ACTA PALAEONTOLOGICA POLONICA
Vol. XX 1975 No. 3

JERZY DZIK

THE ORIGIN AND EARLY PHYLOGENY OF THE CHEILOSTOMATOUS BRYOZOA

Abstract. — The phylogenetic development of the Cheilostomata has tentatively been reconstructed from the oldest, Upper Jurassic forms, not developing heterozoecia, through the successive formation of ovicells, peristomial spines and avicularia, up to the formation of a secondary frontal wall by the development of cryptocyste or by the fusion of spines. Significant similarities in the structure of the zoecial wall of primitive Cheilostomata and Cyclostomata are stated. The hypothesis has been formed that primitive, stomatoporoidal Cyclostomata were the ancestors of the Cheilostomata. The Ctenostomata evolved also from the same forms as the Cheilostomata. A tentative biological interpretation of polymorphism and morphological gradient in a bryozoan colony has also been conducted. Seven species of the Cheilostomata have been described from the Cretaceous of Poland and a new genus, *Wawalia* gen.n. and a new family, Wawaliidae fam.n. have been erected.

INTRODUCTION

Silen's (1942) hypothesis, almost unanimously accepted by other bryozoologists, assumes the evolution of the Cheilostomata from the Ctenostomata through the mediation of forms of the *Labiostomella* type, by forming ovicells and transforming vertically growing branches of colony into peristomial spines. In this sense, the Calloporidae s.s. are the most primitive Cheilostomata. In the times when this hypothesis was formed, it was impossible to correlate it with palaeontological data, since those on the Lower Cretaceous bryozoan faunas were scarce. In addition, an inappropriate determination of the age of some of them was misleading. Thus, Voigt (1942, 1968*a*) proved that part of the bryozoans, described by Reuss (1872, see Voigt, 1942) as Cenomanian, were Danian and those, described by Gregory (1894) as Middle Jurassic, were Maastrichtian. As shown by new data on the early Cheilostomata (Cheetham, 1954; Thomas & Larwood, 1960; Boardman & Cheetham, 1969, 1973; Scott, 1970; Pohowsky, 1973), typical Calloporidae do not occur earlier than in the Cenomanian and all older forms are considerably simpler in structure and not related to the *Labiostomella*.

The findings of new Cheilostomatous Bryozoa from the Lower and Middle Cretaceous of Poland and the comparative materials from the Upper Cretaceous of Poland have served me as a basis for a tentative reconstruction of the early phylogenetic stages of the Cheilostomata and explanation of their origin.

The abbreviations used for marking collections:

JD — the writer's collection, housed in the Palaeozoological Institute of the Polish Academy of Science, Warsaw.

MZ — Museum of the Earth, Polish Academy of Science, Warsaw.

ZPAL UW — Palaeozoological Laboratory, Institute of Geology of the University of Warsaw.

ACKNOWLEDGMENTS

Of the materials used in the present paper, the Cenomanian bryozoans from the environs of Cracow were made available to me by Dr. T. Maryańska, those from the Vesulian of Łęczyca, Kimmeridgian of Wierzbica and Maastrichtian of Nasiłów by dr H. Pugaczewska and those of Campanian of Mielnik by Mr. J. Data. SEM micrographs were taken by Mrs. G. Mierzejewska and Mr. P. Mierzejewski and microscopic photographs by Mrs. M. Radzikowska. My heartfelt thanks are extended to all these persons.

I fell particularly indebted to Professor Adam Urbanek, Dr Richard S. Boardman and to Dr Alan H. Cheetham for their discussions and critical evaluations of the conceptions presented in the paper.

PHYLOGENY OF THE CHEILOSTOMATA

Of all Cheilostomata, the phylogeny of the suborder Cribrimorpha only has so far been described preliminarily (Lang, 1921; Larwood, 1962). Due to the erroneous determination of the age of the faunas important phylogenetically, as well as to the scarcity of the paleontological records of the early stages of their evolutionary development, the remaining Cheilostomata have never been studied from this viewpoint. New data on forms from the Uppermost Jurassic of England (Pohowsky, 1973) and Middle Cretaceous of Texas (Cheetham, 1954; Thomas & Larwood, 1960; Boardman & Cheetham, 1969, 1973; Scott, 1970), along from those on the materials from the Lower and Middle Cretaceous of Poland may already serve as a basis for phylogenetic considerations (text-fig. 1).

Evolution of Cheilostomata Anasca

Pyriporopsis portlandensis Pohowsky, 1973 from the Upper Portlandian of England is the oldest known and probably the most primitive species of the cheilostomatous Bryozoa. It does not display specialization in the structure of zoecia, has a long gymnocyst and a crenulate margin of opesium, without peristomial spines, ovicells and avicularia. Its disorderly system of astogeny may be considered as transitional between the types of astogeny characteristic of the genera *Stomatopora* and *Wilbertopora* (Text-fig. 2c). A similar system of astogeny and the morphology of zoecia is recorded in the Albian species *Pyripora texana* Thomas & Larwood, 1956 and in the Santonian species *Herpetopora parvicauda* Voigt, 1930. The uniserial stage also occurs in the early development of the Albian colony of a form illustrated by Boardman & Cheetham (1973, Fig. 39c), as *Wilbertopora mutabilis*. Colonies of the Albian bryozoans with a similar astogenetic development are described by Scott (1970, Pl. 1, Fig. 2) as *Membranipora kiowana* Scott, 1970. A considerable elongation of gymnocyste (cauda) and a full passage to a triadic proliferation occurred in the Albian and later species of the genera *Pyripora* and *Rhammatopora*. Other development trends were started by *Wawalia* sp. from the Middle Valanginian. In *Wawalia crenulata* gen. et sp.n. from the boundary between the Valanginian and Hauterivian crenulate opesial margin was considerably extended. The boundaries of the zone of crenulation undoubtedly correspond to the margin of soft tissues secreting the skeleton. In the Maastrichtian *Fissuricella* Voigt, 1959 they surround the entire zoecium.

Ovicells first appear in the Middle Albian species *Wilbertopora mutabilis* Cheetham, 1954 and, in the family Alderinidae s.s. derived from it, they make up the only differentiation of zoecia. Avicularia, that is, zooids with operculum transformed into a movable jaw, probably appeared later. The evolutionarily oldest avicularia, differ neither in size nor in the manner of budding from autozoecia (Boardman & Cheetham, 1973, Fig. 40c). Thus, the specialization of operculum probably preceded a decrease in the dimensions of avicularia. In the later, Upper Albian (Text-fig. 7) and Cenomanian (Lang, 1915; Boardman & Cheetham, 1973, Fig. 40b) representatives of the genus *Mystriopora*, avicularia are smaller and more specialized.

The formation of peristomial spines opened new evolutionary prospects to the Cheilostomata, Incipient, small spines were already observed in the Middle Albian forms (Boardman & Cheetham, 1973) and were considerably developed in the Cenomanian genus *Anaptopora* (Text-fig. 8). Their medial fusion led to the formation, in the Lower Cenomanian, of the order Cribrimorpha (Lang, 1921; Larwood, 1969) (Text-fig. 11).

Recent species of the genus *Electra* are devoid of ovicells and avicularia, but, despite this fact, their spines are well developed. Forms marked by such a structure are unknown from the Cretaceous. The presumable spine bases in the Middle Cretaceous *Rhammatopora* (Thomas & Larwood, 1960) are so small that they may make up crenulae of the opesial margin. After all, the genus *Rhammatopora* is sufficiently specialized for the assumption that its relationship to the *Electra* is rather unlikely.

The Recent *Electra, Flustra* and *Membranipora* s.s., along with other, related genera, seem to make up a uniform group marked by a progressive reduction in gymnocyste and in the polymorphism of a colony. Until the phylogeny of this group is studied more accurately, I assume a secondary simplification of forms belonging here as compared with the Calloporidae.

Forms with a strongly developed cryptocyste appear in the Lower Cenomanian. They include both the species having peristomial spines (for example, *Hapsidopora*) and devoid of them (*Rhagasostoma*). This may be interpreted by assuming an independent origin of cryptocyste in various phylogenetical lines, some of them derived from the species of the Calloporidae, not yet having spines and some others from the species which are more advanced evolutionary. We may also assume a secondary reduction of spines occurring together with the development of cryptocyste. Regardless of which of these interpretations is correct, it seems advisable to separate the forms having spines and a large cryptocyste as an independent taxon. In the most primitive Aspidostomatidae, the cryptocyste is porous also in avicularia (reticulocellaria). The muscles which pull the frontal membrane occupy, in the Aspidostomatidae, the corners of opesium, while the Microporidae have separate apertures in cryptocyste.

According to Banta (1970), *Anasca* „appears to be equally artificial" and should be divided into a few suborders. However, as follows from the phylogenetic considerations presented above, the *Anasca* are a monophyletic group. The same is probably true of the *Asciophora* if we exclude from them and transfer to the *Cribrimorpha* the forms having frontal wall of the costal origin. The replacement of the clear division of the Cheilostomata, into three suborders, so far accepted with a more involved one seems to be, therefore unnecessary.

Origin of the Ctenostomata

The oldest Ctenostomata are known from the Ordovician (Pohowsky, 1974). These forms are penetrating in the calcareous substrate. They have been found also in the Devonian (Richards, 1974), Upper Jurassic (Pohowsky, 1974) and in Lower Cretaceous (Voigt, 1973). Forms, developing colonies creeping on the substrate, are known from the Barremian (*Arachnidium brandesi* Voigt, 1968). All these forms are very similar in mode of astogeny and in the morphology of zoecia to primitive Cheilostomata (*Pyriporopsis, Rhammatopora*) and to *Corynotrypa*. They do not display any similarities to Calloporidae nor *Labiostomella*, which does confirm the Silen's hypothesis. Species of Ctenostomata with a long stolon and probably erect zooids are known beginning from the Turonian (*Stolonicella westfalica* Voigt, 1966).

The Paleozoic fossils from the families Ascodictyidae, and Vinellidae were traditionally assigned to the Ctenostomata. This view was fixed by Condra & Ellias (1944). The forms assigned to these families, develop porous, calcareous tubes creeping on the surface of hard objects. Sometimes, fusiform nodi form stellar assemblages. The Recent Ctenostomata do not secrete a mineral skeleton, this fact being a diagnostic character of this order. The *Ascodictyon* was compared by Condra & Ellias (1944) with Recent genera *Walkeria, Farella* and *Aetea*. The first two have erect stolons with bundles of zooids, while the *Aetea* has a creeping stolon and erect zooids. Thus, in the case of *Ascodictyon stellatum* and *Walkeria tuberosa,* they compared fusiform nodi with zoecia and, in the case of *Ascodictyon fusiforme* and *Aetea anguina,* similarly fusiform nodi with a stolon. None of these interpretations can be considered satisfactory. Although the nodi of *Ascodictyon* are porous, these fine pores cannot be considered as the traces of the budding of zoecia and all the more so as opesia.

Thus, the presence of calcareous walls without apertures which might be homologized with opesium or with traces of budding of zooids and, finally, the irregular manner of forming a colony (or, rather pseudocolony) indicate that the Ascodictyidae and Vinellidae are not related with the Ctenostomata. The calcareous, porous walls and the formation of branched, creeping pseudocolony make these organisms (in particular the genus *Allonema*) similar to the Paleozoic foraminiferes Tuberitininae and Ptychocladiidae (see Rich, 1970).

Relationships between the Ctenostomata and Cheilostomata are undoubtedly close (Silen, 1942). If we however accept Silen's hypothesis of the origin of the Cheilostomata from the Ctenostomata, thus the similarities in the microstructure and morphology of zoecia between the Cyclostomata and primitive Cheilostomata would become incomprehensible.

I postulate derivation both the Ctenostomata and Cheilostomata from a common ancestor of similar morphology and microstructure of zoecia and mode of astogeny. These conditions are to be found in *Corynotrypa*. The primitive Ctenostomata (*Arachnidium*) show more similarities to *Corynotrypa* than oldest Cheilostomata. This concerns the round aperture without operculum and the shape of zooids with „cauda". Ctenostomata originated from the *Corynotrypa* line probably in Ordovician.

