# EVOLUTIONARY RELATIONSHIPS OF THE EARLY PALAEOZOIC 'CYCLOSTOMATOUS' BRYOZOA

*by* JERZY DZIK

ABSTRACT. *Wolinella baltica* gen. et sp. n. from the Arenig of Baltic province is the oldest known single-walled bryozoan. It is characterized by cylindrical zooecia, non-pseudoporous exterior wall, and well-developed communication canals between zooecia. *Wolinella* is a supposed ancestor of *Corynotrypa*, which occurs in the lowermost Llanvirn. Evolution from the latter genus to *Dentalitrypa* and to the boring ctenostome *Ropalonaria* originated in the Caradoc. The tendency to develop a common bud in *Wolinella* suggests that *Diploclema* also may be its descendant. The genera *Sagenella*, *Clonopora*, and *Kukersella*, which form a morphological sequence of increasing pseudopore concentration and complexity of communication canals may have also originated from *Wolinella*-like encrusting forms. All post-Palaeozoic Cyclostomata could have been derived from *Kukersella*-like bryozoans. The morphological sequence composed by genera *Wolinella*, *Flabellotrypa*, and *Ceramopora* illustrates evolutionary development of colony-wide hypostegal coelom from a marginal one. *Ceramopora* shows a well-developed single-walled ancestrula with a large hemispherical protoecium. Hederellida are somewhat isolated among Palaeozoic bryozoans in their morphology and astogeny. They resemble Recent phylactolaemate Plumatellida both in the mode of budding, with specialized stolozooids, and shape of zooecia. Corynotrypidae fam. n., *Wolinella* gen. n., *Wolinella baltica* sp. n., *W. polonica* sp. n., *W. brevis* sp. n., *Dentalitrypa infundibuliformis* sp. n., *Clonopora primaeva* sp. n., and *Kukersella erratica* sp. n. are proposed.

ALL Palaeozoic-to-Recent stenolaemate bryozoans lacking a colony-wide hypostegal coelom (the single-walled forms of Borg 1926) are traditionally included in the order Cyclostomata (Bassler 1911*a*, *b*; Brood 1975). On the other hand, all double-walled Palaeozoic bryozoans have been excluded from this order (Astrova 1964, 1965; Utgaard 1973). The lack of the colony-wide hypostegal coelom indicates only the primitiveness of the group and reveals nothing about the internal anatomy of a polypide. There are still too few unequivocal arguments for assignment of particular Palaeozoic 'cyclostomes' to any known higher group of Bryozoa. Many cases of homeomorphy during the 500 Myr of bryozoan evolution have confused the picture of their relationships. A reconstruction of small morphological transformations within fine temporal sequences seems to be a very helpful method in this situation (the stratophenetic approach of Gingerich 1979). It may allow the tracing of evolutionary lines connecting particular groups of early Bryozoa. The aim of this paper is to discuss possible connections between particular groups of early Palaeozoic 'cyclostomes' and related bryozoans in the context of their stratigraphical distribution. Some new sources of information about internal zooecial morphology have been utilized. A reconstruction of the early phylogeny of Bryozoa has been attempted.

*Materials and methods*

The fossils described here were collected from Ordovician erratic boulders of Baltic origin, occurring in the diluvial deposits of central and northern Poland, and from the Ordovician Mójcza limestone (Holy Cross Mts., Poland). Both sources span an age interval from Upper Arenig to Ashgill, and both belong to the Baltic palaeozoogeographical province. Age estimations are based on conodonts (Dzik 1976, 1978). The Baltic Ordovician has supplied a well-known cyclostome bryozoan fauna (Bassler 1911*a*, *b*; Kiepura 1962; Brood 1973, 1974, 1975). Some Silurian species described here are also from Baltic boulders. Estimation of age is based on associated benthic fauna, and is not precise. Cyclostomatous Bryozoa from the Baltic Silurian have been described by Kopajevich (1971) and Brood (1975).

Devonian hederellids have been collected in the Grzegorzowice-Skały section in the Holy Cross Mts., Poland. They occur in two shale series separated by a thick carbonate sequence. The lower one—Grzegorzowice Shale Member of the Grzegorzowice Formation—has been tentatively dated as Eifelian (Adamczak 1976), though no stratigraphically important fossils from it are known. The upper one—Brachiopod Shale of the Skały Formation—contains the pelagic tentaculite *Nowakia otomari* Bouček which is a previously recognized zonal fossil (Bouček 1964; Lütke 1979). 'Cyclostome' bryozoans from Grzegorzowice-Skały section have been partially described by Kiepura (1973).

Some additional cyclostome bryozoans were found in sandy limestones of the Kapp Starostin Formation from Polakkfjellet, Spitsbergen. Samples of rock containing bryozoans have been gathered by Mr. Krzysztof Małkowski M.Sc. during the polar expeditions of the Zakład Paleobiologii PAN in 1975 and 1976. The age of these beds is determined on the basis of associated conodonts as Upper Leonardian or Lower Roadian (Szaniawski and Małkowski 1979).

