

# An unusually large Cyclostome Bryozoan (*Pennipora anomalopora*) from the Upper Cretaceous of Maastricht

by Paul D. TAYLOR & Ehrhard VOIGT

## Abstract

*Pennipora anomalopora* (UBAGHS, 1858) is an erect branching species of cyclostome bryozoan (Family Cerioporidae BUSK) found rarely and only in the Maastrichtian of the Maastricht region. A large and spectacular colony was discovered in 1994 by Fred Michon in the Meerssen Mbr of the Maastricht Fm in the ENCI NV Quarry. This may be the largest Mesozoic cyclostome colony ever found. The branches have well-developed monticules, and sectioned branches reveal the characteristic difference in orientation between autozooezia and kenozooezia, as well as numerous brood chambers which are partially subdivided by internal septa-like walls. Dark growth bands observed within the endozone of a longitudinally sectioned branch are an average of 2.9 mm apart. These bands appear to coincide with levels of brood chambers in the exozone. If larval brooding occurred annually then a distal branch growth rate of about 3 mm per year can be inferred, indicating that the colony lived for more than 35 years.

**Key-words:** Bryozoa - Cretaceous - Netherlands - growth rate.

## Résumé

*Pennipora anomalopora* (UBAGHS, 1858), un bryzoaire cyclostome (Famille Cerioporidae BUSK) branchu et dressé, est une espèce rare qui ne se rencontre que dans le Maastrichtien de la région de Maastricht. Une spectaculaire colonie de grande taille fut découverte en 1994 par Fred Michon à la carrière ENCI NV, dans le Membre de Meerssen de la Formation de Maastricht. Elle est peut être la plus grande colonie de cyclostome mésozoïque jamais trouvée. Les branches présentent des monticules bien développés et les branches sectionnées montrent la différence d'orientation caractéristique entre les autozoécies et les cénozoécies ainsi que de nombreuses chambres d'incubation partiellement divisées par des cloisons internes semblables à des septa. Des bandes de croissance sombres, observées dans l'endozone d'une branche coupée longitudinalement, sont distantes d'environ 2,9 mm. Ces bandes semblent coïncider avec les niveaux de chambres d'incubation de l'exozone. Si l'incubation larvaire avait lieu annuellement, on peut déduire une croissance de la partie distale de la branche d'environ 3 mm par an, ce qui indiquerait que la colonie a vécu plus de 35 ans.

**Mots-clefs:** Bryozoa - Crétacé - Pays-Bas - Taux de croissance.

## Kurzfassung

*Pennipora anomalopora* (UBAGHS, 1858) ist eine seltene erekt-verzweigte cyclostome Bryozoenart (Family Cerioporidae BUSK), die nur im Maastrichtium der Maastrichter Region gefunden wurde. Eine dramatisch grosse Kolonie wurde 1994 von Fred Michon in den

Meerssen-Schichten der Maastricht-Formation im Steinbruch ENCI NV entdeckt. Es koennte sich hierbei um die groesste jemals gefundene cyclostome Bryozoen-Kolonie mesozoischen Alters handeln. Die Zweige zeigen deutlich entwickelte Monticuli. An Duennschnitten kann ein charakteristischer Unterschied hinsichtlich der Orientierung der Auto- und Kenozooezien gezeigt werden sowie zahlreiche Ovicellen, die bisweilen durch innere septenartige Waende unterteilt sind. Dunkle endozonale Wachstumsbaender eines laengsgeschnittenen Zweiges zeigen einen Abstand von durchschnittlich 2.9 mm. Diese Baender scheinen mit Ovicellen-Lagen innerhalb der Exozone Uebereinzustimmen. Falls Larven im Jahresrhythmus ausgebruetet wurden, waere auf eine jaehrliche Wachstumsrate von etwa 3 mm zu schliessen. Fuer die Kolonie ergebe sich damit eine Lebensdauer von ueber 35 Jahren.