Origin of the Cheilostomata

The structure of zoecia and the manner of forming zoaria in primitive Cheilostomata display a considerable similarity to those in primitive Ctenostomata and some of the Cyclostomata. The detailed comparisons presented below allow one to draw the conclusion that the Cheilostomata are most likely to descend from primitive, stomatoporoidal Cyclostomata of the *Corynotrypa* type.

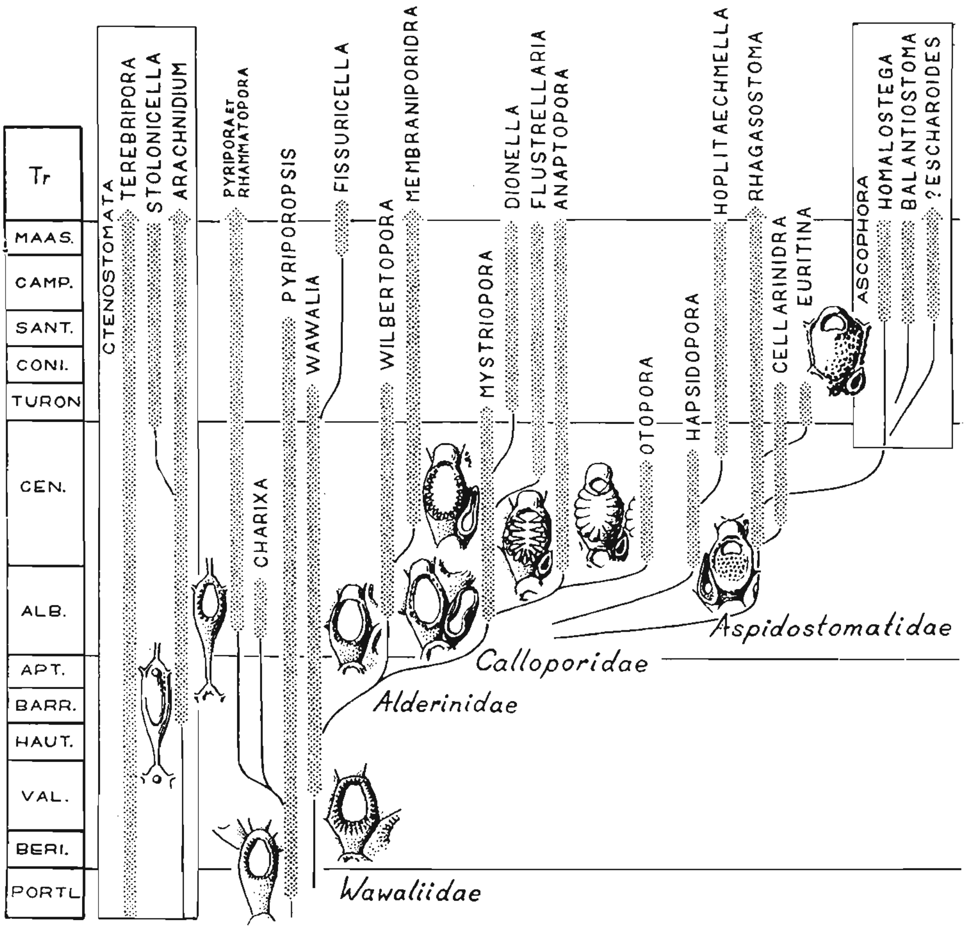


Fig. 1. Early phylogeny of the Cheilostomata.

Microstructure of zoecial walls

As shown by Tavener-Smith & Williams (1972), there are no essential differences in the microstructure of zoecia between the Cheilostomata and Cyclostomata. In the two groups, the wall of zoecium is composed of an avicular primary layer, easily recrystallizable in the process of fossilization, and a lamellar secondary layer. The predominance of the primary over the secondary layer (Pl. XV Fig. 3) occured in the Jurassic *Stomatopora* while the primary layer only occurs in the zoecian walls of the primitive Cheilostomata.

In most Cyclostomata, the wall of zoecium is punctured by many punctae, which sometimes form canals. The gymnocyste of the primitive Cheilostomata displays identical punctae (Pl. XVI, Fig. 2a, b; Text-fig. 4a, b). This punctation is observed only in non-crenulate parts, which are not covered with epithelial folds. The disappearance of the primary punctation from the wall of zoecium in evolutionary process of the Cheilostomata was connected with the reduction in gymnocyste. The Ctenostomata are devoid of a calcareous skeleton.

Morphology of zoecia

Both the stomatoporoidal Cyclostomata and primitive Cheilostomata have opesia situated perpendicularly to the axis of the creeping zoecia. The differences between the stomatoporoids and the primitive Cheilostomata are expressed in the presence in the former of a narrow neck instead of a wide opesium, covered with frontal membrane. We can assume a progressing reduction in the calcareous frontal wall which took place in the evolutionary line from the *Stomatopora* and *Corynotrypa* to *Pyriporopsis*. Under such an assumption, there would take place a shifting and extension of the area of activity of the system of hydrostatic muscles. The Cheilostomata may be directly related with the Paleozoic *Corynotrypa* (as indicated also by similarities in astogeny), but they may be also a continuation of the evolutionary line of the Jurassic stomatoporoids, in which the zoecia become more and more pyriporoidal (Lang, 1907).

The system of communication canals between zoecia is known in considerable part of the Cretaceous Cheilostomata (Canu, 1900), such as species of the genera *Pyriporopsis* (Pohowsky, 1973), *Wawalia* gen.n. (Text-fig, 3a), *Fissuricella* (Voigt, 1959) and ?*Rhagasostoma* (Text-fig. 3b). Characteristically enough, all of them have the system of canals of the *Beania* type (Silen, 1944). This reflects a manner of budding ancestral for Cheilostomata. The communication organs were probably formed by the transformation of stolons and they preserved in part their primitive functions performed during budding (Silen, 1944). The communication organs of the *Callopora* type were formed in connection with the reduction in the thickness of the walls of zoecia and gymnocyste.

Astogeny

The triadic proliferation is typical of the primitive Cheilostomata, which results from the system of communication canals in zoecia. However, in the *Pyriporopsis*, predominant is a uniserial proliferation, with a new row of zoecia sometimes proliferating laterally, while triads are rare (Text-fig. 2c). No regular budding system occurs in the *Pyriporopsis*. The *Stomatopora* and *Voigtopora* (Cyclostomata) mostly display an alternate proliferation of single zoecia and a dichotomy (Lang, 1904; Illies, 1971). Sometimes, it may happen, however, that dichotomies occur considerably more frequently (Text-fig. 2*b*). In the Paleozoic *Corynotrypa*, closely related to the *Stomatopora* as I believe, triadic proliferation is recorded sometimes (Text-fig. 2*a*; Bassler, 1911, Text-fig. 10). This represents a full analogy to the *Pyriporopsis*.

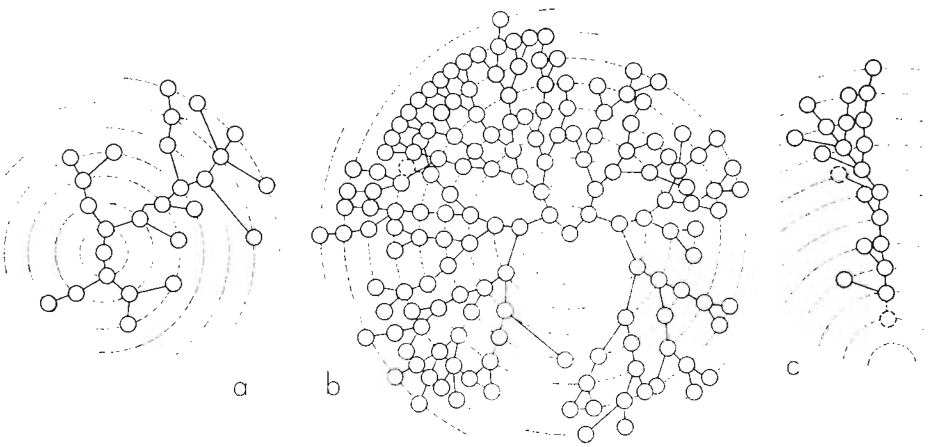


Fig. 2. Hirmer's diagrams of astogeny. *a* — *Corynotrypa schucherti* Bassler, 1911; a colony encrusting the inside of a trilobite carapace, Uppermost Llanvirnian, erratic boulder, JD 1056-E-085 b — *Stomatopora* sp.; a colony encrusting the shell of *Alectryonia*, Lower Kimmeridgian, Wierzbica, ZPAL. UW. No V. IV/5, a specimen illustrated by Pugaczewska (1970, Pl. 1, Fig. 6) *c* — *Pyriporopsis portlandensis* Pohowsky, 1973; a fragmentary zoarium with a particularly cheilostomatous way of budding (Pohowsky, 1973, Pl. 2, Fig. 2). Upper Portlandian, Isle of Portland.

A TENTATIVE BIOLOGICAL INTERPRETATION OF THE MORPHOLOGICAL GRADIENT IN A COLONY AND OF THE DEVELOPMENT OF POLYMORPHISM IN THE BRYOZOA

The system of forming a zooid of three stolons and a further triadic proliferation makes a colony of cheilostomatous Bryozoa fully integrated not only along zoecia, but also transversally. In this connection, Hirmer's diagram only incompletely reflects the connections between zooids and, therefore, it should be treated conventionally. This is the reason why in the present paper such diagrams are used only for depicting the formation of primitive Cheilostomata and not for that of later forms.

The gradient of the size of zoecia (Boardman, Cheetham & Cook, 1969) generally occurs in the astogeny of the Cheilostomata. Frequently, the proportions of zoecia change with the development of a colony. In the astogeny of the ? *Rhagasostoma* sp. from the Cenomanian of Poland, described in the present paper, the zoecia of initial generations have gymnocyste better developed than that of later generations. The ancestrula and zoecia of the first generation of *Sarsiflustra japonica* Silen (Silen, 1938) have a long gymnocyste, which later disappears completely. Generally, the ancestrula has a considerably more primitive morphology than the zoecia formed later. This is a specific recapitulation of phylogeny in astogeny.

Analogous phenomena of the morphological gradient in the graptolites are interpreted by Urbanek (1960, 1973) on the basis of the theory of the morphophysiological gradient. Urbanek's conception assumes the existence of the siculozooid-blastozooid physiological dimorphism and the control of growth and morphology of thecae by a specific physiological agent produced only by the siculozooid. The formation of such a mechanism would require an adaptative character of the morphological gradient in a colony. The suggestion that a juvenile colony exists under different external conditions than those of a mature stage is inapplicable to the sessile colony of the Bryozoa. Since, in the bryozoan colonies, proximal zooids expose evolutionary delay in their characters this implies that they are less adapted to the living conditions of the entire colony than the distal zoids.

According to van Valen (*in* Urbanek, 1963, p. 231), the growth and structure of zooids are controlled by substances active morphogenetically produced by all zoids and accumulated in the colony.

In the Bryozoa, zooids of the formed generation are supplied with food substances by the zooids of parent generation up to the completion of organogeny (Stach, 1938; Boardman & Cheetham, 1969; Cook, 1973). The development of zooids takes place under the conditions of dynamic equilibrium between the stimulation of budding and food resources. An initial depression in alimentary conditions between particular generations disappears with the development of colony first due to a larger number of parent zooids and, second, due to a relative decrease in the number of descendent zooids (a rare triadic proliferation resulting from a limited area and the predominance of uniserial rows and dichotomies). In my opinion, the size of the formed zoecia is limited by food resources of the zooids of parent generations and, indirectly, by the intensity of the stimulation of proliferation. There occurs the supposition that the processes of organogeny taking place under less favourable alimentary conditions are incomplete. The termination of organogeny and formation of a mineral skeleton occur in somewhat earlier stages of ontogeny than in the later generations. This produces an effect of the reflection of ontogeny (and, consequently, sometimes also phylogeny) in astogeny. The evolutionary changes are simultaneusly introduced to onto- and astogeny mostly beginning with earlier developmental stages (Urbanek, 1966). The cases of rejuvenescence (the second zone of astogenetic change — Boardman, Cheetham & Cook, 1969), accompanied by the morphological gradient, may also be explained by an excessive production of the stimulant of proliferation (probably, a non-specific one). Among the Cretaceous Cheilostomata, this phenomenon is rare and abnormal in the development of colony. It is connected with speeding-up of the proliferation of a zooid, which, rapidly forming a fanlike assemblage of descendant individuals, inhibits the proliferation of adjoining zooids of the same generation. It is not unlikely that in such a case there act some physiological mechanisms which inhibit the development of the remaining zooids. The causal nexus between the speeding-up of proliferation and decrease in the size of descendant zoids is here distincly visible.