Almost all previously described Palaeozoic cyclostomes were preserved in shales or marls; they usually formed colonies encrusting surfaces of hard objects (Bassler 1911*a*, *b*, 1939; Solle 1968; Kiepura 1973; Brood 1974, 1975; Kesling and Chilman 1975). This preservation gives some information on the colony shape and astogenetic characters, but distal parts of zooecia are mostly broken. In some genera (e.g. *Dentalitrypa*, *Corynotrypa*) species determination is accordingly difficult. Well-preserved adapertural structures can be studied in undissolved calcite or silicified remnants of zooecia commonly found in residues of acidized limestone samples (Kiepura 1962). The pattern of communication canals and pores between zooecia, and wall pseudopores, may be excellently preserved by phosphate, chamosite, glauconite, or siliceous internal moulds of zooecia. This mode of preservation is similar to, or even better than artificial polystyrene moulds (see Hillmer 1968). Successive solution of a bryozoan colony infilled with chamosite allows observation of early astogeny in very fine, three-dimensional details. Excellent examples of early astogeny can be obtained by delicately etching the surface of moulds of trilobite carapaces and other fossils. After removing the basal layer of a colony, transverse zooecial walls appear, enabling reconstruction of relations between ancestrula and the next zooidal generations. Similar effects are given by a standard method of serial acetate peels (*see* McKinney 1977, 1978) but there are difficulties with the orientation of the plane of sectioning, especially in massive colonies growing on a rough substrate. All of these methods have been employed here, often more than one on a given species.

The course of astogeny has been illustrated by using Harmer's diagrams (see text-fig. 7*b*) in the same manner as in Boardman and Cheetham (1969). Modified Harmer diagrams have been used to show astogeny in hederellids where new buds do not arise from the distal apex of the zooecia (text-fig. 2).

## ZOOECIAL MORPHOLOGY AND ASTOGENY OF THE PALAEOZOIC 'CYCLOSTOMES'

### Hederellidae

This group of single-walled Bryozoa is characterized by a specific shape of zooecia, non-pseudoporous zooecial wall, and mode of budding. Hederellid zooecia are cylindrical, with strong growth lines, and upward-curved apertures. Some specialized zooids (stolozooids) were centres of budding; they produced numerous short, normally-developed zooids. Hederellidae are known from the Wenlock (Bassler 1939; Prantl 1938*b*) to the end of Carboniferous (Missourian; Condra and Elias 1944) but only Devonian faunas are adequately described (Bassler 1939; Solle 1968; Kiepura 1973; Kesling and Chilman 1975). No pre-Silurian ancestor of hederellids is known. The closely-related family Reptariidae differs in the lack of stolozooids. This character connects reptariids with corynotrypid Cyclostomata but in stratigraphical range they do not precede Hederellidae (Bassler 1939; Kiepura 1973).

The irregular budding pattern and very simple shape of zooecia results in many difficulties in estimating the range of species within Hederellidae. The zooecial diameter is almost the only feature

which may be objectively employed in the taxonomy of the group (Bassler 1939; Solle 1968; Kiepura 1973). However, the size of zooecia must be controlled by environmental, and especially trophic, factors (Jebram and Rummert 1978). Therefore identification of species on the basis of this character, particularly in non-topotype localities which may differ in environmental conditions, must involve some difficulties. Biometrical investigations of hederellid intrapopulation variability are very much needed. The methodological basis for the hederellid species concept is provisional, and every specific name is somewhat subjective.

The early astogeny is known in six Givetian species from New York State and Michigan (Bassler 1939; Kesling and Chilman 1975), and in two Givetian (and Eifelian?) ones from Poland (Kiepura 1973; here text-figs. 1, 2). Poorly illustrated early portions of colonies can be found in other papers (Prantl 1938b; Solle 1968). Supposedly the most primitive type of early astogeny, on the basis of similarity with other bryozoan groups, is represented by *Hederella rugosa* Bassler (Bassler 1939: pl. 3, figs. 7-8), *H. reimanni* Bassler (text-figs. 1b, 2f) and *Hederella* sp. (text-fig. 2d, g). The length of the ancestrula is here approximately comparable with that of the autozooids; after budding a few daughter zooids it grows no further. Some zooids of the first to fourth generations become stolozooids during their growth. The second type of astogeny is represented by the North American species *H. thedfordensis* Bassler (Bassler 1939: pl. 6, fig. 8), *H. parvirugosa* Bassler (Bassler 1939: pl. 6, fig. 13), and *H. concinna* Bassler (Bassler 1939: pl. 7, fig. 10). It is characterized by the stolozooidal nature of the ancestrula. The ancestrula grew continuously in length, budding laterally numerous autozooids and a few stolozooids. The boundary between these two types of early astogeny of *Hederella* is not sharp.

*Diversipora bitubulata* Kiepura from Eifelian(?) and Early Givetian of Poland is characterized by a different mode of budding from *Hederella*. Autozooids are budded not laterally but from the upper side of the stolozooid (text-fig. 1a). Inside, each stolozooecium is divided in its proximal part by internal transverse walls. They separate numerous chambers which connect in their distal parts, through large pores, with short autozooecia lying on the frontal side of the stolozooecium. It seems that both the chamber in the stolozooecium and the tube on its surface belonged to a single autozooid. Probably there is no communication between chambers at least in the proximal parts of the stolozooecium.

*D. bitubulata* can be derived from some large-sized species of *Hederella* via '*Hederella*' *magniventra* Bassler from Lower Gravel Point Limestone of Michigan (Bassler 1939: pl. 10, figs. 5-6) as a connecting link. The last species has very short autozooecia which germinated frontally or obliquely from the stolozooecium. Its assignment to *Diversipora* seems to be better substantiated than to *Hederella*.

