Early astogeny and relationships of the Ordovician rhabdomesine bryozoans

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A diverse Ordovician assemblage of juvenile bryozoan colonies, with external phosphatic coatings allowing chemical extraction from the rock, shows a morphologic series probably corresponding to evolutionary step-by-step suppression in the formation of the external colony wall. Its formation was initially delayed leading to formation of the common bud (advanced corynotrypids). Then the permanent double-walled colony organization developed along the colony margin (*Flabellotrypa*-like). In the following evolutionary stage, the external wall was secreted only at the conical creeping stage immediately following ancestrula (typical rhabdomesines). With subsequent evolution the external wall completely disappeared, and the double-walled ancestrula grew vertically (advanced rhabdomesines and phylloporinids). This kind of the early astogeny characterizes also the oldest phyllodictyid cryptostome *Prophyllodictya*, studied in serial peels. Flabellotrypidae fam. n., *Mojczatrypa halysitoides* gen. et sp. n., Kielceporidae fam. n., *Kielcepora ornata* gen. et sp. n., *Ojlepora* gen. n., and *Kielanopora gracilis* gen. et sp. n. are proposed.

K e y   w o r d s : astogeny, evolution, Ordovician, Bryozoa.

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Introduction

Bryozoan faunas of the Paleozoic and Triassic, unlike the later ones, were dominated by forms with the calcareous skeleton of their colonies completely covered from outside by soft tissue. The outer pseudocoelomatic space, common for the whole colony, integrated physiologically all the zooids, thereby enabling free transfer of morphogenetic factors and also controlling development of structures serving functionally for the whole colony. True 'superorganisms' developed in this way, with complex astogeny resulting in very sophisticated Baupläne (see McKinney 1978). The two most widespread kinds of colony organization were represented by massive

colonies, hemispherical or ramose, dominating in the order Trepostomata, and delicate fenestrate colonies typical for the Cryptostomata. Morphologically and presumably phylogenetically transitional forms, with slender cylindrical colonies, are usually classified in the suborder Rhabdomesina within either of these two main Paleozoic bryozoan orders.

It is now rather firmly established that all these bryozoans with the external soft tissue had developed from more primitive palaeotubuliporinids, which had each of their zooids separately protected from the outside environment by a continuous skeleton, with the orifice at the outer end of the peristome being the only exposed soft tissue area. The probable sequence of evolutionary transitions from palaeotubuliporinids to more advanced stenolaemates was from the earliest tubular forms with zooids communicating only basally, through colonies with a common bud in which zooids are unified anatomically until the external and internal skeletal walls separate them, up to true trepostomes and cryptostomes that never develop any individual external skeleton of the zooids other than the basal wall (Fig. 1). The external skeleton covered only the basal part of the colony attachment with less and less distinct ancestrula. With size of the colony base reduced, the external skeleton practically disappeared and the whole zoarium come to be built solely of the internal skeleton.

Somewhat surprisingly, among the oldest known bryozoans of the Arenig there are already forms with gracile ramose colonies, producing secondary colony tissue to increase rigidity of the basal parts of the colony, thus indicating presence of a well developed external soft tissue cover (Taylor & Curry 1985; Gorjunova & Lavrentjeva 1987). Primitive palaeotubuliporinids (corynotrypids) co-occurred with these derived forms, and although having similar colony forms, corynotrypids did not always develop even the common bud (each zooid of *Corynotrypa* and *Wolinella* budded separately; Dzik 1981). It seems unlikely, however, that the transition from a lack to the presence of an external soft tissue took place at the organizational level of ramose erect colonies, since no intermediates have been found in early Paleozoic faunas (even if a remotely similar change has been documented in the Recent stenolaemate *Cinctipora*; Boardman *et al.* 1992).

Although the sequence of events in the development of the soft tissue cover is relatively well recognized in the Trepostomata (Boardman & McKinney 1976; Podell & Anstey 1976; Dzik 1981), in the case of the Cryptostomata a lot of uncertainty remains (see McKinney & King 1984). The crucial role in any interpretation of their relationships is played by the phylloporinids and rhabdomesines. The only report on the early astogeny of the rhabdomesines is that by Tavener-Smith (1974), based on Early Carboniferous materials. Because they show patterns very unlike all other known Paleozoic bryozoans McKinney & King (1984: p. 864) found these data hard to fit in generally accepted evolutionary schemes and suggested that 'studies of rhabdomesoid bases, preferably of Ordovician or Silurian age, must be completed before' their relationships can be resolved.
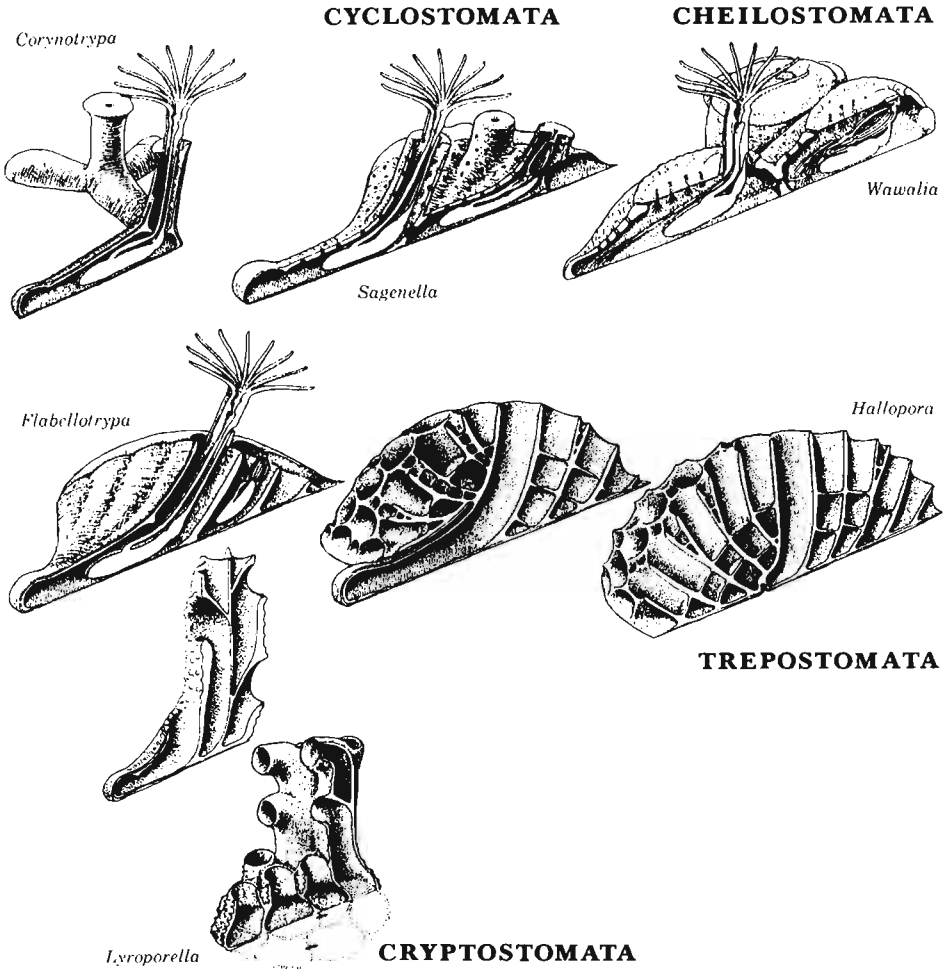
Fig. 1. Transformations in organization of juvenile zoarial morphology within the major groups of the Bryozoa (modified after Dzik 1991).

