella triangularis
Bicornifera laagaiji
Voorthuyseniella lageniformis
Bicornifera(?) longa
'Bicornifera' n. sp. Keij
1
2
3
4
5
ZOOECIA PER UNIT

In the present paper available evidence on the morphology and distribution of these fossils is reviewed and an interpretation of their evolutionary interrelationships is attempted.

The material described is housed at the Institute of Paleobiology of the Polish Academy of Sciences in Warsaw (abbreviated ZPAL).

Morphology of zoarial units in the Bicorniferidae

Voorthuyseniella, *Bicornifera* and *Bifissurinella* have similar external as well as internal morphologies. Their basic structural unit (chamber) is more or less bulbous and provided with three openings. One of these openings, i.e. the aperture, is always oriented upwards, whereas the two others are situated terminally and laterally, opposite each other, at the base of the chamber. The specimens referred to *Voorthuyseniella* have only one such chamber, while *Bifissurinella* consists of two chambers, arranged in a row, and *Bicornifera* has two or more (up to four) chambers. The number of chambers is thus always small.

In *Bifissurinella* and *Bicornifera* a third, smaller chamber was added terminally to the row of chambers. This third chamber seems also to exist in at least some specimens of *Voorthuyseniella*. It has been found in a specimen from the Eocene of Poland, identified as *V. lageniformis* Szczechura 1969, in which it is separated by a septum-like wall (Fig. 3A, F). Keij (1970) and Szczechura (1969) observed septa at both ends of the chambers of *Voorthuyseniella*.

Another internal structure, sometimes present in representatives of *Voorthuyseniella* (Fig. 3C), is a neck-like rim surrounding the basal opening. This basal opening is unknown in *Bicornifera* and *Bifissurinella*.

In all the polycamerate forms (*Bicornifera* and *Bifissurinella*) the neighbouring, large chambers are connected by intercamerate pores. The proximal end is open, while the distal end is open or closed in *Bicornifera*, and invariably closed in *Bifissurinella*.

Unicamerate units of *Voorthuyseniella* have different endings. One of them (Fig. 4B, C, I), pierced by an opening, is joint-like and was probably articulated with a neighbouring unit. The opposite end (at least in some specimens) (Fig. 2A, C, F) is supported (bounded) by two buffer-like short spines and is pierced by at least one large opening (Fig. 3G); it seems to be free. If this interpretation is correct, the joint-like end in *Voorthuyseniella* corresponds to that part of the test in *Bicornifera* and *Bifissurinella* where two chambers adhere, while the free end corresponds to the distal end of *Bicornifera* and *Bifissurinella*. This would mean that *Voorthuyseniella* was at least a bicamerate form, like *Bicornifera* and *Bifissurinella*.

In the oldest bicorniferids, e.g. *'Bicornifera'* sp. n. of Keij 1970 (Fig. 1), from the Paleocene of the Netherlands, chambers are most numerous (up to four) and relatively variable in shape. Younger bicorniferids, e.g. *Bicornifera(?) longa* Lindenberg 1965 (Fig. 1), as described and figured by Keij