The concept of the origin of *Diversipora* as a transformation of typical *Hederella*-type lateral budding into frontal budding is supported by its early astogeny. Recapitulation of phylogeny in astogeny has been suggested by many authors (Dzik 1975, Schopf 1977) but usually simplicity of ancestrular morphology and nearest succeeding generations have not allowed the construction a convincing, unequivocal demonstration of this phenomenon. Phylogeny recapitulation and introduction of evolutionary changes in early astogeny is much better known in colonies of graptolites (Urbanek 1960, 1963, 1973). Data presented by Urbanek shows how evolutionary novelties introduced on the advanced stages of astogeny (distally; on the zone of astogenetic repetition according to Boardman and Cheetham's 1973 nomenclature) expand on the earlier astogenetic stages (on the zone of astogenetic change) with some evolutionary delay. The same phenomenon is represented by the astogeny of *D. bitubulata*. The first autozooid of *D. bitubulata* was germinated laterally by the simple ancestrula of identical morphology with the ancestrulae and zooids of *Hederella* (text-figs. 1a, 2a–c). Zooids of the second generation were produced in the same manner. Zooids of the third and fourth generations budded almost frontally but during subsequent growth they 'crawled' on the lateral side of the stolozooid and grew along it. The first normal, frontally budding, zooid appeared in the sixth generation (text-fig. 2a). All subsequent autozooids are budded frontally and have morphologies different from those of *Hederella*.

The question arises what were the factors involving morphological delay of the first stages in the development of the *Diversipora* colony. Morphophysiologic (Urbanek 1960) and trophic (Dzik 1975) interpretations of such phenomena have been proposed. Urbanek's theory directly concerns only graptolite colonies which basically differ from bryozoan ones in the mode of origin (evolution of graptolite rhabdosomes is rather evolution of behaviour than morphology of zooids; see Crowther and Rickards 1977) but it seems that their astogeny has
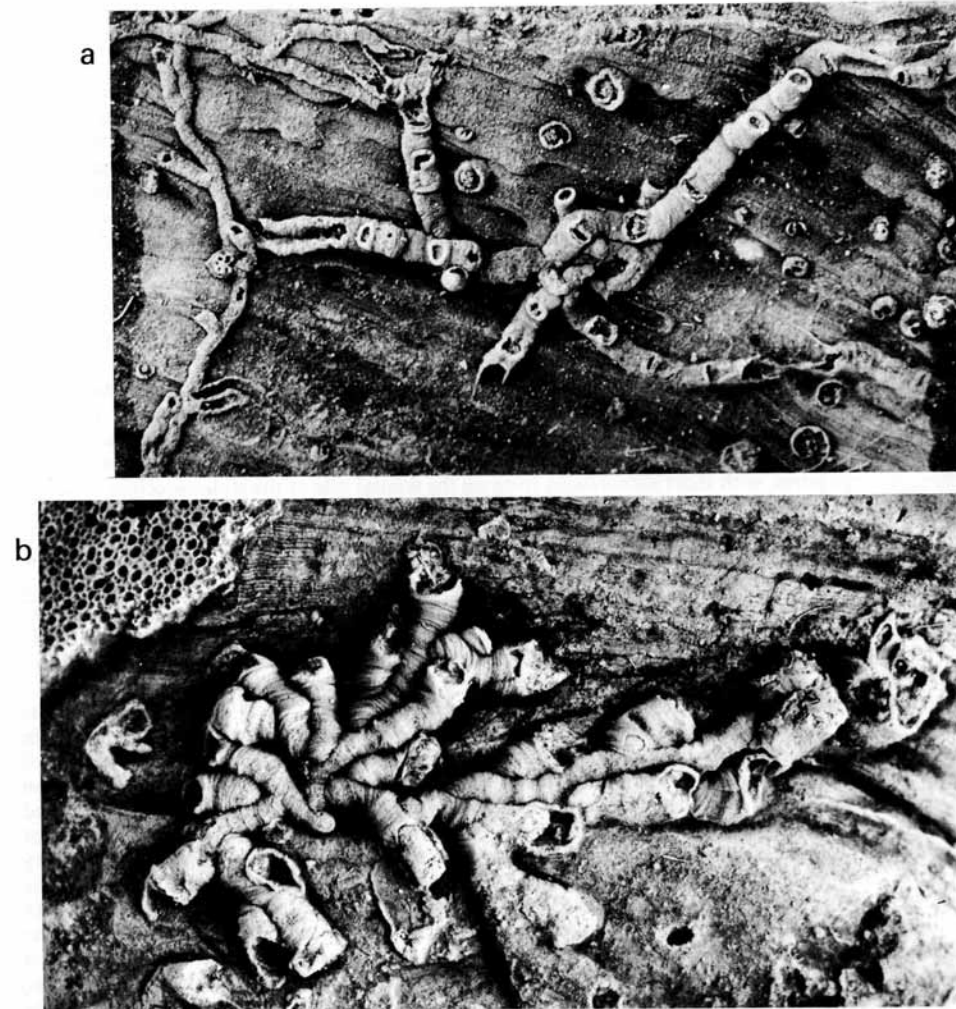