In the present paper such data are presented and an attempt to trace the evolution of the early astogeny leading from single-walled cyclostomatous ancestors, through the rhabdomesids, to early cryptostomes is done. A physiological interpretation of the process is also proposed.

Material and methods

The Ordovician Mojcza Limestone, cropping out at the village Mojcza near Kielce in the Holy Cross Mountains, is an extremely stratigraphically condensed unit, preserving in eight meters of its thickness a record of almost thirty million years of the evolution of the local marine ecosystem,

from the latest Arenig to Ashgill (Dzik *et al.* in press). The rock is mostly composed of detritus of calcareous fossils with thin phosphatic coatings (Fig. 3), the state of preservation exactly the same as in the well-known Early Cambrian 'small shelly fossils' assemblages. Bryozoans are among the more common fossils in Mojcza. An interesting feature of the assemblage is the relative abundance of early colony stages, presumably a result of high juvenile mortality at a muddy bottom devoid of larger objects that could provide stable substrate for older colonies.

A large collection of phosphatized fossils from Mojcza has been assembled by dissolving rock samples in acetic acid, the standard procedure for extracting conodonts. Some illustrations of the cyclostomatous Bryozoa from the locality have been already published (Dzik 1981) and a monographic review of the fauna is to be published (Dzik in press).

Fragmented bryozoan zoaria are preserved in the Mojcza Limestone with their original calcitic skeleton, which is usually completely dissolved during processing of conodont samples. The morphology of the zoaria can be studied owing to thin coatings of calcium phosphate that survive the treatment with acetic acid (see also Conti & Serpagli 1988). A thick coating, although well preserving a general colony form, may completely obliterate details of the surface ornamentation. The most informative are specimens with the thinnest phosphate cover. Such delicate cover, however, is easy to be exfoliated during sample processing. This makes also remounting on SEM stubs extremely risky. Therefore, the best specimens are illustrated, both here and in the review of the fauna (Dzik in press), only with camera lucida drawings taken from different sides of the object.

The Mojcza bryozoan assemblages are unusual in many respects. Extremely gracile colony shapes dominate in them, with the trepostomes and phyllodictyid cryptostomes, most typical for the Ordovician faunas elsewhere, virtually lacking. Unusually diverse and common are the palaeotubuliporinids, but the rhabdomesines contribute the most to the assemblages. Generally, the groups of benthonic organisms that dominate in the Mojcza assemblages are very primitive phylogenetically, and in this respect Mojcza differs from coeval shallow-water localities elsewhere. This is a general feature of phosphatized 'small shelly fossils' faunas known from the earliest Cambrian to Late Silurian. They all seem to represent (like in Mojcza) relatively cold and deep-water environments, with biotas evolutionarily delayed in respect to warmer and shallower ecosystems. The Ordovician Mojcza bryozoans may thus provide an insight into the oldest stage in the phylogeny of the group.

Early astogeny of Ordovician rhabdomesines

The Mojcza materials provide an almost complete spectrum of early astogenetic stages of the rhabdomesines, ranging from colonies with an extensive single-walled stage and horizontally creeping earliest zooecia to those
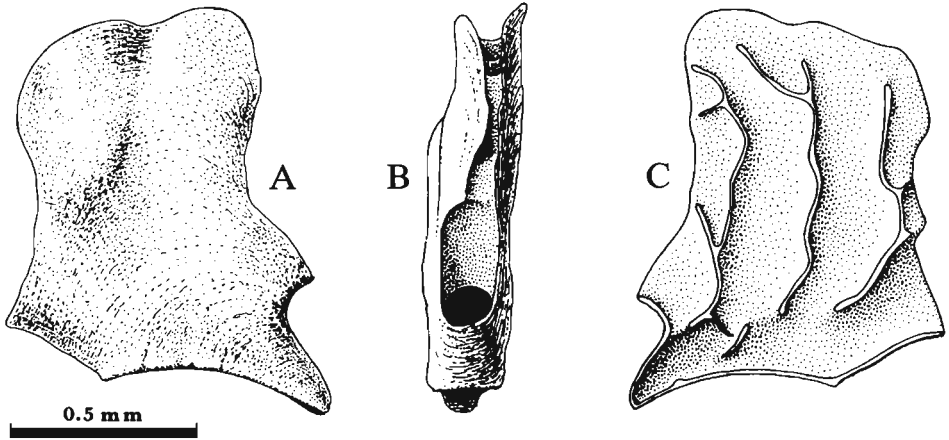
Fig. 2. *Mojczatrypa halysitoides* gen. et sp. n.; type locality of the Mojcza Limestone, Holy Cross Mountains, Poland; reconstruction of juvenile colony based on specimens from sample MA-85 (earliest Caradoc; see also Dzik in press: Text-fig. 6a, b) and MA-62 (latest Llanvirn; Fig. 3A). A-B. Lateral and distal views. C. Medially sectioned colony.

with the single-walled stage completely suppressed and vertically oriented ancestrula (Fig. 3). Beginning from the first, probably erroneous, attempt to interpret astogeny in phylogenetic terms by Elles (1922) a lot of information has been assembled regarding the evolution of early astogeny of both the graptolites (Urbanek 1960, 1963, 1971) and bryozoans (Dzik 1975, 1981; Schopf 1977; Anstey 1987). Several cases of recapitulation of phylogeny in astogeny are known and it is tempting to use the new data on the rhabdomesine astogeny in reconstructions of their early evolution.