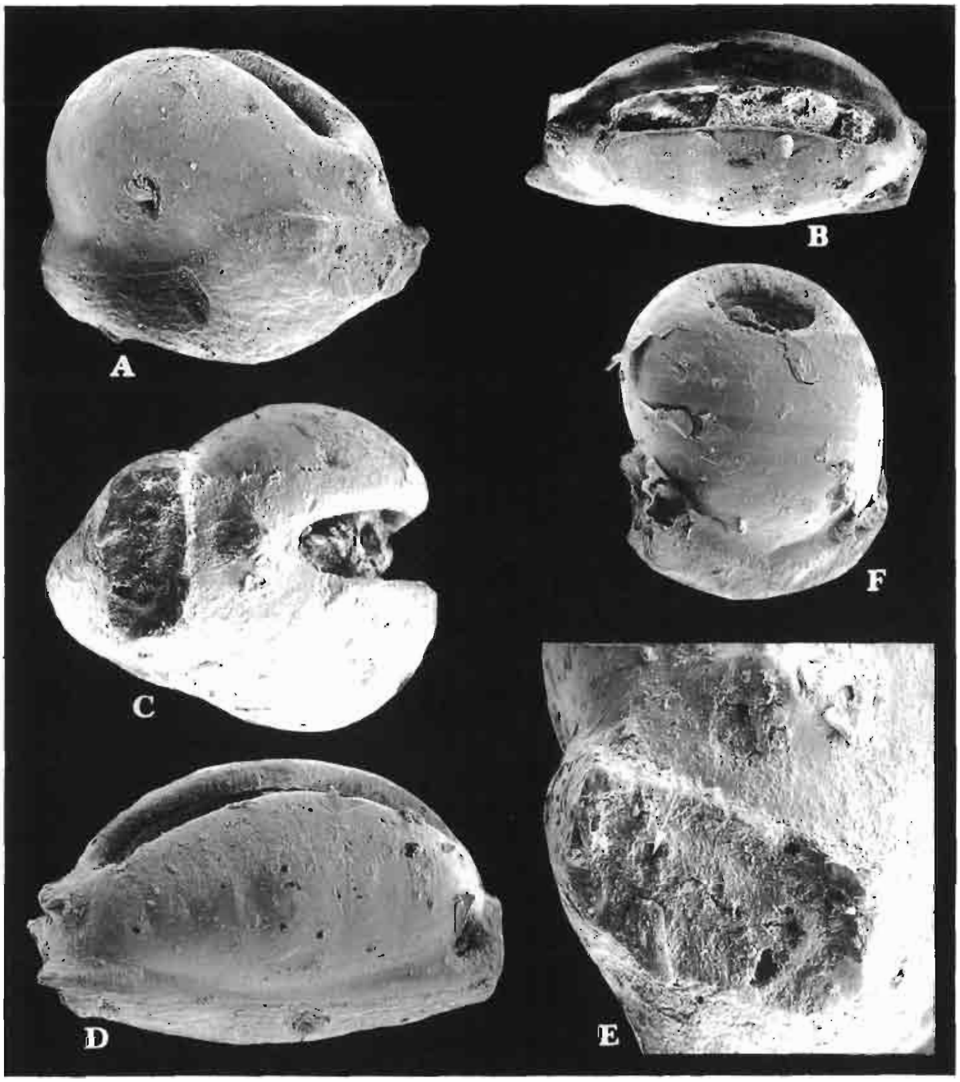


Fig. 2. *Voorthuyseniella lageniformis* Szczechura 1969, Late Eocene, Siemień near Parczew (SE Poland). ❑A-E. Elongated and laterally compressed zooecium ZPAL V II/17. A. Somewhat oblique, lateral view, × 130. B. frontal view, × 100. C. End view showing buffer-like protuberances and rootlet pores, × 160. D. Lateral view, × 140. E. Enlarged details of the terminal end showing buffer-like protuberances and rootlet pores, × 400. ❑F. Globular zooecium ZPAL V II/5, lateral view, × 160.

(1977) from the Late Eocene of Spain, have chambers less numerous, more regular (uniform) in shape, less variable in size and more regularly and tightly arranged. In even younger bicorniferids, e.g. *Bicornifera lagaaiji* Keij 1977 (Fig. 1) from the Late Oligocene of Alabama, there are only two primary, rather tightly joined chambers. Representatives of *Bifissurinella* from the Neogene of Europe, e.g. *B. triangularis* Poignant & Ubaldo 1973

(Fig. 1) from the Early Miocene of France, have much more compact and more closely joined chambers than *Bicornifera lagaaiji*. The bilamellar test wall in *Bicornifera* (Lindenberg 1965, Finger *et al.* 1986) indicates that individual chambers were independently secreted (Haman *et al.* 1984).

Skeletal units of *Bicornifera* and *Bifissurinella* are uniserial fragments of colonies, i.e. internodes or terminal segments connected by non-fossilized organic parts. In *Voorthuyseniella*, the additional basal opening probably served for a rootlet system, strengthening the colony structure and its attachment to the substrate.