TEXT-FIG. 1. Early parts of colonies of Middle Devonian hederellids from the Holy Cross Mts., Poland. *a. Diversipora bitubulata* Kiepura, Skały Formation (Lower Givetian), Skały, specimen ZPAL Br V/4A; on the left side of the photograph fragment of colony of *Hederella* sp. is seen.   *b. Hederella reinmanni* Bassler, Grzegorzowice Formation (Eifelian?), Grzegorzowice, specimen ZPAL Br IV/8606; illustrations of the same specimen in Kiepura (1973: pl. 10, fig. 1, text-figs. 16–17) are mirror images. Both × 10.
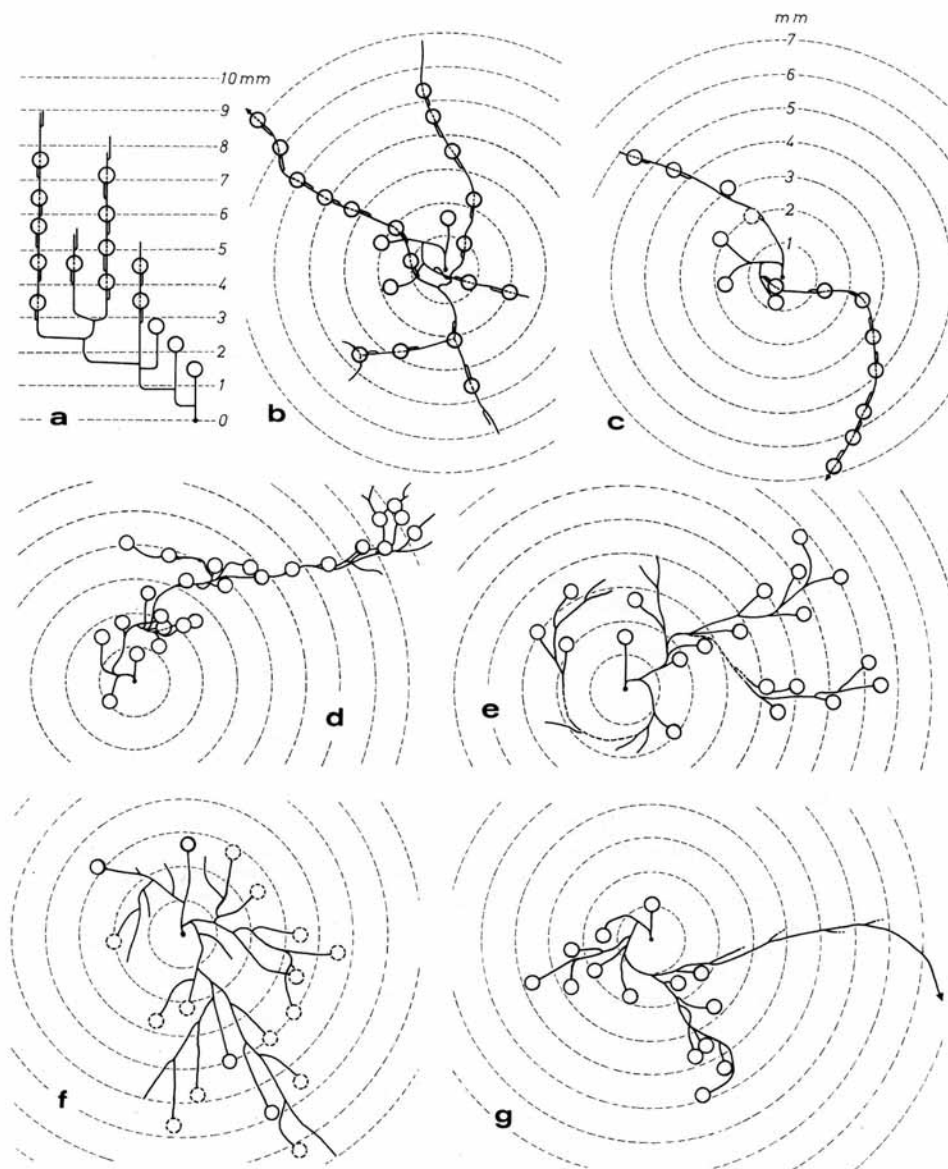
TEXT-FIG. 2. Early astogeny of Devonian hederellids from the Holy Cross Mts., Poland.  *a. Diversipora bitubulata* Kiepura, Skały Formation (Lower Givetian), Skały, diagram illustrating sequence in budding of zooecia, specimen ZPAL Br V/4B (see also text-fig. 1*a*). *b.* same specimen, schematic drawing of budding pattern.  *c.* same species and locality, specimen ZPAL Br V/4C.  *d. Hederella* sp., same horizon and locality (see text-fig. 1*a* for photographic illustration of this species), specimen ZPAL Br V/4D.  *e. Hederella* sp. indet., Lowermost Frasnian, Józefka, specimen ZPAL Br V/6. g. *Hederella* sp., Skały Formation, Skały, specimen ZPAL Br V/4E.  *f. Hederella reinmanni* Bassler, Grzegorzowice Formation, Grzegorzowice, specimen ZPAL Br IV/8606 (see also text-fig. 1*b*).

been controlled by similar mechanisms as bryozoan ones. Urbanek (1960, 1963, 1973) and Taylor and Furness (1978), have assumed that all astogenetic changes have adaptive characters. He has explained the astogenetic gradient as a result of secretion of some morphogenetic 'hormone' by the first zooid in the colony. Decreasing the concentration of these 'hormones' during colony growth involves decreasing the expression of their influence on the development of zooids. Morphogenetic factors control the ontogeny of zooids by inhibition or stimulation of the function of embrional organizers. Evolutionary novelties are introduced by modification of organizer systems, but their appearance in the zone of astogenetic change can be inhibited or stimulated by influence of the morphogenetic factor produced by the first zooid (ancestrula in Bryozoa; siculozooid in graptolites). In short it can be said that Urbanek explains morphological differences between individuals within a colony (clone) by assuming physiologic dimorphism: first zooid (ancestrula or siculozooid) versus other zooids. According to Urbanek (1973) existence of such a dimorphism is indicated by noncontinuous morphological changes between the sicula and other thecae. A similar discrete distinction: ancestrula—other zooecia can also be observed in many bryozoans (*inter alia* single-walled ancestrula—double-walled next zooecia in Trepostomata; Boardman and McKinney 1976). Functional significance of the morphologic gradient is introduced inseparably in the morphophysiologic theory of astogeny. It is needed as a reason for evolutionary development of the complex hormonal system controlling the course of astogenetic changes. According to Taylor and Furness (1978) early developmental stages of zoaria, with zooids of small size, possess higher fitness, expressed in the possibility of occupying ecological niches other than those of competing adult zoaria. There is insufficient evidence of competition in Palaeozoic bryozoans to test this idea.