The early astogeny of the most primitive trepostomes (Podell & Anstey 1979) and rhabdomesines (Figs 3B, 4; Tavener-Smith 1974) suggests that the common ancestor of both groups should have a single-walled organization, non-porous zooecial walls, and a narrow common bud zone at the distal end of a conical encrusting zoarium. Such bryozoans are known to occur in the Early Paleozoic and are here classified in the Flabellotrypidae fam. n., with two genera: *Flabellotrypa* Bassler 1952, characterized by zoaria attached with one of their flat sides to the substrate (see Kiepura 1962, Brood 1975), and *Mojczatrypa* gen. n., with erect colonies (Figs 2, 3A). They thus show traits close to possible ancestors of the trepostomes with massive colonies and ramose rhabdomesines, respectively.

The common bud of the flabellotrypids was permanently immature in respect to the formation of zooecial frontal walls. Neither a separation of zooecia nor any substantial growth of the internal skeleton that would exceed the external colony wall took place. Simple expansion of the bud, up to covering the whole upper surface of the colony, was the way in which, both in the early astogeny and presumably the phylogeny of the trepostomes, a hemispherical massive double-walled colony developed from the conical, single-walled ancestrular bud. Subsequently established centers

that may have hormonally stimulated increased growth resulted in development of massive ramose colonies (Podell & Anstey 1979). One might expect that the gracile erect colonies of the cryptostomes represented a further step in this direction. This may, however, not be the case.

The earliest stage in the astogeny of *Kielcepora ornata* gen. et sp. n. (Figs 3B, 4A-C) shows the same pattern as that described by Tavener-Smith (1974) in Carboniferous rhabdomesids. Not only the ancestrula, but the whole conical initial part of the colony is covered with an external skeletal wall with distinct growth lines. At this stage *Kielcepora* resembles thus *Flabellotrypa*. The differences appear immediately after, when the common bud transforms into a narrow zone of intense vertical growth of the inner colony walls and the typical double-walled zooecia of the colony start to be produced. This species thus represents a combination of a very advanced stage of gracile, erect double-walled colony form and a very primitive early astogeny.

Therefore, either the intermediate stages of hemispherical and massive double-walled colonies were deleted from the astogeny of the rhabdomesid descendants, or the origin of the rhabdomesines was independent of the trepostomes, directly from a *Flabellotrypa*-like ancestor. The latter hypothesis seems more reasonable, and the new Ordovician flabellotrypid *Mojczatrypa* represents a colony form with features one might expect in the ancestor of the rhabdomesines. Unlike *Flabellotrypa*, *Mojczatrypa* colonies were erect (see the extent of the encrusting base in Fig. 3A), even if the primitive common bud persisted throughout the astogeny (Fig. 2). An increase in growth rate of such vertical colonies may potentially result in suppression of the external wall, giving in effect better use of space along the colony axis. Even if *Mojczatrypa*, because its rather late geological age (Llandeilo), cannot be really close to the ancestry of the rhabdomesines, it shows possible paths in which these bryozoans may have originated.

The early astogeny of the most trepostome-like rhabdomesines with relatively thick cylindrical branches and metapores (Fig. 5) provides additional evidence that the origin of the rhabdomesines from ramose trepostomes is rather unlikely. Although the available specimens from Mojcza are not preserved well enough to show whether the earliest stages were single- or double-walled, the budding pattern was clearly polarized, with zooecia of the first generation very short. The center of the morphogenetic field of the branch developed later, the ancestrula did not function as a basilozooid and the position of it was not central as usual for the trepostomes.

The same pattern characterizes rhabdomesines with a few rows of zooecia along one side of the branch. The encrusting stage in the astogeny is there strongly restricted (Fig. 3C) as is the initial cone with the external skeleton (if present at all). This is the most common type of the early rhabdomesine astogeny in the Mojcza material (Dzik in press).

Possibly the next step in the evolution is represented by forms with the encrusting stage other than protoecium completely missing, which in
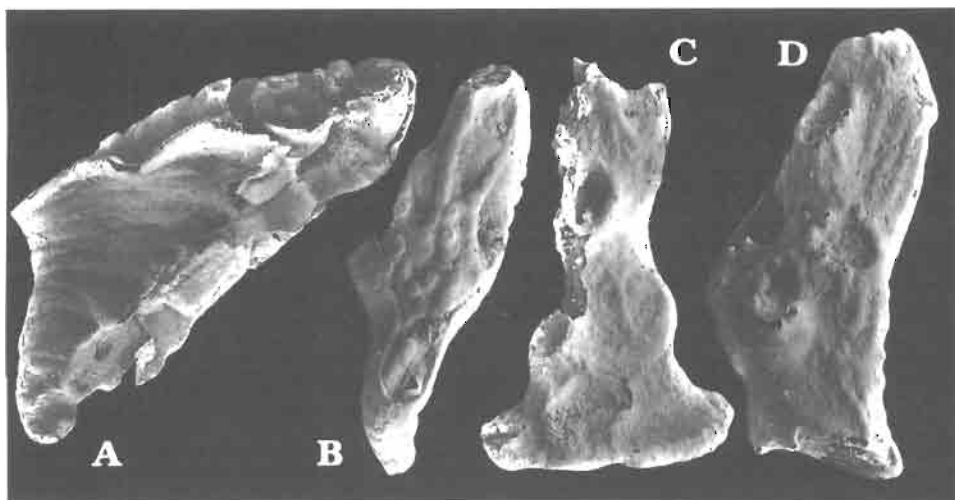
Fig. 3. Phosphatized juvenile bryozoan colonies from the Mojcza Limestone, Holy Cross Mountains, Poland; × 35. ☐A. *Mojczatrypa halysitoides* gen. et sp. n., ZPAL BrV/1018 in lateral view, sample MA-62, *P. anserinus* Zone, Llandeilo. ☐B. *Kielcepora ornata* gen. et sp. n., ZPAL BrV/1020, obverse side, sample MA-57, *E. lindstroemi* Zone, Late Llanvirn. ☐C. *Heminematopora* sp., ZPAL BrV/1028, obverse side, sample MA-87, *A. tvaerensis* Zone, Early Caradoc. ☐D. *Kielanopora robusta* gen. et sp. n., ZPAL BrV/1025, sample MA-85, *A. tvaerensis* Zone, Early Caradoc.