Since no specimens have been found cemented to the substrate the basal parts of colonies were probably not mineralized in the bicorniferids. Haman *et al.* (1984: p. 318) proposed that '*Bicornifera* was attached at its proximal end and not in contact with the sea floor'. Keij (1970) suggested even that *Voorthuyseniella* was an infaunal or nectonic organism.

The great variability of skeletal units within samples of *Voorthuyseniella*, *Bicornifera* and *Bifissurinella* may reflect differences in their positions within the colony. This poses taxonomic difficulties.

Bryozoan affinities of the Bicorniferidae

The Bicorniferidae occur mostly in shallow-water, marine, non-consolidated sediments, and generally are associated with other bryozoan remains. Their zooecia share the same range of size as typical bryozoans. Haman & Kohl (1976a) counted the relative contribution of *Voorthuyseniella* and bryozoans to samples from an Eocene-Oligocene section in the Little Steve Creek in Alabama. They found that 'the abundance of *Voorthuyseniella* appears to correlate with the abundance of bryozoan debris' (Haman & Kohl 1976a: p. 150), and they concluded that these organisms had similar environmental requirements.

The tests of *Voorthuyseniella*, *Bicornifera* and *Bifissurinella* differ greatly in their states of preservation, especially their terminal ends as well as the apertures. The apertures may be simple, round or elongate (depending on the shape of the chamber), and are sometimes surrounded by elevated (even rimmed) shields (Haman 1981, Liszka 1974). Perforated structures around the aperture reminiscent of cryptocysts or calcified frontal walls of blind zooecia(?) were observed in *Bifissurinella* from the Miocene of the Central Paratethys by Szczechura (1985). Calcification of the frontal wall may be present or absent (lost?, damaged?) in anascan cheilostomes associated with the bicorniferids in the Paleocene of Poland. All this means that specimens of the Bicorniferidae with these shields represent more completely calcified zoarial units.

As already pointed out, the terminal ends of the tests of the Bicorniferidae are joint-like structures suggesting that these tests were the segments of articulated colonies. Similar joint-like ends may be seen around isolated zooecia of some articulated cheilostomatous Bryozoa associated with *Bifis-*