**Key-words:** Bryozoa - Kreide - Niederlande - Wachstumsrate

Following von HAGENOW's (1851) early monograph of the type Maastrichtian bryozoan fauna dealing with more than 170 species, HAMM (1881) was the first to recognise and describe the new bryozoan genus *Pennipora* from Maastricht. His description included only a single new species - *P. beyrichi* - named for Professor August H. E. Beyrich (1815-1896). HAMM characterized this species as having an erect, stem-like, ramified colony, with zooecia in the middle of the stem arranged irregularly, and showing larger zooecia surrounded by a pinnate-like arrangement of zooecia of slightly smaller size, hence the name *Pennipora*. No figures were given by HAMM. In his revision of HAMM's paper, VOIGT (1953) provided a full description of *P. beyrichi* and comprehensively figured the species, using the term "Kapsel" for some structures then of uncertain origin but which can now be interpreted as brood chambers. Whereas VOIGT (1953) questionably included *Nodicrescis anomalopora* UBAGHS, 1858 in synonymy with *P. beyrichi*, a new consideration of UBAGHS' description substantiates this synonymy and UBAGHS' species is here given priority over HAMM's. In particular, figure 4 of UBAGHS (1858) shows very clearly the thick, tapering branches with prominent monticules which are a characteristic of *Pennipora*.

BASSLER (1953, p. G77), in the bryozoan *Treatise*, questionably accepted *Pennipora* as a valid genus, not-

ing the “feather-shaped arrangement of tubes and mesopores in longitudinal section”, but inexplicably assigned the genus to the Eleidae. This family, often referred to as the melicerititids, is characterized by operculate zoecia which are clearly not present in *Pennipora*.

*Pennipora* remains a monospecific genus with its sole species being known only from the Upper Maastrichtian of the Maastricht region where it is extremely rare. In 1994, Fred Michon, collecting in the ENCI NV Quarry, discovered numerous branch fragments which were subsequently reassembled into a large colony of *Pennipora anomalopora* (JAGT & MICHON, 1995). This remarkable colony (Fig. 1) is the main subject of this short paper. The unusual internal structure of the branches has been studied using scanning electron microscopy, and inferences are made about the growth rate and age of the colony based on the growth banding visible in some branches.

Order Cyclostomata BUSK, 1852  
Family Cerioporidae BUSK, 1859  
Genus *Pennipora* HAMM, 1881

*Pennipora anomalopora* (UBAGHS, 1858)

- \* 1858 - *Nodicrescis anomalopora* - UBAGHS, p. 130, pl. 26, figs 4-5.
- 1881 - *Pennipora beyrichi* - HAMM, p. 37.
- 1909 - *Heteropora anomalopora* (UBAGHS) - GREGORY, p. 198.
- 1909 - *Pennipora beyrichii* HAMM - GREGORY, p. 302.
- 1953 - *Pennipora beyrichi* HAMM - VOIGT, p. 58, pl. 1, figs 1-5, pl. 2, figs 1-4, pl. 3, figs 1-7.
- 1995 - *Pennipora beyrichi* HAMM - JAGT & MICHON, p. 11, pls 1-2.

MATERIAL

Natuurhistorisch Museum Maastricht No. 1997130,  
Maastricht Fm, Meerssen Mbr, ENCI NV Quarry, near