Polymorphism in the Cheilostomata

The earliest Cheilostomata (*Pyriporopsis, Wawalia, Pyripora, Rhammatopora*) do not produce heterozoecia, which limits the possibilities of tracing their direct origin back to the Ctenostomata and the most primitive Cyclostomata which do not yet form oecia (see Walter, 1969).

Polymorphism appears not before the Middle Albian forms. The occurrence of zooids with ovicells (the type of polymorphism connected with sexual process) is its earliest form. Colonies of Cheilostomatous Bryozoans, having both ovicells and avicularia (Boardman & Cheetham, 1973, Fig. 40c), are known from these same Middle Albian beds. My conclusion is that avicularia are evolutionarily later than ovicells, because so early reduction of avicularia or independent origin of ovicells in both are unlikely.

The evolution of avicularia is only partly related with that of autozoecia, although, for example, the development of cryptocyste is sometimes observed in both autozoecia and avicularia. A considerable evolutionary autonomy of avicularia suggests that their structure is to a considerable extent encoded in a different set of genetic information (as a result of gene duplication), than that concerning autozoecia. The mechanism controlling the realization of one of the two genetic systems (and, consequently, of a separate system of embryonal induction) operates stochastically, which is indicated by a disorderly distribution of avicularia in primitive zoaria (Silen, 1938; Medd, 1966). Its operation requires a certain degree of advancement in astogeny, since in the primitive encrusting Cheilostomata (see Text-figs. 6, 8 and 10c) avicularia appear only in the second, third or even later generation. There occurs the supposition that a certain metabolite may serve here as a sort of a „change-over". The activity of this factor may be expressed only as a lack or presence of fully formed avicularia. Such is the case of all the Cretaceous Cheilostomata I studied. The differentiated expression of the genetic system responsible for the structure of avicularia (as postulated by Cheetham, 1974) would require an additional mechanism. This should be proved by a description, in one and the same population, of a continuous series from the lack of avicularia, through transitional stages of the modification of zoecia, up to normal avicularia. However, the colonies, included by Cheetham in *Wilbertopora mutabilis*, form three distinct groups which, in my opinion, represent different evolutionary stages. A distinct morphological advancement of avicularia in a colony, illustrated by Cheetham (1974) in Pl. 3, Fig. 4 are, as compared with those from his Fig. 2 in the same plate, in conformity with the stratigraphic sequence, that is, the former comes from the Cenomanian and the latter from the Albian.

I think, therefore, that Cheetham's view on the possibility of a differentiated expression of the genotype of avicularia within the range of one and the same species is unfounded. The sporadic occurence of avicularia (Boardman & Cheetham, 1973) cannot be considered as a primitive character. Under the conditions of such a scattered occurrence, in the population, of the phenotypic expression of a set of genus responsible for the organization of avicularia, the selection pressure would be too small to cause the evolution of these structures taking place at the rate observed. The sporadic occurrence of avicularia in some Cheilostomata seems to be a particular atavism, that is, the setting in operation of a normally switched-off set of genes, which has not yet been subject to complete destruction.

Colonies with avicularia appearing as early as the zone of morphological gradient and which occur together with those of *Wilbertopora mutablis,* not having avicularia even in the zones advanced astogenetically (Boardman & Cheetham, 1973, Fig. 40c), should be perhaps assigned to a separate species. The similar structure of autozoecia (according to Cheetham, the colonies with avicularia have peristomial spines, which do not occur in the holotype of *Wilbertopora*) cannot be considered as a specific character. Species from Bohemia, England, Poland and Texas, almost identical in the structure of autozoecia, have, however, quite different heterozoecia, different systems of astogeny and undoubtedly are real, biological species.

DESCRIPTIONS

Class **Bryozoa** Ehrenberg, 1826
Order **Cheilostomata** Busk, 1852
Suborder **Anasca** Levinsen, 1909
Family **Wawaliidae** fam.n.

Diagnosis. — Zoecia with a porous gymnocyste and crenulate opesial margin. Zoaria encrusting. Primary lack of ovicells, spines and avicularia.

Genera assigned: *Wawalia* gen.n., *Pyriporopsis* Pohowsky, 1973, *Charixa* Lang, 1915. *Pyripora d'Orbigny,* 1849, *Fissuricella* Voigt, 1959 and ?*Rhammatopora* Lang, 1915.

Remarks. — The family Wawaliidae differs from the Alderinidae s.s. in the lack of ovicells, from the Electridae in the lack of spines and from the remaining Anasca in the lack of ovicells and avicularia. The genera *Wawalia, Pyriporopsis, Charixa, Pyripora* and *Fissuricella* are most likely to be related directly neither to the *Electra,* nor to the *Membranipora* s.s. Structures suggesting its considerable evolutionary advancement (spines and, probably, vibracularia) occur in the *Electra,* while the *Membranipora,* closely related to it, displays characters of the secondary simplification, that is, a reduction in skeleton (in particular in gymnocyste) and polymorphism.

Stratigraphical and geographical range. — Known from the Upper Jurassic through the Recent (?). America and Eurasia.

Genus *Wawalia* gen.n.

Type species: Wawalia crenulata gen. et sp.n.

Derivation of the name: After the village Wąwał, where the type species was found.

Diagnosis. — Proliferation triadic. Gymnocyste strongly developed, but not forming „cauda".

Spiecies assigned: *W. crenulata* sp.n., *Membranipora kïowana* Scott, 1970, and non-described species from Middle Valanginian of Poland.

Remarks. — *Wawalia* gen.n. differs from the *Pyriporopsis* in the type of astogeny, a short gymnocyste and the number of communication canals. It belongs to a different evolutionary line than the *Pyriporopsis-Pyripora* group.

Stratigraphical and geographical range. — The Valanginian of Poland, Albian of Texas.

Wawalia crenulata sp.n.

(Pls. XV, Fig. 1*a*, *b* and XVI, Figs 1, 2; Text-figs 3*a*, 4*a*, *b*, 5*a-d*, 6)

Holotype: JD 3004—268; Pl. XV, Fig. 1*a*, Text-fig. 4a.

Type locality: Wąwał near Tomaszów Mazowiecki, Central Poland.

Type horizon: Uppermost Valanginian.

Derivation of the name: After a crenulate opesial margin.

Diagnosis. — Opesial margin wide, crenulate, flattened. Gymnocyste perforate. Colony with closely spaced zoecia.

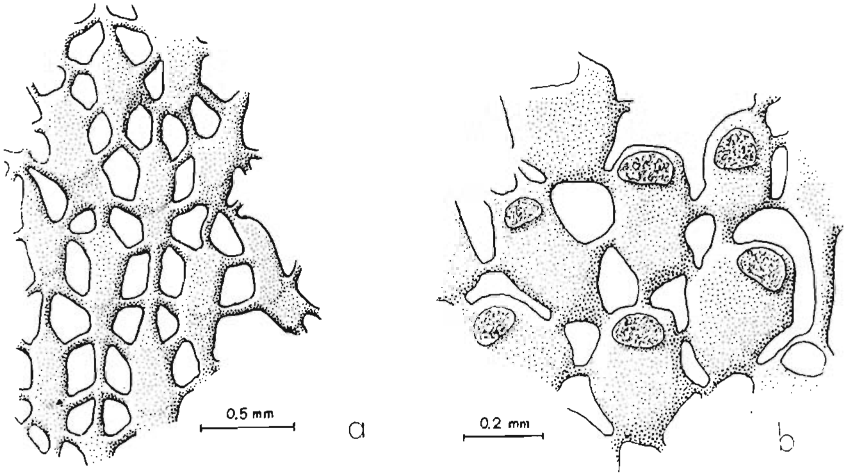


Fig. 3. System of communication canals visible in natural casts of the inside of zoecia. *a* — *Wawalia crenulata* gen. et sp.n., JD 3006—268; *b* — *Rhagasostoma* (?) sp., MZ VIII/Bry-99.

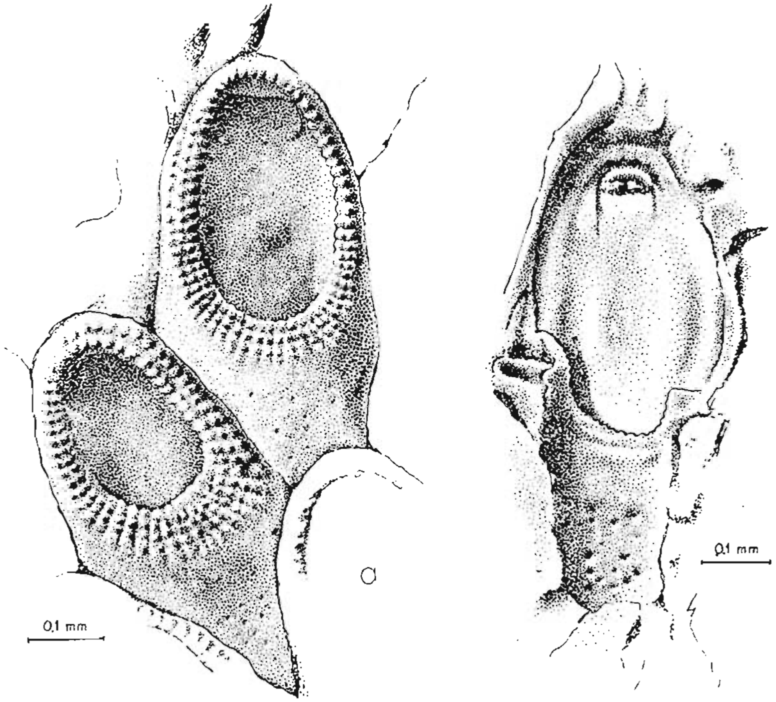


Fig. 4. *Wawalia crenulata* gen. et. sp.n. Uppermost Valanginian and Lower Hauterivian, Wąwał near Tomaszów Mazowiecki, Central Poland. *a* — two zoecia of holotype JD 3004-268; *b* — inner view of a biomurate partly damaged zoecium, the porosity of gymnocyst and morphology of frontal membrane are visible, JD 3007-268.

Dimensions. — Depending on the stage of astogeny, zoecia 0.17 to 0.80 mm long.

Material. — More than 32 colonies encrusting the shells of the oysters *Exogyra* (*Aetostreon*) *latissima* (Lamarck) and *Dichotomites* sp., including five colonies with the ancestrula preserved. Two colonies, biomurated by oysters, display the morphology of the soft parts of body.