Urbanek (1963, 1973) has presented examples of bipolar regeneration of broken graptolite rhabdosomes (a similar phenomenon is also known in Bryozoa: Illies 1974; Blake 1976) which in his opinion can be treated as a natural experiment supporting his theory. He believes that lack of astogenetic changes in the regenerating branch of the rhabdosome is caused by the lack of the siculozooid (broken before regeneration), more strictly by the subsequent lack of secretion of the morphogenetic factor. It must be noted, however, that proximal regenerating zooids were developed synchronously with distal zooids of the rhabdosome and there is no reason for gradient expression. On the other hand, in the cases of 'rejuvescence' of bryozoan colonies the gradient appears without influence of the ancestrula (Boardman *et al.* 1969; Dzik 1975). Only the finding of a very young colony, which had lost its first zooid and then prematurely had begun to bud normally developed large zooids, can be a true natural experiment for the morphophysiologic theory. Loss of the zooid at such an early stage of development must, however, involve teratological perturbations in colony development. Therefore, even if Urbanek's theory is true, finding such a fossil is unlikely. A solution to this question can be expected to come from zoology.

Preference of the trophic interpretation of the astogenetic gradient in Bryozoa (Dzik 1975) can be justified by Occam's razor. This theory does not need the introduction of any concept of a special hormone system, which supposedly occurs in ancestrula but does not occur in the genetically identical remaining zooids. According to the trophic theory two independent factors control early development of the bryozoan colony: ability of food capture by the colony, and rate of budding. During development of the zoarium numerical relations change between functioning parent zooids and daughter zooids nourished by them. During development of the colony, relationships between the parent zooids of each astogenetic generation and their daughter buds change dramatically. A single cheilostome ancestrula buds three zooids (ratio 1:3) but by the third astogenetic generation the ratio is close to 1:1 (Dzik 1975). Similar ratios occur in secondary zones of astogenetic change.

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EXPLANATION OF PLATE 117

Figs. 1-3. *Wolinella polonica* sp. n., erratic boulder E-137, *Eoplacognathus reclinatus* Zone, Lasnamägi stage, Llanvirn, Orłowo, Poland. 1. Fragment of calcitic zoarium ZPAL Br V/496, ×60. 2. Same state of preservation, ZPAL Br V/497, ×75. 3. chamozite(?) internal mould, holotype ZPAL Br V/498, ×75.

Fig. 4. *Wolinella baltica* sp. n., erratic boulder E-089, *Eoplacognathus pseudoplanus* Zone, Kunda stage, Lowermost Llanvirn, Zgierz, Poland, holotype ZPAL Br V/196, chamozite(?) internal mould, ×150.

Fig. 5. *Wolinella brevis* sp. n., erratic boulder E-112, *Prioniodus variabilis* Zone, Kukruse stage, Lowermost Caradoc, Zgierz, Poland, holotype ZPAL Br V/372, ×220. p—communication pore.

PLATE 117
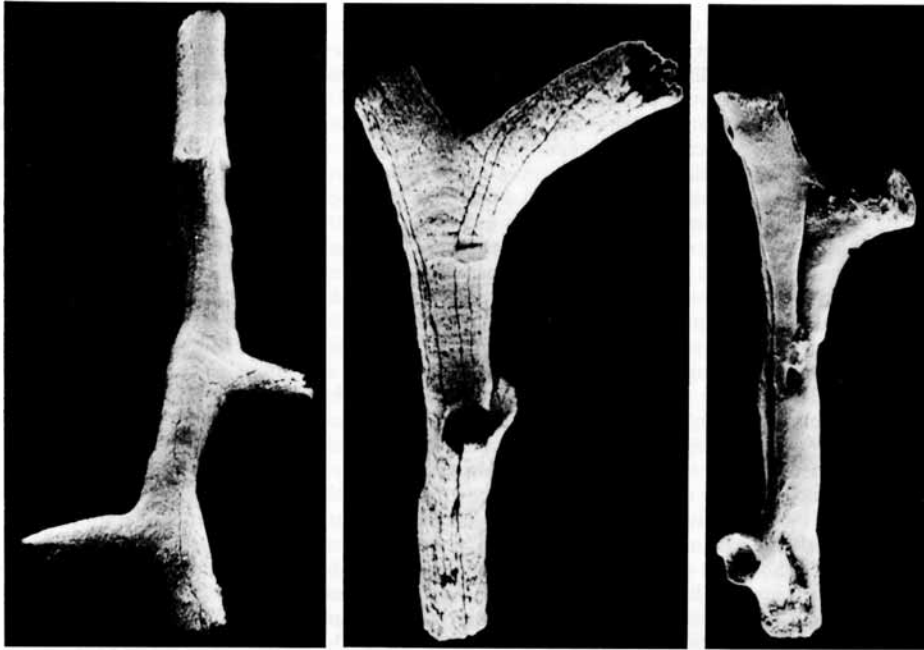


DZIK, Bryozoan *Wolinella*

Within zones of change the dimensions of successive zooids increase sequentially. Therefore under the conditions of stable induction of budding, each successive parent generation is capable of ingesting more and/or different, food particles, and each subsequent daughter generation is better nourished during growth. Influence of trophic conditions on the size of zooecia has been experimentally documented in laboratory material by Jebram and Rummert (1978). It may express itself both in larger zooecial dimensions and in fuller development of newly introduced evolutionary characters of specialization. All disturbances of the state of equilibrium between the two factors mentioned must be expressed in the zooecial morphology. Appearance of the astogenetic gradient in the zone of 'rejuvescence' of the zoarium can be easily explained in terms of this theory. It is impossible, however, to explain on the grounds of the trophic theory features of proximal appearance of evolutionary novelties in a graptolite rhabdosome (see Urbanek 1960, 1973) if they are not effects of expansion of morphological underdevelopment into the distal part of the rhabdosome. Any unequivocal example of proximal evolutionary introduction of features of specialization in bryozoan colony should falsify this theory. The trophic theory cannot be applied to interpretation of synchronously developing morphological gradients in macules and monticules of the double-walled Bryozoa. Although the synchronous development of morphological gradients in macules and monticules may be interpreted as resulting in a trophic function (Taylor 1979) their origin can be satisfactorily explained by the physiologic gradient theory (Pachut and Anstey 1979).