Mojcza material is represented by two species of *Kielanopora* gen. n. Only a small protoecium is attached to the substrate, the tubular, vertically oriented ancestrula being already double-walled (Fig. 3D). In *Kielanopora robusta* gen. et sp. n. a bunch of the first generation zooecia initiate the colony, but in the second, unnamed species from Mojcza the colony is uniserial beginning from the ancestrula (Dzik in press).

The reviewed range of diversity of rhabdomesine early astogeny is wide enough to allow derivation of the patterns known in the cryptostomes. Their evolutionary roots are thus likely to be within the early rhabdomesines.

Early astogeny of oldest ptilodictyid cryptostomes

The studied adult colony of *Prophyllodictya* from the latest Arenig of Hälludden, Öland has a massive stem with the initial group of zooecia hidden under a thick cover of the common colony tissue (Fig. 6A). It is composed mostly of longitudinal ribs (Fig. 6B) with numerous diaphragms and irregular horizontal thickenings that in transverse section resemble trepostome zooecia (Fig. 6C). The attachment surface is irregular, slightly concave. The substrate remains unknown. Longitudinal borings, probably by sipunculid worms, penetrate the zoarium but fortunately the earliest part remained intact.

The first slide that reached the initial part of the colony shows the ancestrula and irregular outlines of two first zooecia (thus probably their bottom walls have been sectioned). The protoecium, being cut off between two peels (at distance approximately 0.1 mm), was apparently not significantly swollen. The two first zooecia are surrounded by a few vesicular chambers, sometimes difficult to distinguish in sections from true zooecia, and this makes the way in which the next three zooecia emerge a little uncertain. Anyway, they form a semilunar group distally to the zooids of the first generation (Fig. 7E). The budding was thus initially strongly polarized, like in the Mojcza rhabdomesines. From this moment it changed in style and the following zooid generations are inserted in between the ancestrula and other zooids (Fig. 7K). The whole group of zooecia kept an oval cross-section and the colony was conically expanding at this stage, with the budding initiation in the center.

Both the ancestrula and other zooecia are very long and tubular. They diverge from the colony axis, with peristomes opened laterally after reaching a few millimeters length. Then the bilateral arrangement of zooecia develops, the median wall approximately following the symmetry plane of the basal group of zooecia.

Evolution of early astogeny in the cryptostomes

Prophyllodictya is the oldest known cryptostome with bifoliate colony branches and it may safely be considered close to the ancestry of the whole branch of the Ptilodictyina Astrova & Morozova 1956 (Gorjunova & Lavrentjeva 1987). Its early astogeny, as follows from the above description, is transitional between multiserial rhabdomesines with radially arranged peristomes at later astogenetic stages (like that in Fig. 5) and some of the phylloporinids with peristomes tending to open on one side of the fenestrate colony branches (like that in Fig. 8). In all these cases the budding is polarized but the ancestrula and first zooids are much shorter in the rhabdomesines.

The *Prophyllodictya* pattern of earliest astogeny, with at least the two first zooids budding at the substrate, has been preserved in the enalloporids (see Brood 1982; Schallreuter & Hillmer 1987) as well as phylloporinids (McKinney & King 1984). They differ in subsequent paths of developing a colony form. In Silurian *Phylloporina? asperatostriata* (Hall 1852) the colony base expands conically but then subdivides radially into branches and, accordingly, a radial budding of zooecia around the ancestrula starts from the beginning of the astogeny (McKinney & King 1984: Fig. 2). The ancestrula and zooecia are elongated in this species, unlike advanced fenestrate cryptostomes, but this radial pattern of the astogeny resembles spirally arranged groups of the basal zooecia in the Carboniferous *Lyroporella* (see McKinney 1978). This is consistent with Blake's (1983: p. 450; also Tavener-Smith 1975) opinion that the fenestellids, characterized by
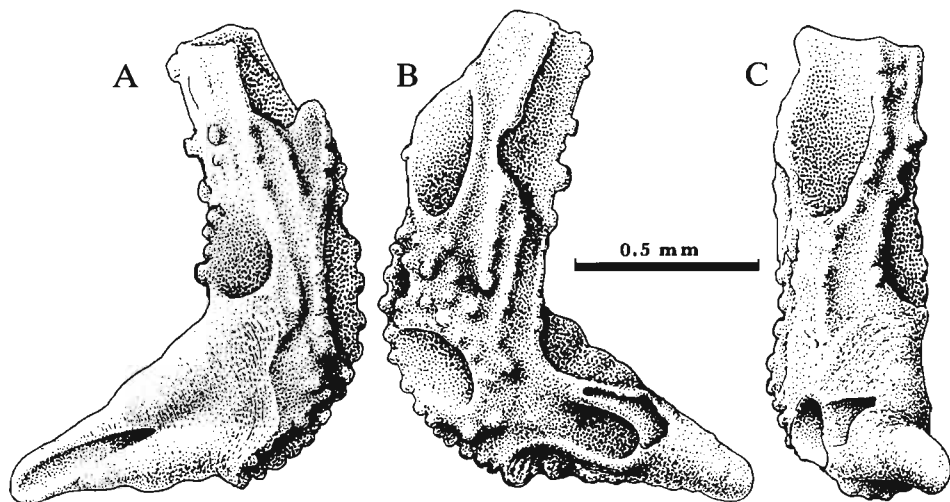
Fig. 4. *Kielcepora ornata* gen. et sp. n.; Mojcza Limestone, Mojcza, Holy Cross Mountains, Poland, sample MA-26, Llandeilo; basal, upper, and proximal views of a juvenile colony with calcium phosphate coating.

short zooecia, derived in Late Ordovician from *Phylloporina* with more elongated, tubular zooecia. If the phylloporinids are really successors of early rhabdomesines with relatively short zooecia it would mean an evolutionary reversal. Actually, also in advanced ptilodictyids, as well as the phylloporinid(?) *Ralfinella* (Dzik in press), zooecia were secondarily shortened and simplified morphologically. The process, widely occurring among the cryptostomes, seems to be a result of simplification of particular zooids in progressively more and more integrated colonies.

The radial arrangement of the colony branches in other phylloporinids developed much earlier in the astogeny, as in the case with Silurian *Chasmatopora?* sp. studied by McKinney & King (1984: Fig. 3) and the Devonian species attributed to *Fenestella* by Cummings (1904, 1905).