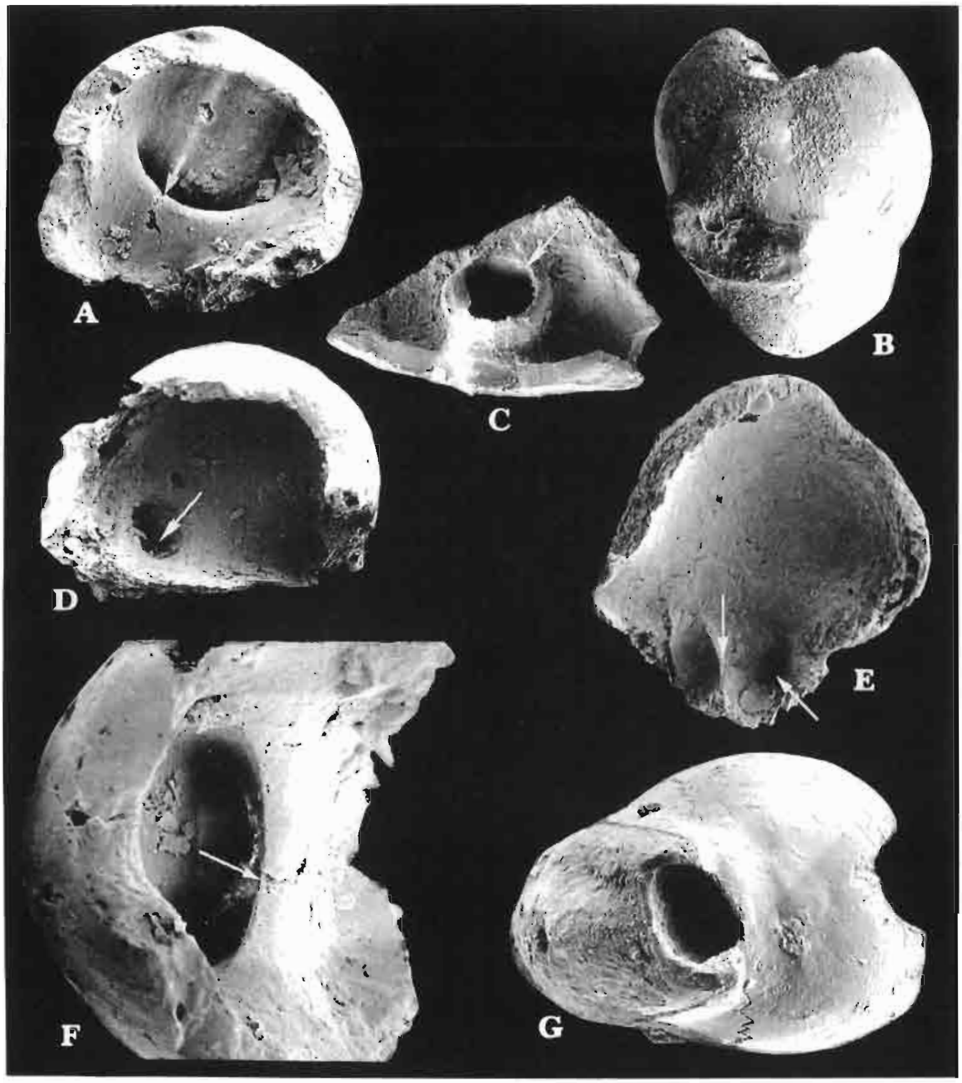


Fig. 3. *Voorthuyseniella lageniformis* Szczechura 1969, Late Eocene, Siemień near Parczew (SE Poland). ❑A, F. Fragment of zooecium ZPAL V XX/1. A. Inner view showing a septum-like wall, × 160. F. Enlarged septum-like wall seen from above, × 400. ❑B. Elongated zooecium in end view ZPAL V II/23, × 160. ❑C. Fragment of zooecium, inner view showing a neck-like ring, ZPAL V XX/2, × 200. ❑D. Damaged zooecium, inner view showing lateral, basal opening, ZPAL V XX/3, × 130. ❑E. Fragment of zooecium, seen from inside and showing a neck-like ring and lateral, basal opening, ZPAL V. XX/4, × 150. ❑G. Elongated zooecium in end view, ZPAL V XX/5, × 200.

surinella (Fig. 4D-H) in the Middle Miocene of the Vienna Basin (Austria). Like the bicorniferids they vary greatly in size and shape.

All these observations indicate, that the Bicorniferidae are aberrant bryozoans. Their oldest representatives from the Paleocene resemble some less derived bryozoans. The Late Cretaceous and Paleocene encrusting bryozoan *Fissuricella* Voigt 1959 had somewhat similar longitudinally elongated opesia (Lindenberg 1965, Keij 1977). The Bicorniferidae may have a similar colony form to *Planicellaria*, *Scrupocellaria*, *Stamenocella* and other bryozoans (Keij 1977).

Lindenberg (1965) found that the aboral opening in *Bicornifera* is similar to that in *Pseudarcella* Spandel 1909 which sometimes cooccurs with the bicorniferids. This fossil had been referred to the foraminifers, calpionellids or tintinnids until Bignot (1989) erected a new systematic unit, Pseudarcellides, and classified it among the microproblematica. In my opinion the pseudarcellids have many features in common with the bicorniferids and could be related to them.

It may be thus concluded that the Bicorniferidae Keij 1977 is a bryozoan family within the Cheilostomata Anasca.

Species concepts in the Bicorniferidae

In 1970 Keij distinguished numerous species of *Voorthuyseniella* (still as problematical taxa) from sediments of different ages (Eocene-Recent) and different areas (Western Europe, North America, South China Sea). Even more species were proposed by subsequent authors (Poignant & Ubaldo 1973, Willems 1975, Spiegler 1976, Haman & Kohl 1976a, b, Ruggieri 1978, Haman 1978, 1979, 1981, Haman & Bailey 1983 and Poignant 1990). By 1990 almost 40 species (including 19 new) had been erected. According to Spiegler (1976) particular species of *Voorthuyseniella* are characteristic of different ages from the Eocene up to Recent in different areas of the world.