Development of *Diversipora* can be described in terms of the trophic theory of astogenetic gradient. If it is assumed that the rate of longitudinal growth of hederellid zooids was similar in the whole colony, then the linear distance between the protoecium and apertures of the zooecia approximately expresses the time relation between gemmation and maturation of particular zooids (text-fig. 2a). Even if full development of a polypide has taken place earlier than the finishing of a zooid bud, this last event must involve the increase of the ability to transfer food substances to buds. In the case of *D. bitubulata* the first two cycles of budding occurred before maturation of the ancestrula; the next two occurred before maturation of the preceding autozooids. The first normally developed, frontally budding autozooid appeared after maturation of three zooids which budded laterally. It belonged to the first generation which certainly utilized in its development food resources actively accumulated by adult zooids of parent generations, but not the ancestrular yolk stock.

### Corynotrypidae

Corynotrypid species differ from those of Hederellidae and Reptariidae in the more or less fusiform shape of zooecia, with frontally curved, long adapertural parts; and from other Palaeozoic single-walled bryozoans in the non-pseudoporous zooecial wall. This is the first group of single-walled Bryozoa which appeared in the fossil record.

The oldest occurrence of Corynotrypidae is in the Baltic Ordovician (*Wolinella baltica* gen. et sp. n.). It is characterized by reptant, reticulate initial parts of zoaria and erect uniserial branches in the later stages of astogeny. *W. baltica* occurred from Middle Volkhovian (B IIβ; Middle Arenig) up to Aseri stage (Lower Llanvirn). Species of *Wolinella* differ from those of *Corynotrypa*, apart from the erect colonies, in the subcylindrical shape of zooecia, which are without the strong proximal constrictions typical of *Corynotrypa*. The mode of budding can be estimated on the basis of growth lines on the surface of zooecia (Pl. 117, figs. 1, 2) and by the shape of internal moulds of zooecia (Pl. 117, figs. 3–5). Budding took place in the following manner: the zooid aperturally accreted cuticle and the primary calcareous layer and, after maturation of the zooid, the inside of the zooecium was subsequently constricted by secretion of a secondary layer (text-fig. 9c). Thickening of the secondary layer involved separation of longitudinal, irregular canals connecting particular zooecial spaces. These canals run along the zooecia in erect branches; in the reptant part of the colony they were weakly developed. In the case of *W. baltica* each zooid was connected with the longitudinal canals through two communication pores. One of them was situated proximally as an extension of the zooid, the second one obliquely joined the distal basal part of the zooecium with the underlying bundle of canals. The shape and number of canals are variable. Their pattern is most variable in *W. polonica* sp. n. from Lasnamägi stage (Middle Llanvirn). In this species several canals commonly
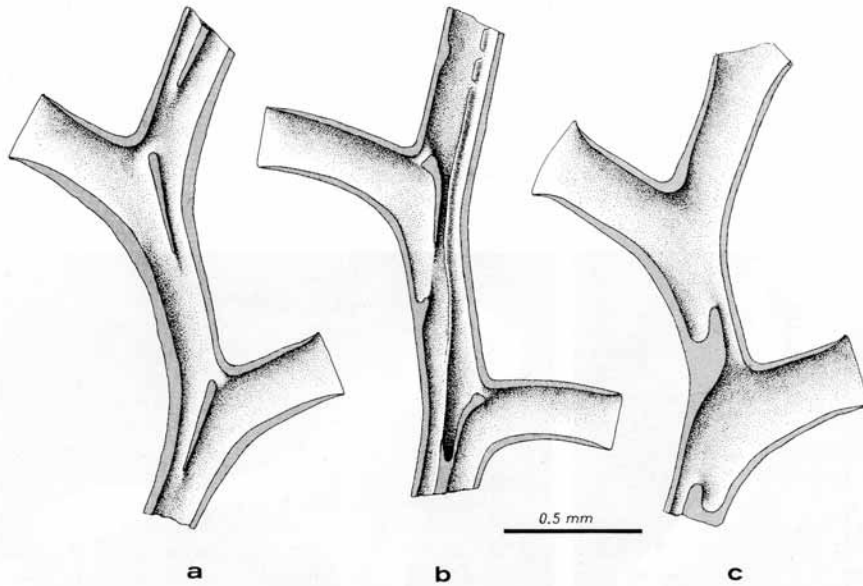
TEXT-FIG. 3. Reconstructions of internal zooecial structures of species of *Wolinella* gen. n.; medial sections of zoarial branches. *a. W. baltica* sp. n., based on specimens from erratic boulder E-089, Lowermost Llanvirn. *b. W. polonica* sp. n., based on specimens from erratic boulder E-137, Middle Llanvirn. *c. W. brevis* sp. n., based on specimens from erratic boulder E-112, Lowermost Caradoc.

run along the branch, connected with zooecia only through a single, distal pore (Pl. 117, fig. 3). Its descendant, *W. brevis* sp. n., occurring in Uhaku and Kukruse stages (Llandeilo—Lowermost Caradoc), presents a highly simplified pattern of internal canals (Pl. 117, fig. 5; text-fig. 3c). The proposed next link of the *Wolinella* evolutionary lineage is represented by Upper Caradoc '*Mitoclemella*' *kullsbergiana* Brood, but only external characters of this species are known (Brood 1974). Erect uniserial species such as '*Clonopora*' *gotlandica* Brood from the Baltic Wenlock (Brood 1975) perhaps also belong to *Wolinella*. '*Corynotrypa*' *hennigi* Brood may be a reptant part of the '*C.*' *gotlandica* colony.