Description. — Ancestrula with an elongate gymnocyste and opesial margin having few crenulae. It originates three zoecia, provided that a rapid development of one of the rows does not block the remaining ones. Triadic proliferation maintained if not stopped by area limitation (Text-fig. 5*a*-*d*). With a regular development of zoecium, eight communication canals, more or less uniform in transverse section (Text-fig. 3), detach from it. The occurrence of porous plates is suggested by changes in the color of calcite, which fills canals on the boundary between zoecia. Each zoecium contacts other, adjoining zoecia through two lateral canals. It also contacts three zoecia of the next generation and receives the canals of three zoecia of the preceding generation. In drawing Hirmer's diagrams of astogeny, I assumed that the zoecium, which produces the medial communication canal, is a parent zoecium. The length of zo-

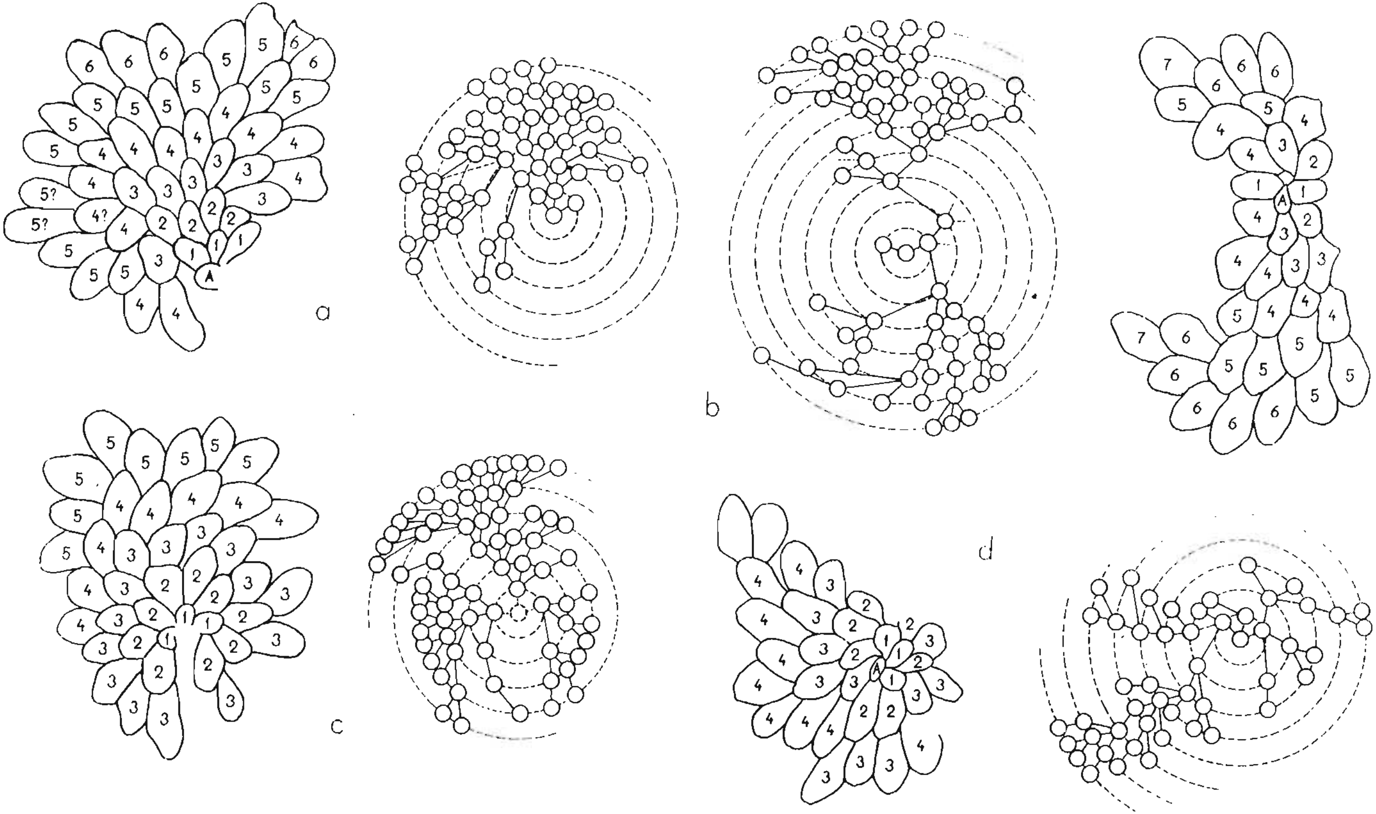


Fig. 5. *Wawalia crenulata* gen. et. sp.n., outlines of the early astogenetic stages and Hirmer's diagrams of: *a* — holotype JD 3004-268; *b* — JD 3005-268; *c* — JD 3003-268; *d* — JD 3002-268.

ecia increases with astogeny (Text-fig. 6). The rate of growth gradually drops, but it is at least up to the ninth generation that no distinct stabilization is visible in the dimensions of zoecia. The microstructure of zoecial walls is typically cheilostomatous - acicular. Gymnocyste is perforated by thin canals, identical with those in the Cyclostomata (Pl. XVI, Figs. 2, 3; Text- fig 4*a*, *b*). These pores occur only on the rough and non-crenulate surface of gymnocyste. The wide, crenulate opesial margin is smooth and lustrous, which indicates that at the animal's life-time it was covered with a fold of soft tissues. On the biomurated zoecia, the mold of a soft membrane encircles a wide opesial margin (Text-fig. 4*b*). Operculum semicircular, rather indistinct.

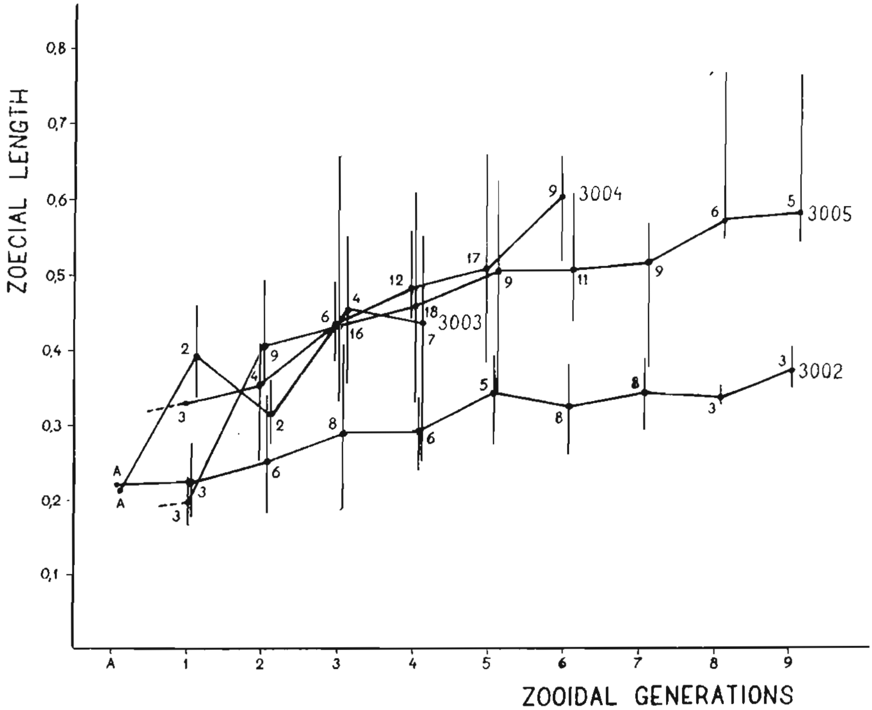


Fig. 6. *Wawalia crenulata* gen. et sp.n., a change in the size of zoecia in the ostogeny of four colonies: JD 3004-268, JD 3005-268, JD 3003-268 and JD 3002-268.

Occurrence. — Wąwał, Central Poland. In this locality, *W. crenulata* has been found in the upper part of the zone of occurrence of *Neohoploceras arnoldi* (Pictel & Campiche) above the bed containing *Saynoceras verrucosum* (d'Orbigny), *Valanginites nucleus* (Roemer), *Dobrodgeiceras wilfridi* (Karakasch). *D. ventrituberculatum* (Nikolov), *D. perinflatus* (Matheron), *Neocraspedites complanatus* (Koenen), and *Bochianites neocomiensis* d'Orbigny (Kokoszyńska, 1956; Dimitrova, 1967) (Upper Valanginian, Saynoceras verrucosum Zone) and, finally, in the beds with *Dichotomites* sp. The last-named beds are assigned to the Lower Hauterivian (Witkowski, 1969) but this assignment is not sufficiently documented.

Family **Calloporidae** Norman, 1903 emend.

Diagnosis. — Avicularia, peristomial spines and ovicells occurring primarily.

Remarks. — The genera *Wilbertopora* Cheetham, 1954, *Alderina* Norman, 1903 and *Aplousina* Canu & Bassler, 1927, having a well-developed gymnocyst, but primarily without avicularia and spines, have here been assigned to the family Alderinidae Canu & Bassler, 1927 emend.

Numerous species of the Bryozoa with well-developed avicularia, but without spines (of the genera *Ramphonotus* Norman, 1894, *Pyriporella* Canu, 1911, *Ellisina* Norman, 1903, *Cranosina* Canu & Bassler, 1933) occur in the Cretaceous. Thus, the necessity arises to separate a taxa which would include the genera, which originally have not spines. This should be, however, preceded by detailed phylogenetic studies. Despite its depressed ovicell, *Cranosina praecursor* (Brydone), considered to be the earliest representative of the Hincksinidae (Shaw, 1967) cannot be an ancestor of the genus *Hincksina*, since it is devoid of spines. The depression of ovicell occurred independently of each other in various evolutionary lines of the Calloporidae, much the same as in the Onychocellidae and Microporidae. The separation of the polyphyletic family Hincksinidae should be given up.

The genera *Callopora* Gray, 1848, *Mystriopora* Lang, 1915, *Anaptopora* Lang, 1916 and (?) *Hincksina* Norman, 1903, having strongly developed spines and a faint cryptocyst, make up a group of typical Calloporidae.

In my opinion, the calloporids having zoecia with a strongly developed cryptocyst and with simultaneously occurring peristomial spines (the genera *Hoplitaechmella* Voigt, 1949, *Hapsidopora* Lang, 1917, *Tylopora* Lang and (?) *Distelopora* Lang, 1915) should be distinguished as a separate subfamily.

Genus *Mystriopora* Lang, 1915

Type species: *M. moeckleri* Lang, 1915.

Remarks. — In addition to *M. moeckleri* Lang, 1915 and *M. perforata* (Reuss, 1846), mentioned by Lang, I include in this genus primitive species having avicularia with a well-developed gymnocyst and proliferations as one of the zooids of a triad. They are: *Mystriopora* sp. and the species, which were illustrated in Boardman & Cheetham, (1973) as *Wilbertopora mutabilis* (Fig. 40c) and *Wilbertopora* sp. (Fig. 40b).

? *Mystriopora* sp.

(Pl. XVI, Fig. 2; Text-fig. 7)

Material. — A fragmentary colony encrusting the shell of *Aucellina gryphaeoides* (Sowerby).

Dimensions. — Lengths of fifteen zoecia: mean — 0.55 mm, max. — 0.65 mm., min. — 0.46 mm. Lengths of six avicularia: mean — 0.33 mm, max. — 0.38 mm, min. — 0.30 mm.

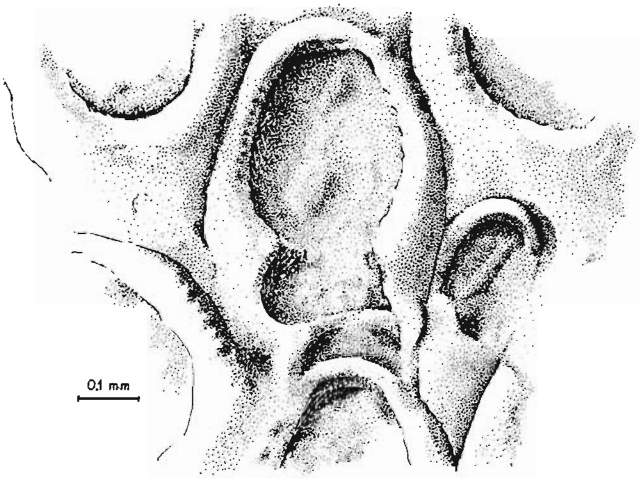


Fig. 7. *Mystriopora* ? sp., Upper Albian (or Lower Cenomanian), Annopol near Sandomierz, a frontal view of a autozoecium of a zoecium with a damaged ovicell and an avicularium. JD 3010-374.

Description. — Zoecia with a well-developed gymnocyst and poorly visible crenulation of opesial margin. Avicularia (zoeciulae) without specialization characters, with a round opesium and large gymnocyst, differing from autozoecia in small dimensions only. Presumed traces of a hyperstomial ovicell occur on a zoecium.

Remarks. — In the outline of gymnocyste and avicularia this species is similar to some representatives of the genus *Mystriopora,* especially an oval opesium of avicularia makes it similar to a form illustrated by Cheetham (Boardman & Cheetham, 1973, Fig. 40a), from which it differs, however, in considerably smaller dimensions of avicularia. It remains to be solved if the lack of spines is here original or secondary. It is not unlikely that small spine bases, characteristic of primitive species of *Mystriopora,* were destroyed as a result of the corrosion of the surfaces of zoecia. Type species of *Mystriopora* is more evolutionary advanced.