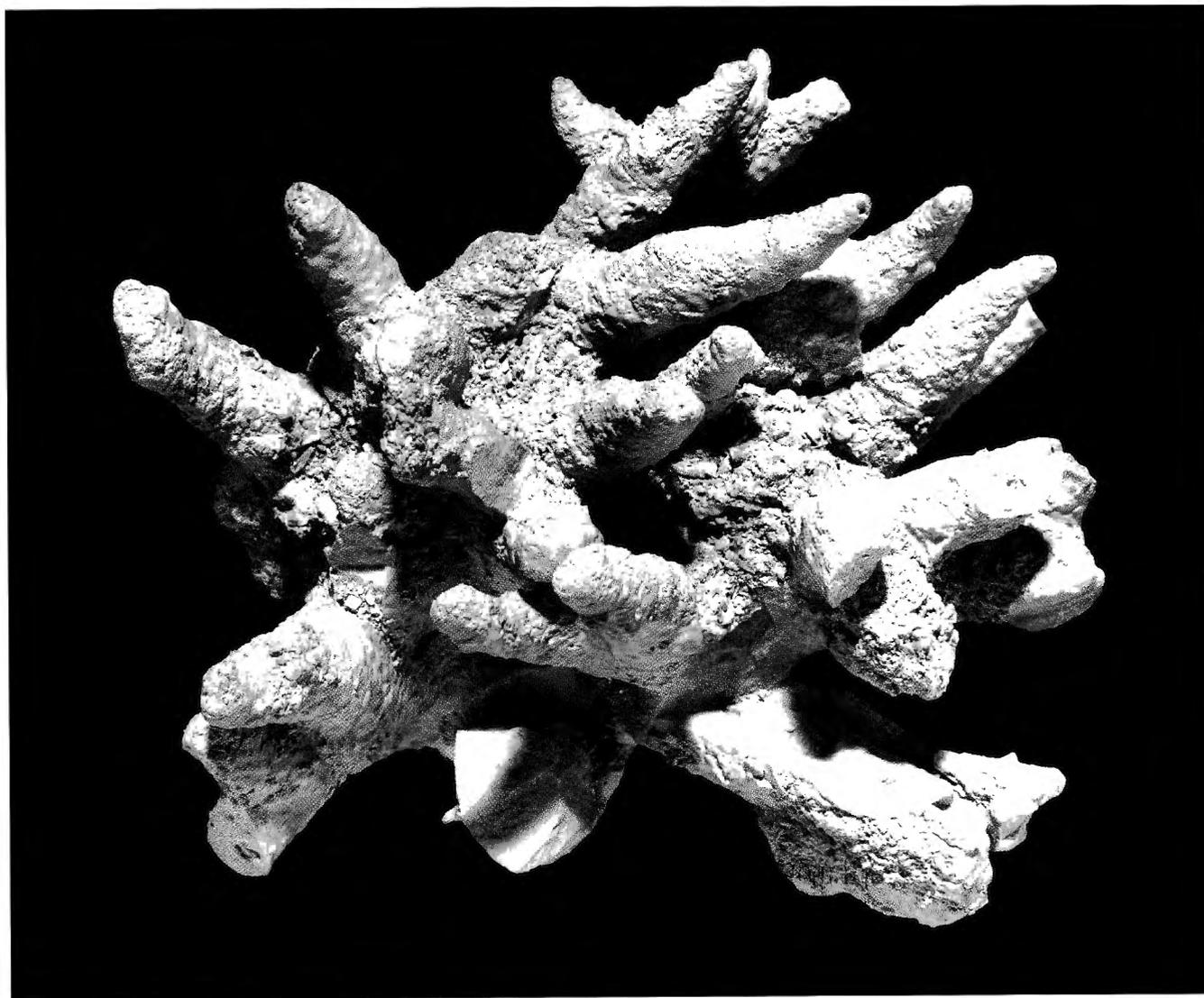


Fig. 1 - *Pennipora anomalopora* (UBAGHS, 1858). Maastrichtian, Maastricht Fm, Meerssen Mbr; ENCI NV Quarry, near Maastricht, The Netherlands; Natuurhistorisch Museum Maastricht No. 1997130. x 0.7.

Maastricht, The Netherlands. Branch fragments from this specimen are in the Voigt Collection, Hamburg, registered as Nr 15024 and SEM stubs as Nr 14144-7.

#### DESCRIPTION

The new specimen (Fig. 1) has a maximum dimension of 21 cm. However, the base is apparently not preserved and some branches are broken; therefore, the full size of the colony during life cannot be ascertained but was undoubtedly larger. The colony has a branching, dendroid morphology, comprising thick branches which bifurcate occasionally. Branches have a distinctive finger-like shape (Fig. 2.1), tapering gently in diameter towards the rounded distal apex. At these growing tips, branch diameter is about 5 mm, 20 mm proximally of the growing tip it has increased to about 15 mm, while the thickest branches yet more distant from growing tips may attain diameters of at least 22 mm.

Branch surfaces are everywhere covered by prominent monticules (Figs 2.1, 3.1). These rounded hummocks are

spaced about 4 mm apart measured centre to centre, and measure about 3 mm in diameter. The height of the monticules above intermonticular regions is 0.5 mm.