The shape of the ancestrula of *Wolinella* species is similar to encrusting autozooecia. It differs from autozooecia only in the presence of a small hemispherical protoecium (text-fig. 4b). The first two encrusting zooids were budded from the distal end of the ancestrula laterally at a wide angle. The range of the reptant part of the colony is unknown. Some fragments of colonies are attached to calcite rods, the supposed remnants of calcified algal stems (text-fig. 10b). It is unknown if they are juvenile parts of the colony or adult branches occasionally coiled around other objects.

The genus *Corynotrypa* appears in the Baltic palaeozoogeographical province in the Upper Kundan stage (Lowermost Llanvirn). It is regarded as having originated from *W. baltica*-like forms. Development of the zooecia in *Corynotrypa* species is similar to that of *Wolinella*; even the pattern of constriction of the zooecial interior is very similar to this genus. Within the same sample of *Corynotrypa* zooecia with convex and flat basal sides occur together. The shape of basal parts of the zooecia may depend on the character of the substrate on which colony grew. Among the oldest Llanvirn corynotrypids zooecia with basal constrictions formed by a hemiphragm occur (Pl. 118,

figs. 1, 5). This morphological separation of the adapertural part of the zooecium achieves its culmination in the zooecia of the genus *Dentalitrypa* Kiepura. This genus, known from the Upper Caradoc to Ludlow(?) of the Baltic region, is characterized by zooecia with very wide, infundibular necks. The Ashgill *D. bidens* Kiepura shows a pair of long spines in the aperture (Pl. 118, figs. 2, 6). This structure is supposedly homologous with the lunarium of Ceramoporidae and Fistuliporidae. The Silurian *D. infundibuliformis* sp. n. has a wide apertural neck, much larger than the remaining parts of the zooecium (Pl. 118, fig. 3; text-fig. 5d–f). Both species probably represent a single evolutionary lineage derived from the *Corynotrypa schucherti* group in the lower Caradoc, which evolved in the direction of enlargement of the zooecial neck.
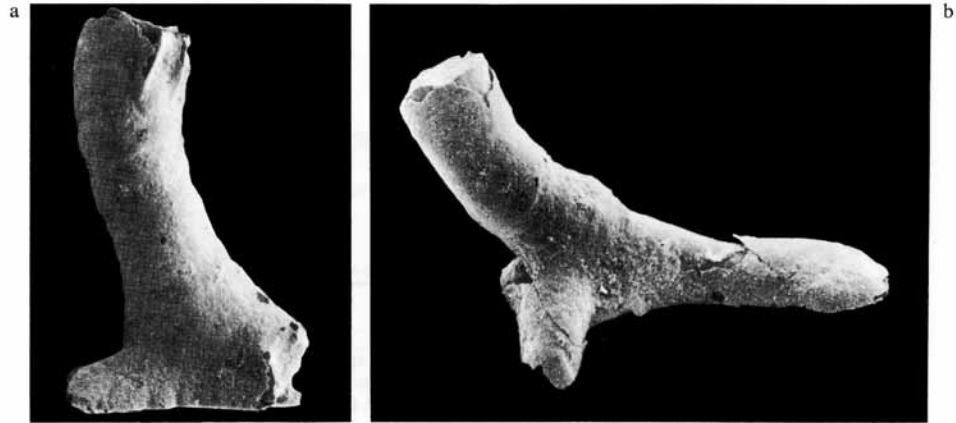


TEXT-FIG. 4. Incrusting parts of zoaria of *Wolinella polonica* sp. n., Mójcza Limestone, sample A-10, *Eoplaco-gnathus reclinatus* Zone, Middle Llanvirn, Mójcza, Holy Cross Mts., Poland. *a. incomplete autozooecium* ZPAL Br V/1011, ×60. *b.* ancestrula ZPAL Br V/1012, ×100.

The family Corynotrypidae underwent its highest differentiation in the Baltic Ashgill. A single rock sample may contain up to five co-occurring species of the genera *Corynotrypa*, *Lagenosypho*, and *Dentalitrypa* (see Pl. 118, figs. 2, 4; text-fig. 6a–d). It is easy to distinguish these species on the basis of their zooecial morphology (especially adapertural parts). They are undoubtedly distinct biological species. The size and course of astogeny do not seem to be important features in the taxonomy of corynotrypid species. Therefore, the identification of Baltic species of *Corynotrypa* on the characters of the North American material described by Bassler (1939) seems to be almost impossible without additional data.

EXPLANATION OF PLATE 118

Figs. 1, 5. *Corynotrypa* sp. (aff. *C. schucherti* Bassler), erratic boulder E-113, *Eoplacognathus robustus* Zone, Lasnamägi stage, Llanvirn, Rozewie, Poland, chamosite internal mould, ZPAL Br V/374: 1. ×180, 5. ×600.