The specimens referred to the numerous species of *Voorthuyseniella* differ in their morphological details as a result of varying states of preservation as well as variations in the shape of the internode, the shape of the substrate and other factors. I am unable to find any features of taxonomic value which would allow delimitation of boundaries between species within this genus.

Lindenberg (1965) distinguished two species within *Bicornifera*: *B. alpina* and *B. longa*. The characters used to separate these species concern the general appearance of the tests, i.e. length: height ratio, shape of openings and distinctness of sutures between chambers. However in 1969 Keij described *Bicornifera* n. sp. from the Late Oligocene of Alabama intermediate in size between *B. alpina* and *B. longa*. Liszka (1974) distinguished a species of *Bicornifera* in the Late Eocene and Early Oligocene of the Polish flysch Carpathians with four instead of two large chambers of similar size, all tightly arranged. He suggested also that specimens from the same strata determined by Grzybowski (1894) as *Marginulina ostiata* (Foraminifera) may belong to *Bicornifera*. Keij (1977) introduced another new species, *B. lagaaiji* from the Late Oligocene of Alabama, and identified

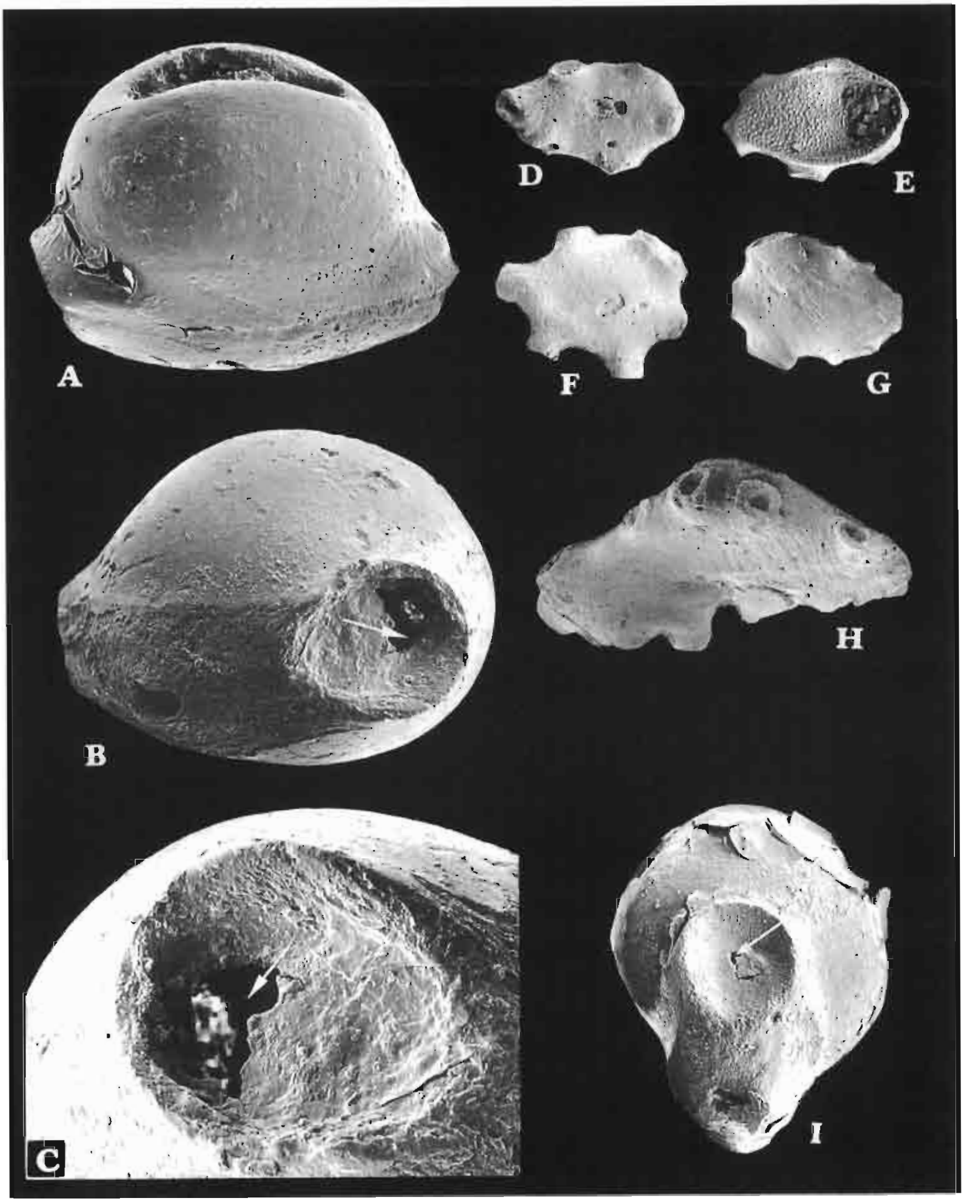


Fig. 4. A-C, I. *Voorthuyseniella lageniformis* Szczechura 1969, Late Eocene, Siemień near Parczew (SE Poland). ❑A. Elongated zooecium, external lateral view, ZPAL V II/18, × 160. ❑B, C. Elongated zooecium in outer view, ZPAL V XX/6. B. End view showing a joint-like terminal end pierced by an opening, × 200. C. Enlarged details of the joint-like terminal end pierced by an opening, × 400. ❑I. Bulbous zooecium in external end view, showing a joint-like terminal end pierced by an opening, ZPAL V XX/15, × 160. D-H. Cheilostomatous bryozoan zooecia, Middle Miocene, Sooss, Vienna Basin (Austria). ❑D, F-H. Back sides showing joint-like terminal ends, ZPAL V XX/7-10, × 40, except for H, which is × 60. ❑E. Zooecium seen frontally, ZPAL V XX/11, × 40.

B. n. sp. from the Paleocene of the Netherlands. In opposition to this general trend a large intraspecific rather than interspecific variation within the genus has been pointed out (Szczechura 1990). Also Haman *et al.* (1984) found a considerable variation concerning the external morphology of their specimens of *Bicornifera*; in the opinion of these authors some structures in *Bicornifera* (e.g. closure of their distal ends) are unstable. In consequence the differences used to distinguish various species of *Bicornifera* are actually not sufficient to separate them.