Occurrence. — Upper Albian (or Lower Cenomanian) of Annopol near Sandomierz (Cieśliński, 1960).

Genus *Anaptopora* Lang, 1916

Type species: *A. disjuncta* Lang, 1916

Remarks. — The genus *Anaptopora* was assigned by Lang (1921) to the family Otoporidae (Cribrimorpha). Since, however, its spines are not fused together, I transfer it to the family Calloporidae despite its undoubtedly close relationship to the Cribrimorpha. It differs from the genus *Dionella* Medd, 1965 in the presence of avicularia of one type only.

Anaptopora sp.

(Pl. XVII, Fig. 1; Text-fig. 8*a*, *b*)

Material. — A colony encrusting echinoid test.

Dimensions: Lengths of zoecia varying within limits of 0.33 and 0.90 mm, depending on the stage of astogeny.

Description. — Zoecia with a well-developed gymnocyst, opesial margin with large bases of about 16 spines. Opesium small, oval with a tu-

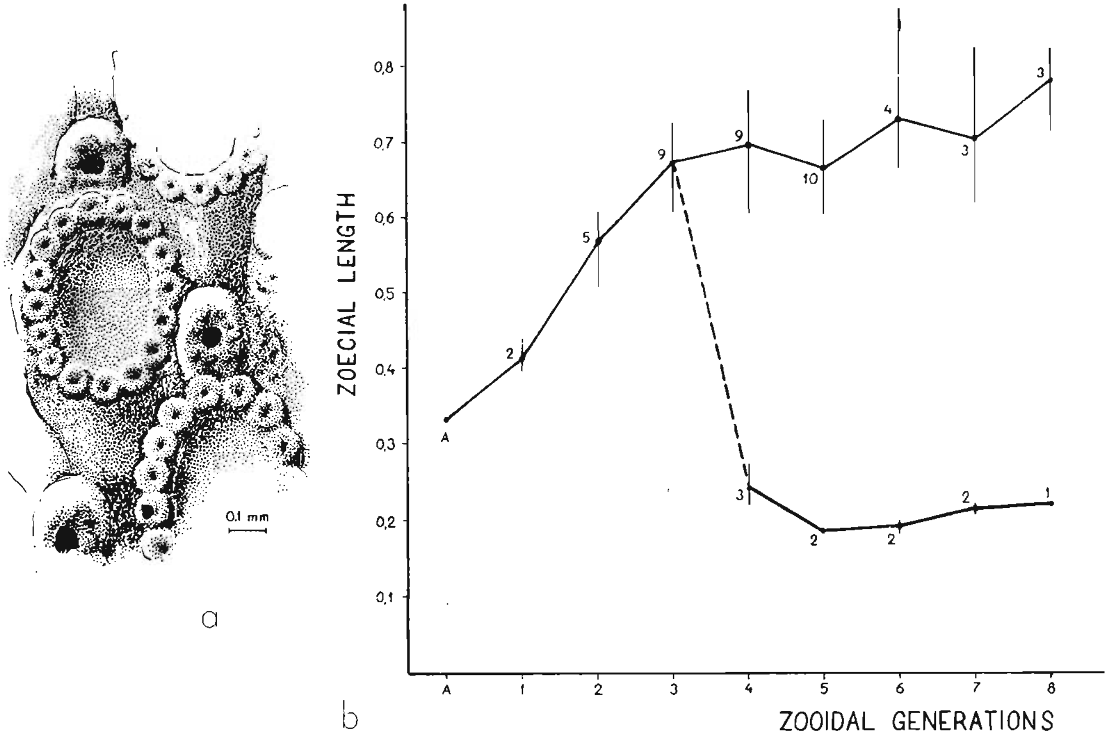


Fig. 8. *Anaptopora* sp., Lower (or Middle) Cenomanian, Korzkiew near Cracow. MZ VIII/Bry-101. *a* — a frontal view of a zoecium and an avicularium of the sixth generation; *b* — astogenetic changes in the size of zoecia and avicularia (bottom part of the diagram).

berculate margin and interzoecial avicularia usually situated distally of zoecia. An astogenetic increase in the size of zoecia and avicularia is shown in Text-fig. 8*b*.

Remarks. — It differs from the remaining species of the genus *Anaptopora* in the shape of avicularia.

Occurrence. — Lower (or Middle) Cenomanian of Korzkiew near Cracow (Marcinowski, 1974).

Family **Aspidostomatidae** Jullien, 1888

Remarks. — The families Onychocellidae, Microporidae and Aspidostomatidae are so similar to each other that assigning the most primitive Middle Cretaceous forms to any of them is arbitrary. It would be advisable to limit the range of the Microporidae to forms having distinctly separated opesiulae.

Genus *Rhagasostoma* Koschinsky, 1885

Type species: *R. hexagona* Koschinsky, 1885

Rhagasostoma acmon (d'Orbigny, 1851)

(Pl. XVIII, Fig. 1; Text-fig. 9)

1852. *Eschara acmon* d'Orbigny; A. d'Orbigny, p. 115, Pl. 662, Fig. 13—14.
1900. *Rhagasostoma acmon* d'Orbigny; F. Canu, p. 431, Pl. 7, Fig. 27.
1930. *Onychocella acmon* d'Orbigny; E. Voigt, p. 462, Pl. 18, Fig. 10.

Material. — Two fragmentary colonies encrusting echinoid test.

Dimensions (in mm); Length of 15 zoecia of specimen M. Z. VIII/Bry-102: mean — 0.48, max. — 0.57, min. — 0.35; of 13 zoecia of specimen M. Z. VIII/Bry-100: mean — 0.42, max. — 0.57, min. — 0.35. Two avicularia of the last-named specimen are 0.44 mm long.

Description. — Gymnocyste margin wide, descending distally, fine-crenulate. Cryptocyst porous, opesium with small opesial indentations. Zoecia polygonal in outline, gymnocyst nearly invisible. Avicularia large, asymmetric, with a long troughlike distal part. Avicular cryptocyste porous.

Occurrence. — Poland: Lower (or Middle) Cenomanian of Korzkiew near Cracow (Marcinowski, 1974); western Germany and France: Santonian through Campanian.

?*Rhagasostoma* sp.

(Pl. XVIII, Fig. 2; Text-figs 3*b* and 10*a-c*)

Material. — A colony encrusting an echinoid test.

Dimensions: Lengths of zoecia varying within limits of 0.23 and 0.65 mm, depending on the stage of astogeny.

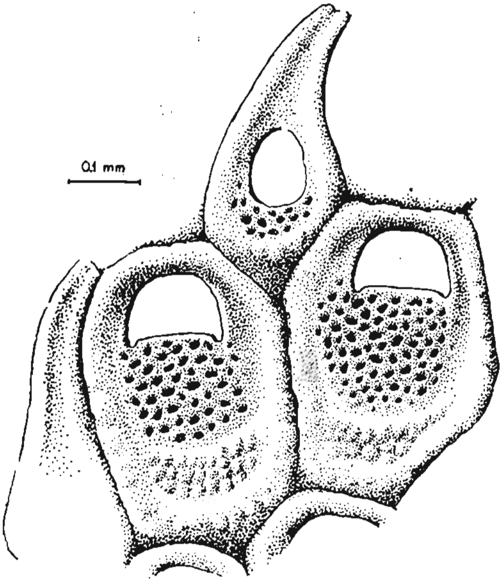


Fig. 9. *Rhagasostoma acmon* (d'Orbigny), Lower (or Middle) Cenomanian, Korzkiew near Cracow, a frontal view of zoecia and an avicularium, both advanced astogenetically. MZ VIII/Bry-100.

Description. — In early astogenetic stages, zoecia have a distinctly separated, rounded gymnocyste with its margin encircling an oval aperture (Text-fig. 10*a*). In later astogenetic stages, zoecia assume a polygonal shape, gymnocyst decreases and appertural margin extends proximally (Text-fig. 10*b*). Zoecia contact each other by communication canals more or less uniform in transverse section (Text-fig. 3*b*). Cryptocyste and, probably, zoecial walls porous. Autozoecial opesia semicircular, slightly convex proximally.

Avicularia, appearing in the second generation, are nearly symmetrical, with a tapering, troughlike distal end. Ovicells probably hyperstomial, semicircular in transverse section, appearing from the seventh generation. Only their basal parts are preserved (Text-fig. 10*b*).

Remarks. — It is not unlikely that the colony described may be assigned to the species *R. acmon* (d'Orbigny). The differences, consisting in the presence of gymnocyst, lack of opesiular indentations and a smaller specialization of avicularia may be ascribed to the interspecific variability, astogenetic changes and state of preservation. The specimen differs from the species *R. turonica* Canu, 1900 (Canu, 1897) from the Turonian of France in the lack of opesiular indentations.

Occurrence. — Lower (or Middle) Cenomanian of Iwanowice near Cracow.

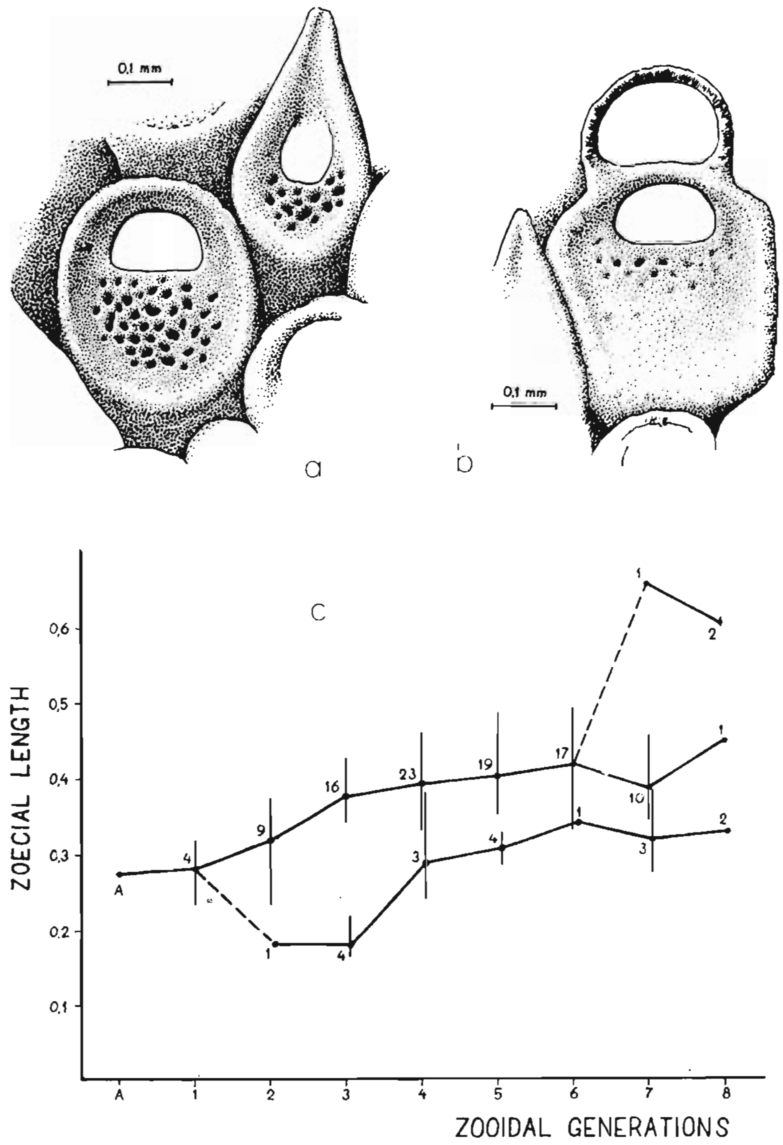


Fig. 10. (?) *Rhagasostoma* sp., Lower (or Middle) Cenomanian, Iwanowice near Cracow, MZ VIII/Bry-99, *a, b* frontal views of zoecia with a damaged ovicell of the seventh generation; *c* astogenetic changes in the size of autozoecia, avicularia (bottom part of the diagram) and zoecia with ovicells (top part of the diagram).