Several fenestrates do not show radial colony organization from the beginning of their astogeny. Their branches were arranged in a half-funnel, presumably oriented parallel to a bottom current. In such case only one erect colony branch emerge from the group of the basal zooecia. In Carboniferous *Lyroporella* peristomes of this branch are facing the basal group of vertically gaping short zooecia (McKinney 1978).

Ordovician *Moorephylloporina? reticulata* (Hall 1847) as interpreted by McKinney & King (1984: Fig. 1) is somewhat enigmatic in having allegedly creeping, tubular ancestrula with zooecia of subsequent generations parallel. The illustrated specimen resembles thus rather a cut in half funnel-like advanced fenestrate colony than any of the rhabdomesines of phyllodictyids discussed above.

Physiological interpretation

A sequence of evolutionary events leading to the development of the advanced cryptostome colony organization through the rhabdomesids as an intermediate stage can thus be proposed.

At the very beginning a tubular skeleton was produced by the earliest bryozoans, similar to that of the corynotrypids and their possible non-colonial ancestors (see Dzik 1991; Weedon 1991). In some derivatives of the Corynotrypidae the formation of internal walls was fast enough, preceding both the branching of ramose colonies and formation of frontal walls in the zooids, to result in a common-bud at the distal end of the colony.

Development of frontal walls was completely suppressed in the Flabellotrypidae although their double-walled margin of the colony is morphologically undistinguishable from the common bud in more primitive cyclostomes. The sole difference is the complete lack of any zooecia with separate external walls in the flabellotrypids. Vertical colony growth then developed in some of them, with the double-walled surface still quite restricted in area. The next factor then appeared: a suppression of the external colony wall.

Unlike the trepostome encrusting colonies, which produced the external wall basally, while expanding over the substrate, in the rhabdomesines the external wall continued to be developed only for a short time after the common bud was established by the ancestrula and then suddenly disappeared. A small growing front developed at the double-walled margin of the colony and this was solely responsible for the colony vertical growth. The budding pattern of *Prophyllodictya* shows that the factor stimulating budding was produced at the tip of a growing branch. The extend of the external wall at the proximal end of the colony became more and more restricted until the ancestrula transformed into a double-walled zooid.

At least some parts of the above sequence of events were repeated in the evolution of the Bryozoa several times. They must have been thus controlled by rather simple morphogenetic mechanisms. Actually, one may reduce the whole process to a gradual suppression in the formation of the external colony wall. Its formation was initially delayed, in respect to the internal walls, at newly secreted zooid peristomes, leading thus to formation of the common bud. It is generally accepted that the external pseudocoelom common for the whole colony developed from a retarded common bud. Finally, except for the stage immediately following the ancestrula, the external wall was no longer secreted at all.

The ancestrula is the only zooid in the bryozoan colony produced sexually and it depends in its development on the egg yolk. Its organogeny may thus be controlled by different morphogenetic factors than in the following generations. Urbanek (1960) proposed this feature of the sexually produced zooid in graptolites to explain its morphologic distinction and this idea can be applied also to the rhabdomesid bryozoans. A decrease in
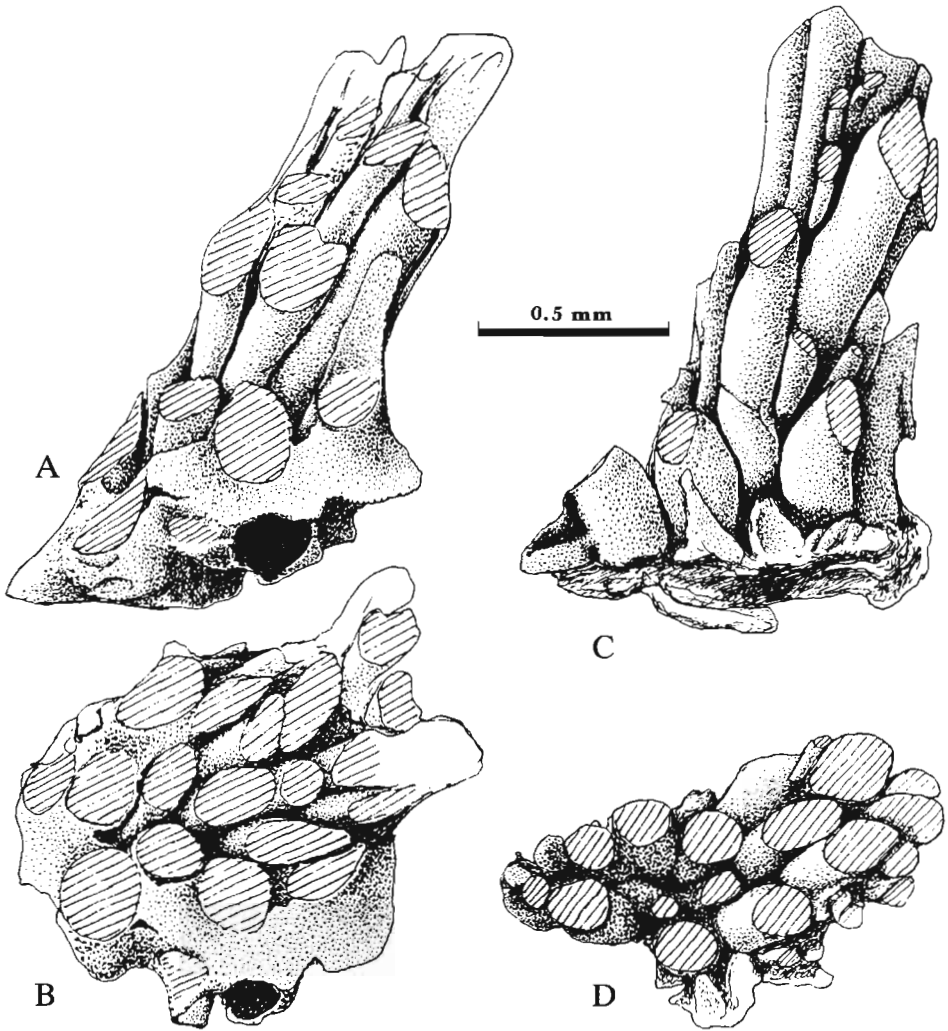
Fig. 5. *Nematotrypa*(?) sp., phosphatic nuclei of juvenile colonies from the Mojcza Limestone at Mojcza, Holy Cross Mountains, Poland; lateral and upper views. ☐A-B. Sample MA-84. earliest Caradoc. ☐C-D. Sample MA-98, latest Caradoc.

expression of a physiologic factor inherited from the egg may thus result in final evolutionary suppression of the external wall in the rhabdomesines.