Poignant & Ubaldo (1973) described *Bifissurinella* as a monospecific genus. In 1977 Keij added more species, including one formerly referred by him to *Bicornifera*. Species of *Bifissurinella* distinguished by Keij differ in size, general appearance, morphological details and especially the so-called carina. The last feature, if present, always varies in shape and arrangement.

Additional representatives of *Bifissurinella* have been since reported (Szczechura 1985), including one supported with distinct terminal corn-like protuberances. These species shows great variability. *Bifissurinella cornifera* varies in its general shape and size as well as more subtle morphological details. The dorsal side of the zoarium may be rounded or flattened depending on the morphology of the substrate to which it was attached. Thus these features can hardly be of taxonomic value.

Therefore the numerous species so far attributed to the Bicorniferidae do not seem to be biologically meaningful. Diagnostic features on which they were created are insufficient to distinguish different populations of colonies. Other criteria to distinguish species and genera within this group of microfossils should be chosen, criteria that take account of their nature as fragments of colonial organisms. The profound morphological changes in the evolution of the group suggest that it may have some stratigraphical value.

Evolution of the Bicorniferidae

The oldest representative of the family (Fig. 1) is known (as *Bicornifera* n. sp.) from the Paleocene of the Netherlands (Keij 1977) and (as *B.* sp.) from the Paleocene of Poland (Szczechura 1990). This *'Bicornifera'* produced much elongated internodes of unstable size and shape, with zooecia that also vary in shape being more or less tightly packed up to four in number.

Species of both *Voorthuyseniella* and *Bicornifera*(?) occur in the Eocene. The oldest known *Voorthuyseniella* is *V. bearnensis* Poignant 1990 from the Early Eocene of SW France (Aquitanian Basin). Younger species of *Voorthuyseniella* are known from the Netherlands, Belgium, France, Italy (Sicily), Portugal, Spain, Germany and Poland as well as from Alabama, Texas, Louisiana and Taiwan. Since the Eocene (up to Recent) the geographical extent of *Voorthuyseniella* has enlarged and reached the South China Sea and the Gulf of Mexico.