Zooecial apertures open on the branch surface and are polygonal to rounded in shape (Fig. 3.5) and small, measuring about 0.07-0.11 mm in diameter. In some areas between monticules it is possible to distinguish slightly larger, more rounded apertures surrounded by smaller, more angular apertures (e.g. VOIGT, 1953, pl. 1, figs 1-2). The former are interpreted as autozoecia (feeding zooids) and the latter (the "mesopores" of VOIGT, 1953) as kenozoecia (non-feeding polymorphs). Monticule summits do not show this dimorphism. Instead, they tend to be abraded and/or may have zooecial tubes oriented subparallel to the colony surface.

No thin sections are available but fractured and sawn branches adequately reveal the internal morphology of the colony (Figs 2.2, 3.2, 3.3). Branches have an axial endozone in which the zooecia are oriented parallel to the

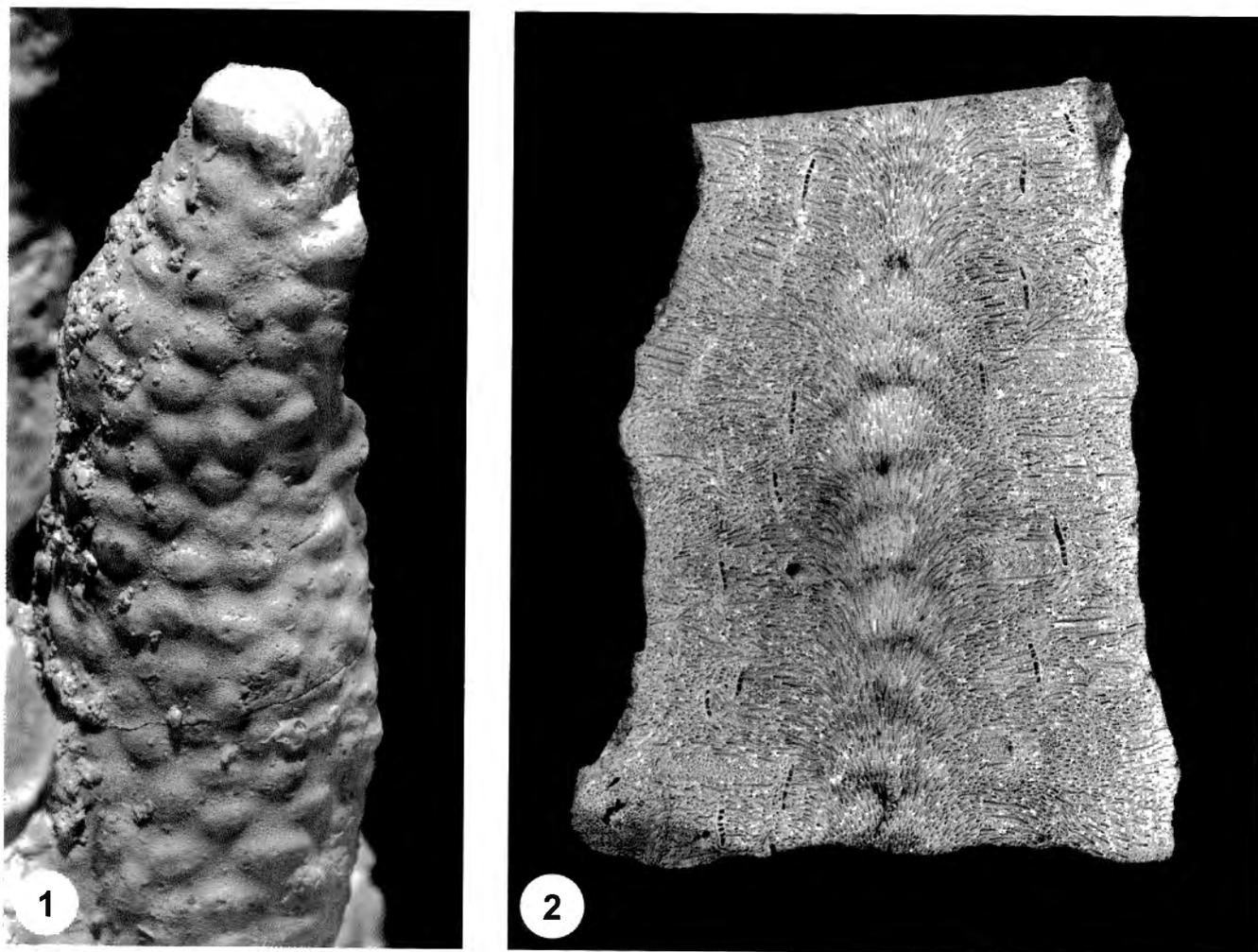
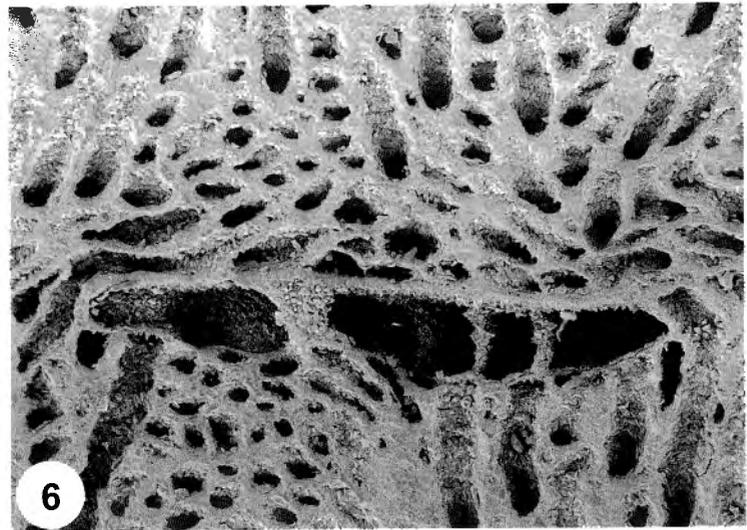
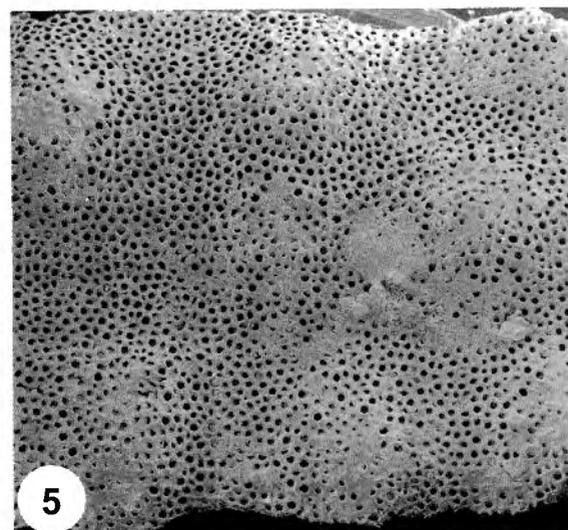
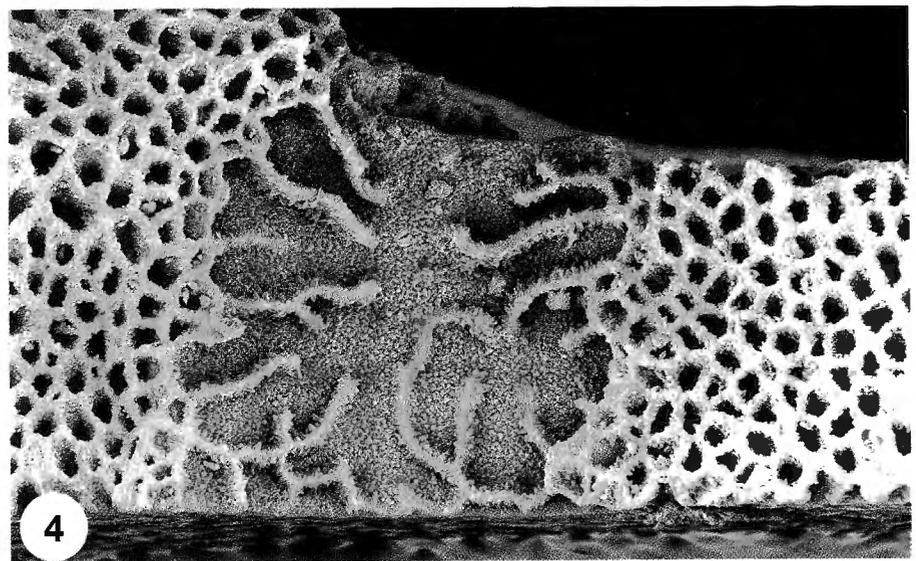
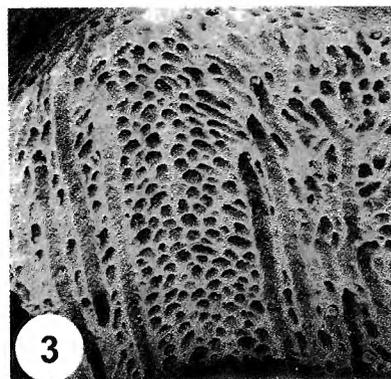
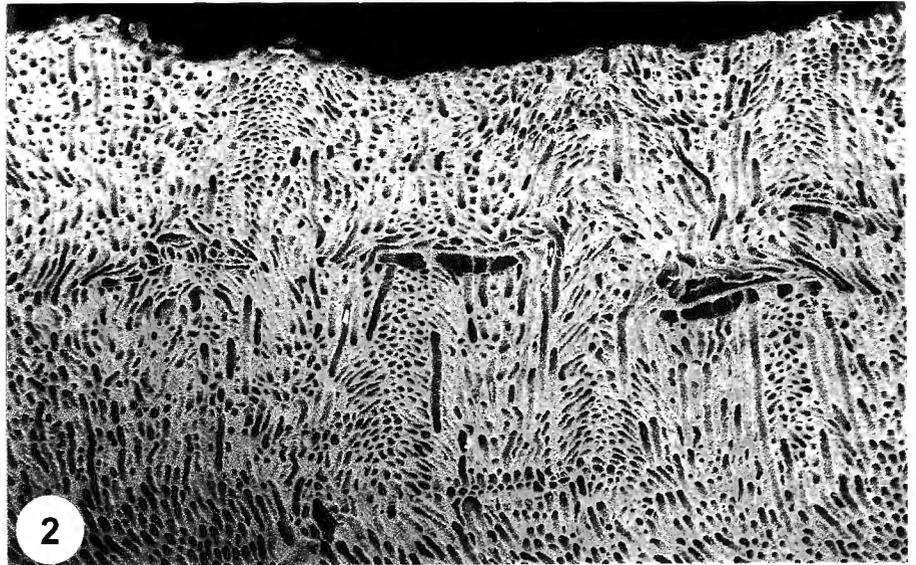
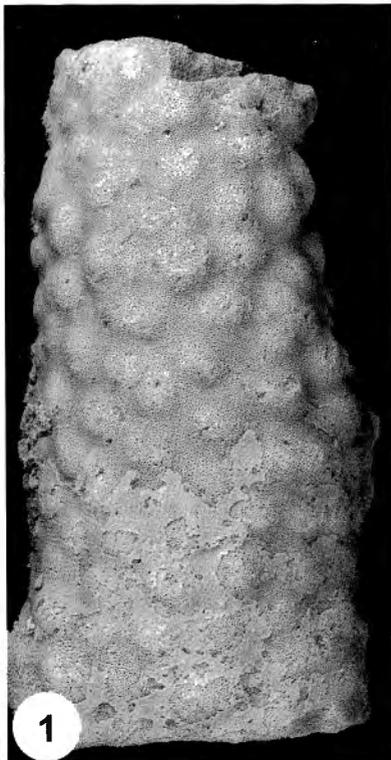