The evolution of the rhabdomesines was thus probably controlled by changes in that part of the genome which controls development of the external wall. To go further and to interpret properly the process of their morphologic evolution one needs more information on the genetic control of histogeny of the frontal wall in Recent cyclostomatous Bryozoa.

Most interestingly, the final result of the discussed evolutionary process, a funnel-like cryptostome colony with the vertically growing first zooid, thin branches connected in a network by dissepiments, and the

stem strengthened with a secondary tissue, imitates organization of den-drograptid colonies, built of completely different skeletal material in basi-cally different way. While the organization of a bryozoan colony directly depends on the anatomy of zooids, the collagenous graptolite rhabdosome is a product of evolutionarily modified behavior of particular zooids. If results are so similar, the background selection forces must have been closely similar, too.

Diagnoses of new taxa

Flabellotrypidae fam. n.

Diagnosis.– Fan-like expanding encrusting colonies with double(free)-walled zooids opening their peristomes in a narrow zone at the distal end. External wall imporous, with distinct growth lines, pores in internal walls may communicate between adjacent zooids.

Remarks.– The morphologic organization of the bryozoans included in the family is transitional between the palaeotubuliporinid Cyclostomata (*Woli-nella*), primitive Trepostomata, and rhabdomesine Cryptostomata. It re-mains thus a matter of convenience to which of these higher rank units it is assigned.

Genera included: *Flabellotrypa* Bassler 1952, *Mojczatrypa* gen. n.

Mojczatrypa gen. n.

Type species: *Mojczatrypa halysitoides* gen. et sp. n.

Diagnosis.– Vertically oriented, laterally flattened fan-like colonies with usually a single series of peristomes opening along the margin of the fan. Species included: Only the type species.

Mojczatrypa halysitoides gen. et sp. n.

Figs 2A-C, 3A.

Holotype: ZPAL BrV/1018. Fig. 3A.

Type horizon and locality: *P. anserinus* Zone. Llandeilo, sample MA-62, Mojcza Limestone, Holy Cross Mountains, Poland.

Diagnosis.– As for the genus.

Distribution.– *P. anserinus* to *A. tvaerensis* Zones, Llandeilo and Early Caradoc.

Kielceporidae fam. n.

Diagnosis.– Ancestrula attached to the substrate with its side, trans-formed into a more or less conical initial part of the colony with well developed external skeleton and the common bud restricted to its distal end. Narrow colony branches usually with peristomes opening on one side; no axial zone or joints.

Remarks.– New data on the early astogeny of Ordovician bryozoans provide additional evidence for the fact that similar colony forms may develop in unrelated bryozoans with basically different colony develop-ment. This especially concerns the rhabdomesines with their geometrically
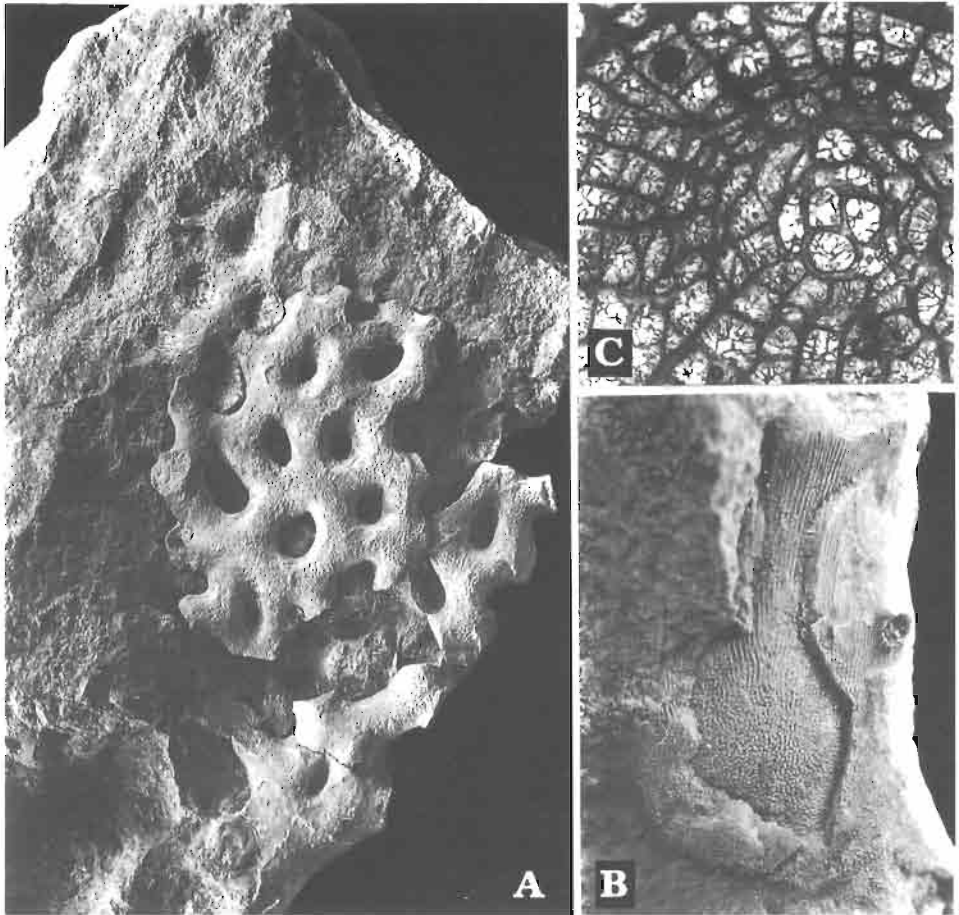
Fig. 6. *Prophyllodictya* sp., Kundan (latest Arenig) of Hälludden, *Asaphus raniceps* Zone, 1.6 m above the base, Öland island, Sweden; specimen ZPAL Br V/1024. ☐A. Lateral view of the colony; × 1. ☐B. Surface ornamentation of the stem; × 5. ☐C. Acetate peel of transverse section of the colony base with the ancestrula and five daughter zooecia (see Fig. 7F).