It is probable that in the early Paleogene (?Eocene) *Voorthuyseniella* emerged from the ancestor of the true *Bicornifera*. The Eocene *Bicornifera*(?) species from Spain assigned by Keij (1977) to *B. longa* Lindenberg 1965 (Fig. 1) has internodes more regular in their general appearance, still consisting of up to four zooecia (generally with a distinct smaller kenozooecium) that are generally more evenly and more tightly packed. In their overall appearance they are intermediate between the type species of *Bicornifera* and the Paleocene *'Bicornifera'*. Eocene species of the *Bicornifera* group are known only from Europe: Spain and the Polish Carpathians. Specimens from Poland, referred by Liszka (1974) to *B. longa* are associated with other representatives of the *Bicornifera* group (consisting of four very compact zooecia) that seem to represent an endemic form.

Bicornifera(?) *longa* persisted up to the Oligocene in Austria and Turkey, but close to the end of the Eocene the typical *Bicornifera* (including the type species *B. alpina* Lindenberg 1965) appeared in Poland. *Bicornifera* is known also from the Oligocene of Europe (Austria, France, Yugoslavia, Poland) as well as from the Oligocene of the Gulf Coastal Plain and Mississippi. In comparison with its Eocene ancestors it is represented by rather short, compact, similarly shaped internodes, consisting of only two large, tightly packed zooecia and one small kenozooecium.

Bifissurinella is an obvious descendant of *Bicornifera*. It is known from Europe only, i.e. from the Oligocene of France and Germany, and from the Miocene of France and Italy as well as the Central Paratethys (Austria, Poland). It is represented by triangular segments of articulated zoaria consisting of three tightly joined zooecia (two autozooecia and one kenozooecium). The presence of a so-called carina (Keij 1977) proves that it was a sessile organism. Frontal walls of the kenozooecia in *Bifissurinella* may be supported with horn-like protuberances (Szczechura 1985). *Bifissurinella* seems to be the most specialized form of the Bicorniferidae.

If *Bifissurinella* zoarial units really represent complete colonies (in contrast to internodes in other Bicorniferidae), in the evolution of Bicorniferidae there was a tendency not only to diminish the number of zooecia and to strengthen their connections within internodes but also to reduce the size of the colonies.

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Streszczenie

Od ponad 40 lat znane są z osadów kenozoicznych mikroskamieniałości wapienne zaliczane do rodzajów: *Bicornifera* Lindenberg 1965, *Voorthuyseniella* Szczechura 1969 (= *Lagena*-x Voorthuysen 1949) i *Bifissurinella* Poignant i Ubaldo 1973. Liczne gatunki wyróżnione w obrębie tych rodzajów zaliczane są (na ogół) do mikroproblematyków bądź mszywiołów Cheilostomata, Anasca; Keij (1977) zaliczył *Bicornifera* i *Bifissurinella* do nowej rodziny Bicorniferidae.

Autorka uznaje pogląd, że wymienione mikroskamieniałości należą do mszywiołów (Cheilostomata, Anasca) i że reprezentują one tę samą rodzinę Bicorniferidae. Jest też zdania, że *Voorthuyseniella* reprezentuje pojedyncze zooecia (za życia połączone w segmenty), natomiast *Bicornifera* i *Bifissurinella* to kompletne segmenty kolonii osiadłych, płożących. Segmenty te składały się z nielicznych (3-4) zooeciów ułożonych szeregowo; także segmenty tworzyły szeregi.

Zdaniem autorki skamieniałości te pochodzą od wspólnego przodka t.j. paleoceńskich przedstawicieli "*Bicornifera*", występujących w osadach centralnej i NW Europy. W eocenie nastąpiło oddzielenie się od pozostałych bicorniferidów linii *Voorthuyseniella*, która w raczej niezmienionej postaci przetrwała do dziś.

Druga linia bikorniferidów uległa szybkiej ewolucji w kierunku kompakcji, oraz redukcji liczby zooeciów i ich specjalizacji; wydaje się też że nastąpiła redukcja wielkości kolonii i jej ściślejszy związek z podłożem.