Fig. 2 - *Pennipora anomalopora* (UBAGHS, 1858). Maastrichtian, Maastricht Fm, Meerssen Mbr; ENCI NV Quarry, near Maastricht, The Netherlands.

1. Finger-like branch with prominent monticules, x 2. Natuurhistorisch Museum Maastricht No. 1997130.

2. Longitudinally-sectioned branch showing growth bands in the endozone and brood chambers in the exozone, x 3. Voigt Collection, Universität Hamburg Nr 15024.



long axis of the branch. Endozonal diameter is about 5 mm, and there is no distinction between different polymorphs. One longitudinally sectioned branch (Fig. 2.2) exhibits dark convex bands within the endozone which are spaced an average of 2.9 mm apart. Although the endozone is typical of that present in many dendroid cyclostomes, the surrounding exozone is atypical (Fig. 3.2). Normally in cyclostomes, zooecia in the exozone are all oriented parallel to one another and approximately perpendicular to the colony surface. This can be seen clearly in transverse and longitudinal sections of branches which closely follow the long axes of the exozonal zooecia. In *P. anomalopora*, however, such sections pass along the axes of only some of the zooecia: zooecia cut longitudinally and forming long tubes which may pass through the entire exozone are mixed with other zooecia cut obliquely and appearing to be short. Often a single column of "short zooecia" occurs between two "long zooecia", but in other instances a wide band of "short zooecia" is present (Fig. 3.3). Such bands of short zooecia may have a chevron or pinnate configuration, with zooecia of opposite orientation meeting in the centre of the band.

Interpreting the unusual exozonal structure of *P. anomalopora* is difficult because sections provide only two-dimensional information. Nevertheless, it appears that the "long zooecia" are oriented conventionally for a cyclostome exozone (i.e. approximately perpendicular to the colony surface), whereas the "short zooecia" have a more variable, non-perpendicular and oblique orientation relative to the colony surface. This difference in orientation is not readily apparent on the surface of the colony but it is presumed that the "long zooecia" represent autozooecia with slightly larger apertural diameters, and the "short zooecia" are kenozoecia. The wide bands of "short zooecia" may be the kenozoecia that open on the

monticules, as suggested by VOIGT (1953). Further disruptions in zooecial orientation are related to the presence of brood chambers.

Brood chambers have been seen only in sections (Fig. 3.2, 3.4, 3.6). They are developed only in the exozones of branches, but their location relative to the monticules is uncertain. Based on sections, it is estimated that the colony contains more than one hundred brood chambers, surpassing the maximum number known in any other cyclostome. In vertical sections cut parallel to the growth direction of the surrounding zooecia, brood chambers appear as low horizontal cavities, up to 0.3 mm in height, with slightly concave floors and flat roofs (Fig. 3.6). Vertical walls subdivide the brood chambers, and their roofs are overgrown by subhorizontal zooecia, sometimes overarched a space on top of the roof where it is possible that a soft-bodied fouling organism was once present. Directly beneath the brood chamber, the zooecia may diverge slightly. Tangential sections of brood chambers show that they are roughly circular in outline shape, and about 2 mm in diameter. The vertical dividing walls resemble coral septa and can be observed to originate at the outer margin of the brood chamber and grow centripetally towards the centre of the chamber (Fig. 3.4). The walls are not straight but instead meander slightly and sometimes bifurcate. Occasionally individual walls may meet, causing part of the brood chamber to be partitioned off, but usually there is no contact between the walls and the central part of the brood chamber remains free of these septa. Cyclostome brood chambers are often penetrated by autozooecia and/or kenozoecia which act as roof supports. These zooecia are sometimes linked by radial, septa-like walls (e.g. NYE, 1976, pl. 51, fig. 1; SCHAEFER, 1991, pl. 26, figs 1-2), but it is rare to find septa subdividing a brood chamber without associated zooecia. However, a close analogue to the septa found in the brood chambers of *Pennipora anomalopora* occurs in the unrelated Maastrichtian cyclostome *Reteporidae georgiknetschi* VOIGT, 1984 (see VOIGT, 1984, pl. 4, figs 5-6). Ooeciopores have not been observed. The microstructure of the brood chamber roof is obscured by diagenetic crystals of calcite and it is not possible to ascertain whether it represents a pseudoporous exterior wall or a porous interior wall, although the former is more likely based on comparison with other cerioporids.



Fig. 3. — Photomicrograph (1) and scanning electron micrographs of *Pennipora anomalopora* (ÜBAGHS, 1858). Maastrichtian, Maastricht Fm, Meerssen Mbr; ENCI NV Quarry, near Maastricht, The Netherlands. Voigt Collection, Universität Hamburg.