Suborder **Cribrimorpha** Lang, 1916
Family **Otoporidae** Lang, 1916

Diagnosis. — Spines fused medially, avicularia „somewhat or decidedly elongate and pointed, and where decidedly so, with curved rostra" (Lang, 1921).

Genus *Otopora* Lang, 1916

Type species: *O. auricula* Lang, 1916

Otopora sp.

(Text-fig. 11)

Material. — A colony encrusting, together with *Rhagasostoma acmon*, an echinoid test.

Remarks. — Small avicularia, pointed distally and distally fused spines make this specimen similar to the only species of this genus, that is, *O. auricula*, from which it, however, differs in the number of spines (costae), having about eleven while *O. auricula* has 15 to 20 of them. Zoecia about 0.46 mm long. A strongly corroded surface of colony precludes more accurate measurements.

Occurrence. — Lower (or Middle) Cenomanian of Korzkiew near Cracow (Marcinowski, 1974).

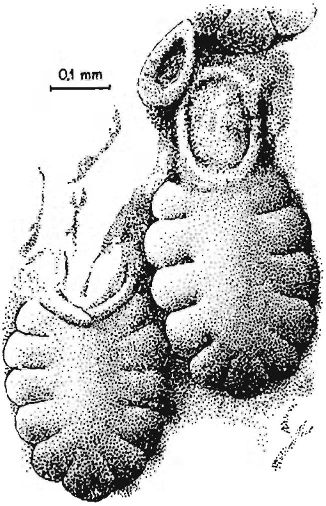


Fig. 11. *Otopora* sp., Lower (or Middle) Cenomanian, Korzkiew near Cracow, a frontal view of an avicularium and zoecium, probably with remains of an ovicell. MZ VIII/Bry-102.

Suborder **Ascophora** Levinsen, 1909

Family **Exochellidae** Bassler, 1935

Genus *Homalostega* Marsson, 1887

Homalostega cf. *inflata* Henning, 1894

(Text-fig. 12*a*-*b*)

1959. *Aechmella inflata* (Henning); E. Voigt, Abb. 4f.
1965. *Homalostega* sp.; H. Pugaczewska, p. 88, Pl. 11, Fig. 2a, b.

Material. — Two colonies encrusting the shell of *Pycnodonta vesicularis* (Lamarck).

Description. — Ancestrula differing from the remaining zoecia in a larger opesium. Zoecia of early generations less slender. Gymnocyst redu-

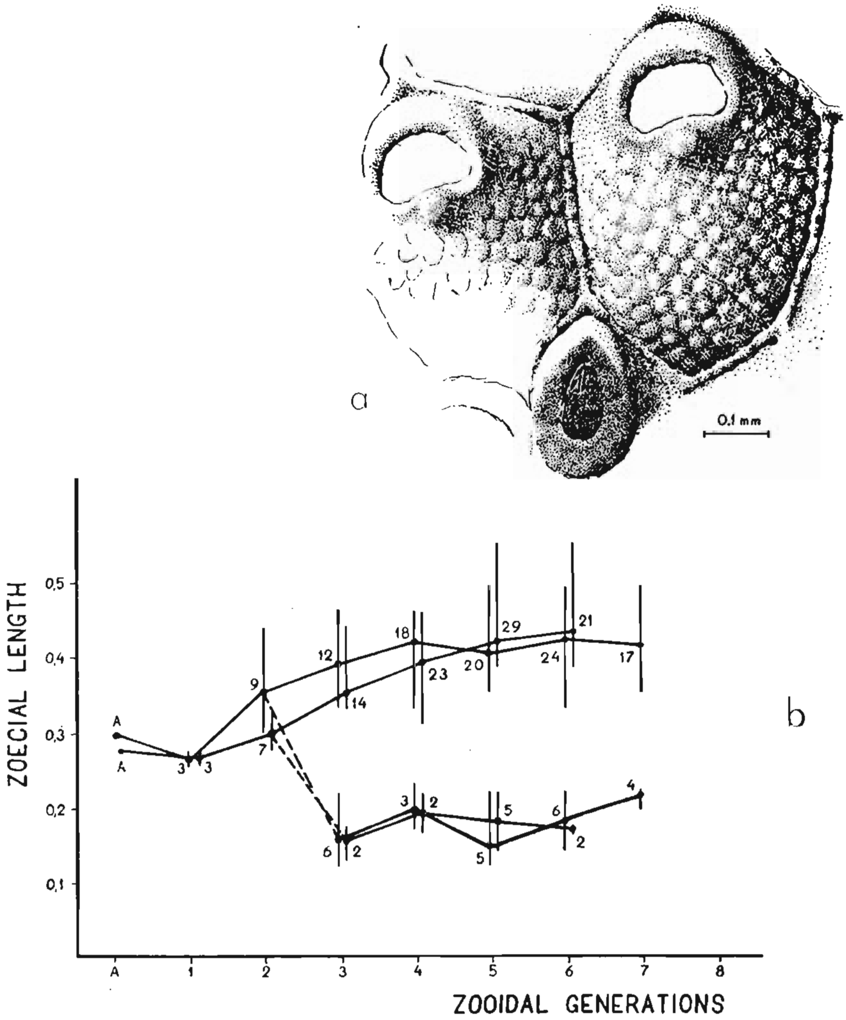


Fig. 12. *Homalostega* cf. *inflata* Henning, Lower Maastrichtian, Nasiłów near Puławy, *a* — a frontal view of zoecia of the fifth generation, ZPAL. UW. V/I.40a; *b* — an astogenetic change in the size of zoecia in two colonies, ZPAL, UW. V/I.40a and b.

ced and forming tuberculate lists separating zoecia. Cryptocyst strongly convex (covering ascus?) with tubercles arranged in rows crossing each other obliquely. A spiny process (or perhaps an ascoporus?) occurs below opesium. Opesium semicircular, with a concave proximal margin. Avicularia small with a pointed and erect distal end. They appear in the third generation parallel to zoecia.

Occurrence. — Upper Campanian of Nasiłów, Poland, and Senonian, Sweden.

Polska Akademia Nauk
Zakład Paleozoologii
Al. Żwirki i Wigury 93, 02-089 Warszawa
May, 1974

REFERENCES

BANTA, W. C. 1970. The body wall of Cheilostome Bryozoa, III. The frontal wall of Watersipora arcuata Banta, with a revision of the Cryptocystidea. — *J. Morph.*, **131**, 37—56, Philadelphia.

BASSLER, R. S. 1911. The Early Paleozoic Bryozoa of the Baltic provinces. — *Bull. U. S. Nat. Mus. Washington,* **77**, 1—382. Washington.

BOARDMAN, R. S. & CHEETHAM, A. H. 1969. Skeletal growth, intracolony variation, and evolution in Bryozoa: a review. — *J. Paleont.*, **43**, 205—233, Menasha.

— 1973. Degrees of colony dominance in Stenolaemate and Gymnolaemate Bryozoa. — in: Animal colonies, development and function through time, edit. R. S. Boardman, A. H. Cheetham, W. A. Oliver jr., 121—220, Stroudburg.

— , — & COOK, P. L. 1969. Intracolony variation and the genus concept in Bryozoa. — *Proc. N. Amer. Paleont. Conv.*, Part C., 294—320.

CANU, M. F. 1897. Bryozoaires du cenomanien des Janières (Sarthe). — *Bull. Soc. Geol. France.*, Ser. 3, **25**, 147—157, Paris.

— 1900. Révision des Bryozoaires du Crétacé figurés par d'Orbigny. Deuxième Partie — Cheilostomata. — *Ibidem,* **28**, 334—463.

CHEETHAM, A. H. 1954. A new Early Cretaceous Cheilostome Bryozoan from Texas. — *J. Paleont.,* **28,** 177—184, Menasha.

— 1971. Functional morphology and biofacies distribution of Cheilostome in the Danian Stage (Paleocene) of Southern Scandinacia. — *Smithsonian Cont. Paleobiol.*, **6**, 1—52, Washington.

— 1974. Taxonomic significance of autozooid size in some early multiserial Cheilostomes from the Gulf Coast of the USA — *In*: David, L. edit. Proceedings of the third International Bryozoology Association Conference, Lyon, 1974. *Docum. Lab. Geol. Fac. Sci. Lyon* (in press).

CIEŚLIŃSKI, S. 1960. Biostratygrafia i fauna albu Polski (bez prowincji alpejskiej). — *Prace Inst. Geol.*, **30**, 1—30, Warszawa.

CONDRA, G. E. & ELIAS, M. K. 1944. Carboniferous and Permian Ctenostomatous Bryozoa. — *Bull. Geol. Soc. Amer.,* 55, 517—568, New York.

COOK, P. L. 1973. Settlement and early colony development in some Cheilostomata. — *In*: Living and Fossil Bryozoa, G. P. Larwood edit., 65—73, Glasgow.

DIMITROVA, N. 1967. Fosilite na Blgarija, IV, dolna kreda, Glavonogi (Nautiloidea i Ammonoidea). 1—236, Sofia.

GREGORY, J. W. 1894. On some Jurassic species of Cheilostomata. — *Geol. Mag.* 2, 61—64, London.

ILLIES, G. 1971. Drei Arten der Gattung Stomatopora (Bryozoa Cyclostomata) aus den mittleren Lias bei Goslar und deren verschiedene Knospungsmuster. — *Oberrh. Geol. Abh.*, **20**, 125—146, Karlsruhe.

KAUFMANN, K. W. 1973. The effect of colony morphology on the life-history parameters of colonial animals. — *In*: Animal colonies, development and function through time., edit. R. S. Boardman, A. H. Cheetham, W. A. Oliver jr., 121—220. Stroudsburg, Pennsylvania.

KOKOSZYŃSKA, B. 1956. Dolna kreda okolic Tomaszowa Mazowieckiego. — *Biul. Inst. Geol.,* **113**, 5—50, Warszawa.

LANG, B. A. 1904. The Jurassic forms of the „genera" Stomatopora and Proboscina. — *Geol. Mag.*, Dec. V, **1**, 7, 315—322, London.

— 1907. The evolution of Stomatopora dichotomoides (d'Orbigny). *Ibidem,* Dec. V, **4**, 1, 20—24.

— 1915. On some new uniserial Cretaceous Cheilostome Polyzoa. *Ibidem,* Dec. VI, **2**, 11, 456—504.

— 1921. Catalogue of the fossil Bryozoa (Polyzoa) in the Department of Geology, British Museum (Natural History). The Cretaceous Bryozoa (Polyzoa). Volume III. The Cribrimorpha. — Part I, 1—269, London.

LARWOOD, G. P. 1969. Frontal calcification and its function in some Cretaceous and Recent Cribrimorpha and other Cheilostome Bryozoa. — *Bull. British Mus.* (*Nat. Hist.*), *Zoology*, **18**, 172—182, London.

MARCINOWSKI, R. 1974. The transgressive Cretaceous (Upper Albian through Turonian) deposits of the Polish Jura Chain. — *Acta Geol. Pol.*, **24**, 1, Warszawa.

MARSSON, T. 1887. Die Bryozoen der Weissen Schreibkreide der Insel Rugen. — *Palaeont. Abh.*, **4**, 1, 1—110, Berlin.

MEDD, A. W. 1965. Dionella gen. nov. (superfamily Membraniporacea) from the Upper Cretaceous of Europe. — *Palaeontology*, **8**, 492—517, London.

POHOWSKY, R. A. 1973. A Jurassic Cheilostome from England. — in: G. P. Larwood (edit.). Living and fossil Bryozoa, 447—461, London.

— 1974. Notes on the study and nomenclature of boring Bryozoa. — *J. Paleont.*, **48**, 2, 556—564, Lawrence.

PUGACZEWSKA, H. 1965. Les organismes sédentaires sur les rostres des Belemnites du Crétacé supérieur. — *Acta Palaeont. Pol.*, **10**, 73—92, Warszawa.

— 1970. Traces of the activity of bottom organisms on the shells of the Jurassic ostreiform Pelecypods of Poland. — *Ibidem*, **15**, 415—440.

RICH, M. 1970. The genus Tuberitina (Foraminiferida) in Lower and Middle Pennsylvanian rocks from the Eastern Great Basin. — *J. Paleont.*, **44**, 6, 1060—1066, Menasha.