simple arrangement of morphologically uniform zooecia. Their classification based solely on morphology of adult colony branches may thus result in polyphyletic groupings. I propose therefore to restrict the family Arthrostylidae Ulrich 1882 to forms with articulated colonies (*Arthrostylus* Ulrich 1882, *Arthroclema* Billings 1865, *Arthrostyloecia* Bassler 1952, *Cuneatopora* Siegfried 1963, *Helopora* Hall 1851, *Moyerella* Nekhoroshev 1956, *Osburnostylus* Bassler 1952, *Sceptropora* Ulrich 1888, *Ulrichostylus* Bassler 1952). The new family Kielceporidae is proposed for early rhabdomesines that share with the Rhabdomesidae Vine 1884 conical initial part of the colony with well developed external skeleton but lacking the axial cylinder or any axial zone. It is somewhat inconvenient to make the type of a family a species known solely from phosphatized remnants, but in type
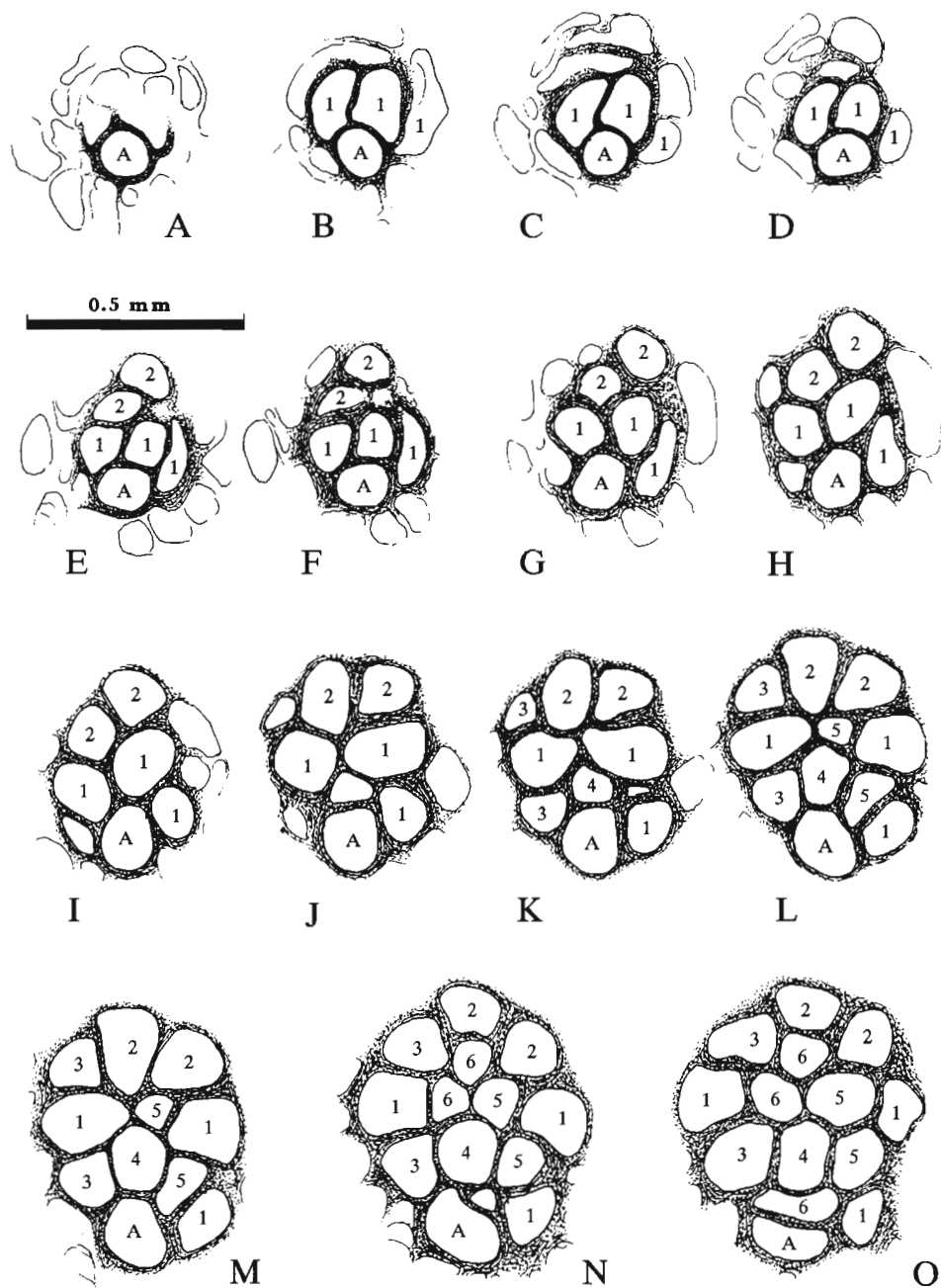
Fig. 7. *Prophyllodictya* sp., Kundan (latest Arenig) of Hälludden, *Asaphus raniceps* Zone, 1.6 m above the base, Öland island, Sweden; specimen ZPAL Br V/1024. A-O. Camera-lucida drawings of acetate peels taken from serial sections of the colony base; zooid generations indicated with numbers.
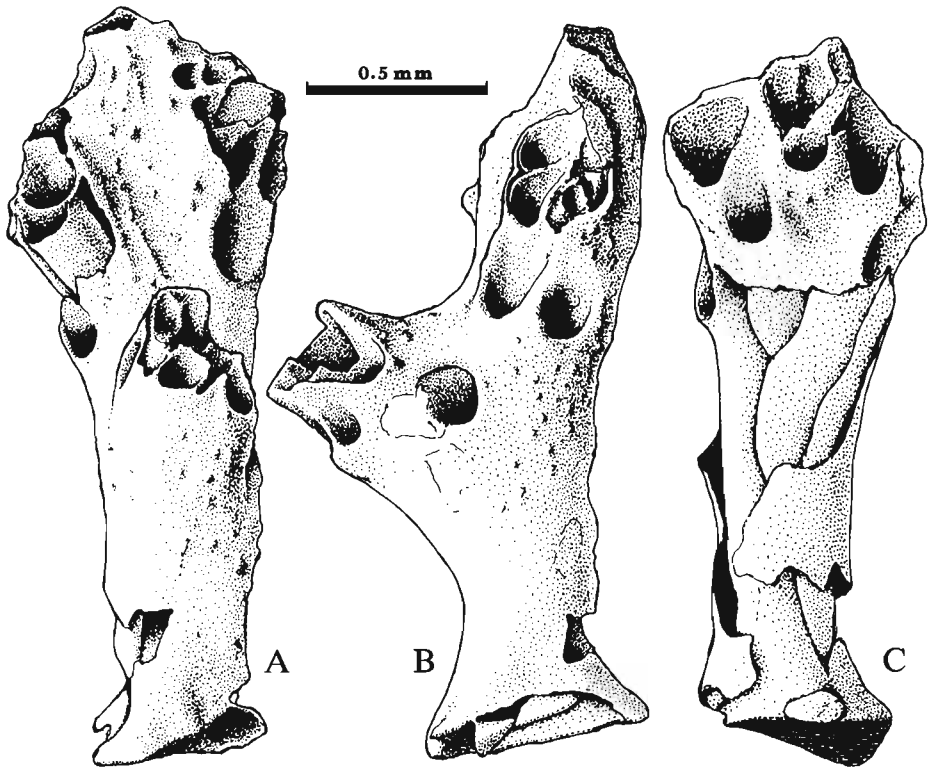
Fig. 8. *Parachasmatopora*(?) sp.; type locality of the Mojcza Limestone, Holy Cross Mountains, Poland, sample MA-20, early Caradoc. A-C. Proximal, lateral, and distal views of a juvenile colony with calcium phosphate coating (artificially exfoliated in C).