1. Branch with broken tip and conspicuous monticules, x 2. Nr 15024.
2. Slightly oblique longitudinal section of the exozone showing mixture of "long" and "short" zooecia and a few brood chambers, x 9. Nr 14144.
3. Vertical section through a monticule with "short" zooecia flanked by some "long" zooecia in the intermonticular areas on either side, x 12. Nr 14145.
4. Tangential section showing the underside of the roof of a brood chamber and the septa-like partitions, x 27. Nr 14147.
5. Branch surface, x 9. Nr 14145.
6. Vertical section through a brood chamber with septate internal partitions and a flat roof overgrown by subsequent zooids, x 33. Nr 14144.

#### DISCUSSION

The Maastrichtian bryozoan fauna of the Maastricht region is enormously abundant and diverse. However, it remains poorly known and includes a great many undescribed species, despite the early monograph of von HAGENOW (1851). Some of the bryozoans are associated with sea-grasses (VOIGT, 1981), some with hardgrounds (VOIGT, 1987) and others with still different habitats. More than one hundred cyclostome species are present at Maastricht. Of these, the rare *Pennipora anomalopora* builds the largest colonies.

The size of the newly-discovered colony is exceptional not only for Maastricht but for living and fossil cyclos-

tomes as a whole. Although living colonies of the New Zealand cyclostome *Cinctipora elegans* HUTTON (see BOARDMAN *et al.*, 1991) can reach at least 15 cm in height, such large colonies of this narrow branched species may depend upon the presence of a diverse associated fauna of encrusting epizoans to strengthen and bind the inactive proximal branches of the colonies. In contrast, the integrity of the large colonies of *Pennipora anomalopora* must have been maintained by the thick, robust branches themselves. We are unaware of any other Mesozoic cyclostome colonies as large as the new colony of *P. anomalopora* from Maastricht. In its sheer size and dendroid colony-form, the specimen is more comparable with some Palaeozoic trepostome bryozoans (e.g. BOARDMAN, 1960, pl. 9) than it is with typical Mesozoic cyclostomes.

It would be interesting to know the age at death of the large colony of *P. anomalopora*. The existence of growth banding in the endozone of a longitudinally sectioned branch (Fig. 2.2) provides tentative estimates of growth rate and longevity. Convex, darker coloured bands cross the endozone parallel to inferred positions of former branch distal growth tips. The bands are relatively evenly-spaced, averaging about 2.9 mm apart, and gradually pass into the surrounding exozone. Areas of endozone between the bands are paler in colour whereas the exozone has a similar colouration to the dark bands. The dark bands appear to result from an increased density of brown ferruginous material. They may represent levels containing brown bodies formed by cyclical polypide degeneration, although the incomplete filling of chambers by diagenetic calcite and non-availability of thin sections make this hypothesis difficult to prove. In some stenolaemate bryozoans, the original organic material of brown bodies may be permineralized by authigenic aluminosilicates (MORRISON & ANSTEY, 1979), but in others they are apparently represented by framboidal pyrite

(PDT unpubl.). The latter, on oxidation, could potentially give the brown colouration seen in *Pennipora anomalopora*. This explanation for the origin of the dark bands is consistent with the overall dark colouration of the endozone because skeletal growth rates characteristically slow down in bryozoan endozones (see KEY, 1990) and therefore the proportion of brown bodies relative to skeletal mass should be greater. As noted above, it is difficult to trace the dark bands into the exozone. However, exozonal brood chambers are generally aligned with projected trajectories of the dark bands into the exozone. In some instances, successive endozonal growth bands can be correlated with successive layers of exozonal brood chambers.

As sexual reproduction in many non-tropical bryozoans, including the cyclostome *Crisia eburnea*, occurs annually (RYLAND, 1970, p. 83), the most reasonable assumption is that the bands represent annual growth bands formed at times of sexual reproduction with an associated growth check and widespread polypide degeneration across the endozone to give a concentration of brown bodies. If this inference is correct, then distal branch growth averaged about 3 mm per year, and the Michon colony which has branches more than 100 mm long would have lived for at least 35 years. Given the very large number of larval brood chambers present in colonies of *P. anomalopora*, suggesting a high fecundity, it is surprising that this long-lived bryozoan is so uncommon.

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