RICHARDS, P. 1974. A Devonian Immergentia (Ectoprocta, Ctenostomata) from Ohio. — *Ibidem.*, **48**, 5, 940—946, Lawrence.

SCOTT, R. W. 1970. Paleoecology and paleontology of the Lower Cretaceous Kiowa Formation, Kansas. — *Contrib. Univ. Kansas Paleont.*, **52**, 1—94, Kansas.

SHAW, N. G. 1967. Cheilostomata from Gulfian (Upper Cretaceous) rocks of Southwestern Arkansas. — *J. Paleont.*, **41**, 178—182, Menasha.

SILEN, L. 1938. Zur Kenntnis des Polymorphismus der Bryozoen. Die Avikularien der Cheilostomata Anasca. — *Zool. Bidrag Uppsala*, **17**, 149—366, Uppsala.

— 1942. Origin and development of the Cheilo-Ctenostomatous stem of Bryozoa. — *Ibidem*, **22**, 1—59.

— 1944. On the formation of the interzooidal communications of the Bryozoa. — *Ibidem*, **22**, 433—488.

STACH, L. W. 1938. Colony-formation in Smittina papillifera (MacGillivray, 1869) (Bryozoa). — *Porc. Zool. Soc. London*, Ser. B., **108**, 401—415, London.

TAVENER-SMIRTH, R. & WILLIAMS, A. 1972. The secretion and structure of the skeleton of living and fossil Bryozoa. — *Philos. Trans. Roy. Soc. London* (B), **264**, 97—159, London.

THOMAS, H. D. & LARWOOD, G. P. 1960. The Cretaceous species of Pyripora d'Orbigny and Rhammatopora Lang. — *Palaeontology*, **3**, 370—386.

URBANEK, A. 1960. An attempt at biological interpretation of evolutionary changes in graptolite colonies. — *Acta Palaeont. Pol.*, **5**, 127—234, Warszawa.

— 1963. On generation and regeneration of cladia in some Upper Silurian Monograptids. — *Ibidem*, **7**, 135—254.

— 1966. On the morphology and evolution of the Cucullograptinae (Monograptidae, Graptolithina). — *Ibidem*, **11**, 291—536.

— 1973. Organisation and evolution of graptolite colonies. *In*: ed. R. S. Boardman, A. H. Cheetham, W. A. Oliver jr., Animal colonies, development and function through time. 121—220, Stroudsburg, Pennsylvania.

VOIGT, E. 1930. Morphologische und stratigraphische Untersuchungen über die Bryozoenfauna der oberen Kreide. I Teil. Die cheilostomen Bryozoen der jungeren Oberkreide in Nordwestdeutschland, im Balticum und in Holland. — *Leopoldina*, **6**, 379—579.

— 1942. Kreidebryozoen aus New Jersey (USA) unter A. E. Reuss Originalen zu seiner Monographie der Bryozoen und Foraminiferen des Unteren Pläners (1872) in H. B. Geinitz Das Elbthalgebirge in Sachsen. — *Ztschr. Deutsch. Geol. Ges.*, **94**, 326—338, Berlin.

— 1959*a*. Uber Fissuricella n.g. (Bryozoa foss.). — *Abh. Jb. Geol. Paläont.*, **108**, 260—269, Stuttgart.

— 1959b. Revision der von F. v. Hagenow 1838—1850 aus der Schreibkreide von Rugen veröffentlichen Bryozoen. — *Geologie*, **8**, 25, 1—80, Berlin.

— 1966. Die Erhaltung vergänglicher Organismen durch Abformung infolge Inkrustation durch sessile Tiere unter Berücksichtigung einiger Bryozoen und Hydrozoen aus der Oberen Kreide. — *Abh. Jb. Geol. Paläont.*, **125**, 401—422, Stuttgart.

— 1967. Oberkreide-Bryozoen aus den asiatischen Gebieten der UdSSR. — *Mitt. Geol. Staatsinst. Hamburg*, **36**, 5—95, Hamburg.

— 1968*a*. A contribution to the knowledge of the Polyzoa-fauna of the Maastrichtian in the Cotentin (Manche). On the Cretaceous age of the so-called Jurassic Cheilostomatous Polyzoa. — *Bull. British Mus. (Nat. Hist.), Geology*, **17**, 1—45, London.

— 1968*b*. Eine fossile Art von Arachnidium (Bryozoa, Ctenostomata) in der Unteren Kreide Norddeutschland. — *Abh. N. Jb. Geol. Paläont.*, **132**, 87—96, Stuttgart.

— & SOULE, J. D. 1973. Cretaceous burrowing Bryozoans. — *J. Paleont.*, **47**, 21—33, Menasha.

WALTER, B. 1969. Les Bryozoaires jurassiques en France. Etude systématique. Rapports avec la stratigraphie et la paleoécologie. — *Docum. Lab. Geol. Fac. Sci. Lyon*, **35**, 1—328, Lyon.

WITKOWSKI, A. 1969. Budowa geologiczna Niecki tomaszowskiej. — *Prace Inst. Geol.*, **53**, 1—105, Warszawa.

JERZY DZIK

POCHODZENIE I WCZESNA FILOGENEZA MSZYWIOŁÓW Z RZĘDU CHEILOSTOMATA

Streszczenie

W ściankach zoeciów prymitywnych Cheilostomata (*Wawalia*, górny walanżyn) stwierdzono występowanie porowatości identycznej jak u Cyclostomata. Wcześniej Tavener-Smith & Williams (1972) wykazali brak istotnych różnic w mikrostrukturze zoeciów między Cyclostomata i Cheilostomata. Najprymitywniejsze Cheilostomata (*Pyriporopsis*, górny portland) mają system pączkowania pośredni między Cyclostomata (szeregi jednorzędowe i diady) i Cheilostomata (triady). Prostopadłe do osi płożących się zoeciów ustawienie apertury zbliża Cheilostomata najbardziej do *Stomatopora* i *Corynotrypa* z Cyclostomata. Powstanie Cheilostomata było prawdopodobnie związane z rozszerzeniem opesium a tym samym pola działania mięśni hydrostatycznych.

Koncepcje postulujące powstanie Cheilostomata z Ctenostomata (Silen, 1942) nie znajdują potwierdzenia w dokumentacji paleontologicznej. Postuluje się wyprowadzenie Ctenostomata z prymitywnych Cheilostomata drogą pełnej redukcji szkieletu wapiennego. Najpierwotniejsze Ctenostomata (*Arachnidium*, od barremu) wykazują daleko idące podobieństwo w morfologii zoeciów i systemie pączkowania do wczesnych Cheilostomata (*Pyripora*).

Dominacja pączkowania triadami, charakterystyczna dla większości Cheilostomata tworzących inkrustujące kolonie, występuje już u form z górnego walanżynu (*Wawalia*). Brak polimorfizmu kolonijnego jest tu pierwotny. Owicelle znane są dopiero od środkowego albu (*Wilbertopora*) i wtedy też pojawiły się formy z awikulariami — zooidami o rozrośniętym, tworzącym szczękę operculum (*Mystriopora*). Początkowo niewielkie kolce otaczające opesium rozrastają się (*Anaptopora*, dolny cenoman) i zlewają się tworząc wtórną przednią ścianę (*Otopora*, dolny cenoman). W innej linii ewolucyjnej wtórna ściana frontalna powstaje przez rozrost blaszkowatej tylnej krawędzi opesium — kryptocystu (*Rhagasostoma*, dolny cenoman). Kompensujące zmniejszenie pola opesium, wpuklenie pod kryptocyst membrany frontalnej i uwypuklenie kryptocystu prowadzi do powstania worka kompensacyjnego (*Homalostega*, *Balantiostoma*, ?*Escharoides*, dolny kampan).

Wysunięto przypuszczenie, że powstanie polimorfizmu było poprzedzone przez rozdzielenie systemów informacji genetycznej odpowiedzialnych za końcowe etapy organogenezy różnych typów zooidów. Realizacja jednego z tych niezależnie ewoluujących systemów indukcji embrionalnej zależy od zadziałania odpowiedniego mechanizmu przełącznikowego.

Zmiany morfologii i rozmiarów zoeciów w rozwoju kolonii (gradient morfologiczny) interpretuje się jako wynik zmian stanu równowagi między stymulacją pączkowania a kumulującymi się zasobami pokarmowymi kolonii.

ЕЖИ ДЗИК

ПРОИСХОЖДЕНИЕ И РАННИЙ ФИЛОГЕНЕЗ МШАНОК ОТРЯДА CHEILOSTOMATA

Резюме

В стенках цистидов примитивных Cheilostomata (*Wawalia*, верхний валанжин) наблюдалась пористость аналогичная пористости у Cyclostomata. Ранее Тавенер-Смис и Уильямс (1972) констатировали, что в микроструктуре ячеек Cyclostomata и Cheilostomata не наблюдается существенных различий. Самые примитивные Cheilostomata (*Pyriporopsis*, верхний портланд) обладают промежуточной системой почкования между Cyclostomata (однорядное и диадное) и Cheilostomata (триадное). Положение апертуры перпендикулярно осям стелющихся учеек больше всего приближает Cheilostomata к *Stomatopora* и *Corynotrypa* из Cyclostomata. Возникновение Cheilostomata было, вероятно, обусловлено расширением опезия и, следовательно, площади действия гидростатических мускулов.

Предположения о развитии Cheilostomata из Ctenostomata (Силен, 1942) не находят обоснования в палеонтологических данных. Выдвигается взгляд о происхождении Ctenostomata за счет примитивных Cheilostomata путем полного редуцирования известкового скелета. Самые простые Ctenostomata (*Arachnidium*, с баррема) проявляют значительное сходство в морфологии цистидов и системе почкования с ранними Cheilostomata (*Pyripora*).

Преобладание триадного почкования, характерное у большинства Cheilostomata образующих инкрустационные колонии, наблюдается уже в формах из верхнего валанжина (*Wawalia*). Отсутствие колониального полиморфизма представляет здесь первичное явление. Овицеллы известны только лишь со среднего альба (*Wilbertopora*). Тогда же появились формы с авикуляриями — зооидами с разросшимся и образующим челюсть оперкулюм (*Mystriopora*). Первоначально небольшие шипы, окаймляющие опезий, разрастаются (*Anaptopora*, нижний сеноман) и соединяются, образуя вторичную переднюю стенку (*Otopora*, нижний сеноман). В другой эволюционной линии вторичная фронтальная стенка образуется за счет разрастания пластинчатой задней грани опезия — криптоциста (*Rhagasostoma*, нижний сеноман). Компенсирующее сокращение площади опезия, погряжение под криптоцист фронтальной мембраны и выгибание криптоциста ведет к образованию компенсационной сумки (*Homalostega*, *Balantiostoma*, *Escharoides*, нижний кампан). Предполагается, что появлению полиморфизма предшествовало разделение систем генетической информации, управляющей завершительной стадией развития разных видов зооидов. Выполнение одной из развивающихся независимо систем эмбриональной индукции стимулируется импульсами соответствующего переключающего механизма.

Изменения морфологии и величины цистидов в эволюции колонии (морфологический градиент) рассматривается в качестве результата изменения состояния равновесия между стимуляцией почкования и накопляющимися пищевыми запасами колонии.

EXPLANATION OF PLATES

Plate XV

Wawalia crenulata gen. et sp.n.
Uppermost Valanginian, Wąwał

Fig. 1. Holotype, JD 3004-268; ×50.
Fig. 2. Paratype, JD 3009-268; scanning electron micrograph, appr. ×400

Stomatopora dichotoma Lamouroux
Vesulian, Łęczyca

Fig. 3. Longitudinal section of zoecium, JD 3013-002, pl primary layer. sl secondary layer; ×400.

Plate XVI

Wawalia crenulata gen. et sp.n.
Uppermost Valanginian, Wąwał

Fig. 1. *a* and *b* fragments of paratype specimen, JD 3009-268; scanning electron micrograph, ×600.
Fig. 2. Tangential section of gymnocyste, JD 3011-268; ×400.
Fig. 3. Longitudinal section of gymnocyste, JD 3012-268; ×400.

Plate XVI

Anaptopora sp.
Cenomanian, Korzkiew

Fig. 1. Specimen MZ VIII/Bry 101; ×50.