species of presumably related genera the early astogeny remains unknown and their morphologic similarity may appear misleading.

Genera included: *Kielcepora* gen. n., *Heminematopora* Bassler 1952, *Ralfinella* Lavrentjeva 1985, *Glauconomella* Bassler 1952, *Ojlepora* gen. n.

Kielcepora gen. n.

Type species: *Kielcepora ornata* gen. et sp. n.

Diagnosis.– Narrowly cylindrical colony branches with more or less radially arranged zooecial peristomes alternating in rows. Peristome margins and the surface of the branch covered with prominent stylets.

Kielcepora ornata gen. et sp. n.

Figs 3B, 4A-C.

Holotype: ZPAL BrV/1020, Fig. 3B.

Type horizon and locality: *Eoplacognathus lindstroemi* Zone, Uhakuan, Late Llanvirn, sample MA-57, Mojcza Limestone, Holy Cross Mountains, Poland.

Diagnosis.– Colony branches with usually four rows of large (approximately 0.25 mm) oval peristomes with a dozen stylets around the margin. Rows of similar stylets cover the surface between the peristomes. A slight dorsoventral asymmetry of branches may develop.

Distribution.– *Eoplacognathus robustus* to *E. lindstroemi* Zones, Uha-
kuan, Late Llanvirn, Mojcza Limestone.
Species included: Only the type species.

Ojlepora gen. n.
Type species: *Thamniscus*(?) *orosus* Wiman 1901

Diagnosis.– Dichotomous colony branches with a few rows of zooecia
(usually 4-6), reverse side with longitudinal riblets, the medial one usually
stronger.

Remarks.– The initial colony part of the type species illustrated by Spjeld-
naes (1984: Pl. 5: 5) shows clearly polarized early astogeny shared with the
Mojcza rhabdomesids. Although the stage with external wall seems to be
restricted or even missing, the close similarity to *Kielcepora* in the morpho-
logy of zooecia suggests this family placement.

Species included: The type species and a few yet unnamed forms from the
Mojcza Limestone.

Family Nematotrypidae Spjeldnaes 1984

Emended diagnosis.– Vertically growing double-walled ancestrula located
marginally in the encrusting part of the colony. The erect stage follows after
a few generations of short zooecia attached to the substrate. Zoarial
branches with radially arranged zooecia. Spaces between zooecia in
multiserial forms may be filled with metapores.

Remarks.– Blake (1983: p. 592) removed *Nematotrypa* from the Rhabdo-
mesina. Without examining the type species of the genus I am not able to
evaluate Spjeldnaes' (1984) decision to erect a family based on it within the
rhabdomesines. However, the presence of cylindrical multiserial rhabdo-
mesines with metapores and extensive encrusting parts in Mojcza (Fig. 5)
supports his view. The interpretation of *Nematopora* here accepted is based
on the attribution of colony bases from the Devonian of Ohio to this genus
by Blake (1983: Fig. 221.4).

Genera included: *Nematotrypa* Bassler 1911, *Nematopora* Ulrich 1888,
Tropidopora Hall 1886, *Kielanopora* gen. n.

Kielanopora gen. n.
Type species: *Kielanopora robusta* gen. et sp. n.

Diagnosis.– Vertically growing tubular ancestrula, the first zooid buds
above the substrate. Colony branches thin, zooecia sparsely distributed
along the axis with more or less radially oriented peristomes, which are
usually armed with a circle of short stylets.

Remarks.– The species of the genus, especially an unnamed one from the
Early Caradoc of Mojcza (Dzik in press), represent the extreme stage in
suppression of the encrusting colony stage within the family. Because of
radial (or alternating opposite) distribution of peristomes along the colony
branches they are unlikely to be directly related to the phylloporinids.

Species included: The type species and unnamed gracile species from the
Mojcza Limestone.

Kielanopora robusta gen. et sp. n.
Fig. 3D.
Holotype: ZPAL BrV/1025, Fig. 3D.
Type horizon and locality: *Amorphognathus tvaerensis* Zone, Kukrusean, Early Caradoc, sample MA-85, Mojcza Limestone, Holy Cross Mountains, Poland.
Diagnosis.– Relatively robust colony branches with peristomes of tubular, coarsely ornamented zooecia only slightly elevated.
Distribution.– *Amorphognathus tvaerensis* to *A. superbus* Zones, Early to Late Caradoc, Mojcza Limestone.

Acknowledgements

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Streszczenie

Dzięki licznym okazom młodocianych kolonii mszywiołów z otoczkami fosforanowymi, wytrawionym z ordowickich wapieni z Mójczy, możliwe stało się skompletowanie pełnego szeregu morfologicznego wzrostu złożoności astogenezy w ewolucji Rhabdomesina. Generalna tendencja polegała na redukcji stadium z zewnętrznym szkieletem aż do objęcia wspólną jamą ciała nawet ancestruli. W dalszej kolejności doprowadziło to do daleko posuniętej fizjologicznej integracji kolonii; struktury wspólne dla kolonii podlegać poczęły ewolucyjnej komplikacji zaś poszczególne zooecia uproszczeniu.