? *Mystriopora* sp.
Upper Albian or Lower Cenomanian, Annopol

Fig. 2. Specimen JD 3010-254; ×50.

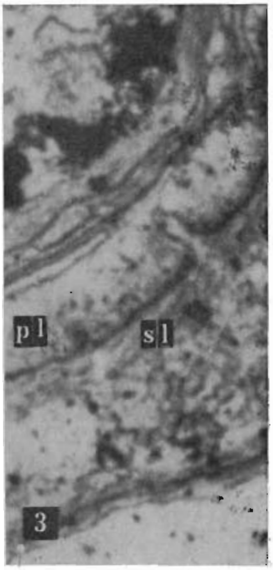
Plate XVIII

Rhagasostoma acmon (d'Orbigny)
Cenomanian, Korzkiew

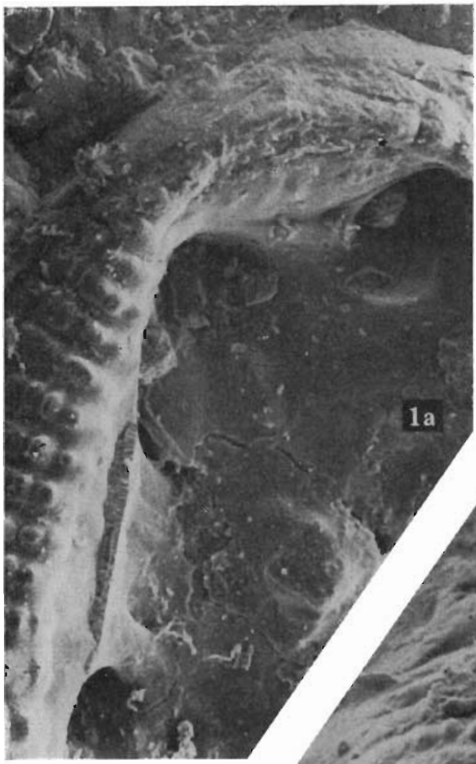
Fig. 1. Specimen MZ VIII/Bry-100; ×50.

?*Rhagasostoma* sp.
Cenomanian, Iwanowice

Fig. 2. Specimen MZ VIII/Bry-99; ×50.



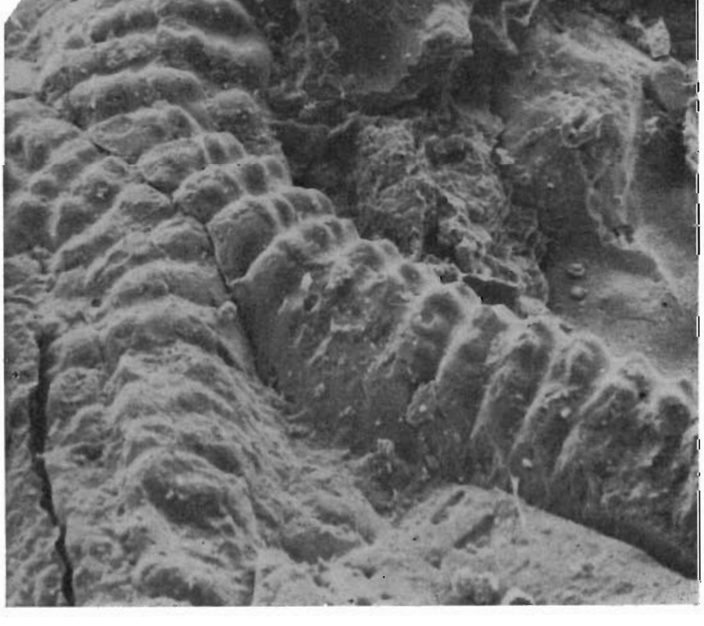
Figs 1, 3 phot: M. Radzikowska
Fig. 2 phot: G. & P. Mierzejewscy



1a

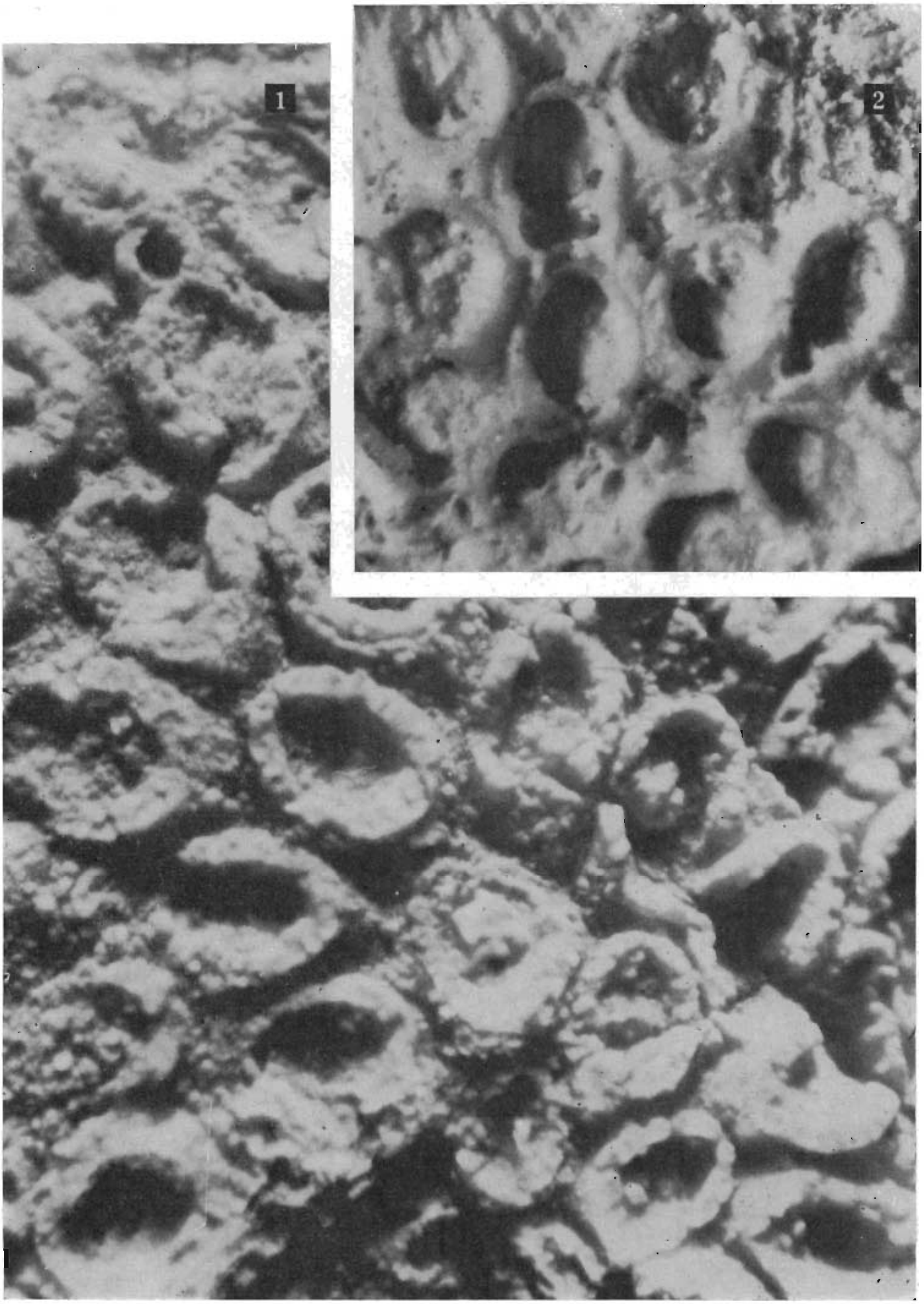
2

1b

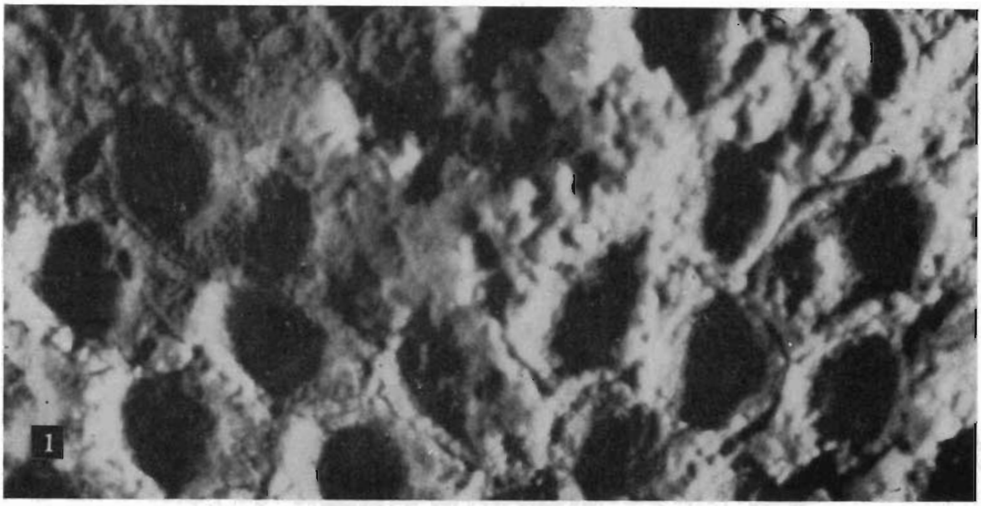


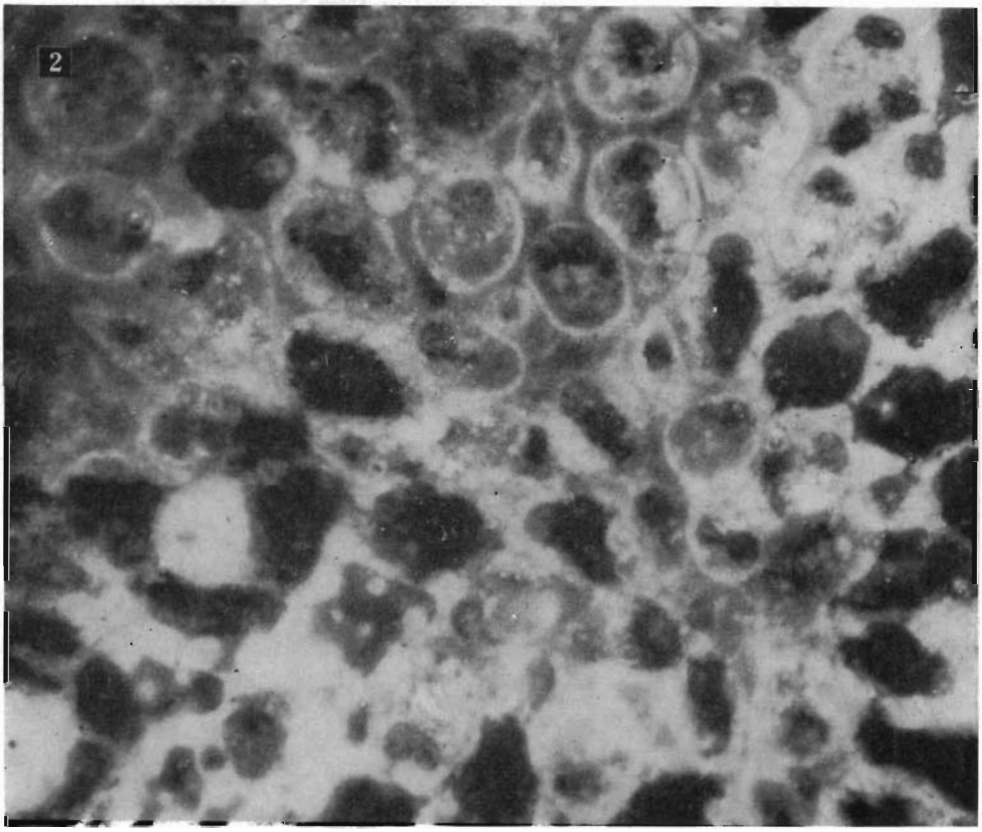
3

Fig. 1a, b phot: G. & P. Mierzejewscy



Figs 1, 2 phot. M. Radzikowska





Figs 1, 2 phot. M. Radzikowska