Figs. 2, 4, 6. *Dentalitrypa bidens* Kiepura, erratic boulder E-090, Ashgill, Zgierz, Poland, calcitized zooecia: 2. lateral view, ZPAL Br V/257, ×100, 4. upper view, ZPAL Br V/258, ×100, 6. opesium of the same specimen, ×400.

Fig. 3. *Dentalitrypa infundibuliformis* sp. n., erratic boulder E-161, Ludlovian(?), Międzyzdroje, Poland, holotype ZPAL Br V/627, lateral view, ×100.

PLATE 118



DZIK, *Corynotrypa, Dentalitrypa*
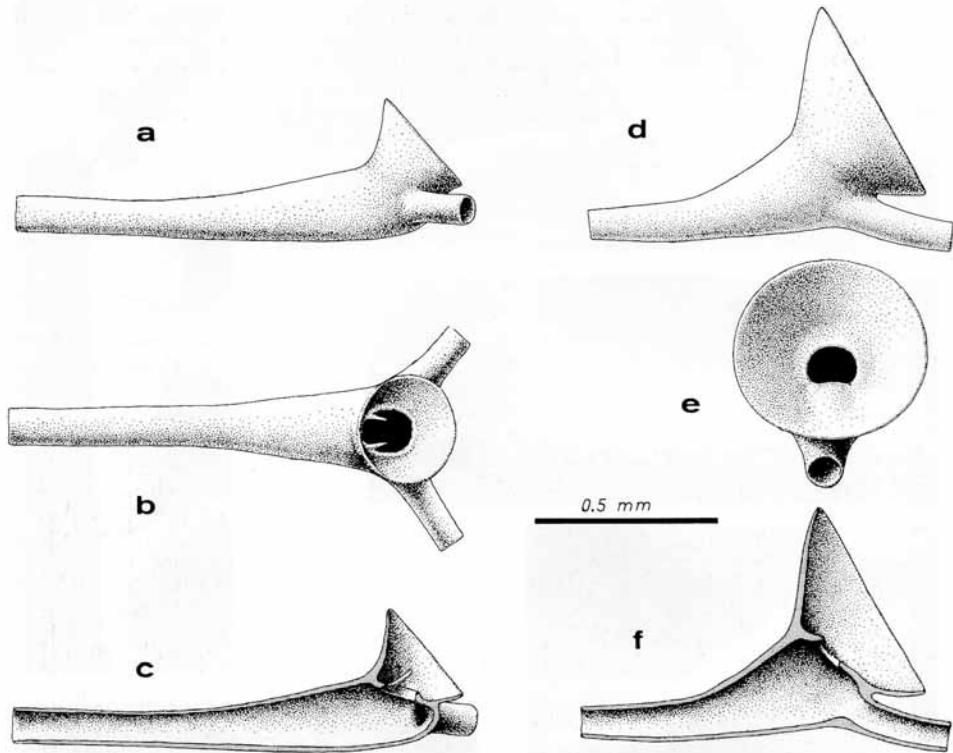
TEXT-FIG. 5. Reconstructions of zooecial morphology of the species of the genus *Dentalitrypa* Kiepura. *a–c.* *D. bidens* Kiepura, lateral, upper view, and medial section, based on specimens from erratic boulder E-090, Ashgill. *d–f. D. infundibuliformis* sp. n., lateral, distal view, and medial section, based on specimens from erratic boulder E-161, Ludlow(?).

The mode of budding in typical corynotrypids was similar to that in primitive *Pyripora*-like Cheilostomata. One to three zooids were germinated from a single parent zooid. Uniserial rows of zooecia are typical for the elongate, delicate species, like *Lagenosypho gibbosus* (Kiepura) (text-fig. 6d). Relatively short, wide species (e.g. *C. schucherti* Bassler), usually budded in diads; triads were not uncommon (text-fig. 7a, b; Bassler 1911a, b). Variability of the budding pattern is very wide. The ancestrula of *Corynotrypa* has a shape similar to autozooecia (text-fig. 7a). The zone of astogenetic changes is clearly developed (text-fig. 7c) though its expression is very variable. The first two zooids germinated from the distal end of the ancestrula at an angle of 180° in the same way as in *Wolinella*. In Jurassic species of the genus *Stomatopora* zooids of the second generation germinated in this manner from a single zooid of the first generation. This similarity is superficial and is an effect of similar functional adaptation rather than phylogenetic relationship.

Typical representatives of the genus *Corynotrypa* are known up to the Pennsylvanian (Condra and Elias (1944); *Lagenosypho* occurred up to the Upper Permian (Langer 1980). Taylor (1980) redescribed '*Stomatopora*' *voigtiana* from Guadalupian of England which shows a mode of budding and the zooecial shape almost identical to the Pennsylvanian *C. thomasi* Condra and Elias. Lack of evidence for wall pseudoporosity suggests that this form cannot be placed in *Stomatopora* from which it differs in its mode of budding (see Illies 1968, 1971).

The genus *Diploclema* Ulrich differs from all other Corynotrypidae in the multiserial organization of erect branches, but it developed in the same manner as uniserial branches of *Wolinella*, i.e. there was a well-developed common bud. Zooecia are separated longitudinally by walls with a secondary lamellar layer (Ross 1967; Kopajevich 1971; Boardman and Cheetham 1973). *Diploclema* could be derived from *Wolinella* by an increase of the number of rows of zooecia. *Diploclema* ranges from Trenton (Upper Caradoc) to Wenlock (Brood 1975; Kopajevich 1971).

*Crownoporidae*

All single-walled pseudoporous Early Palaeozoic Cyclostomata are included in this family. In the Baltic province Crownoporidae appears in the Lasnamägi stage (Middle Llanvirn). *Clonopora primaeva* sp. n. is the oldest and most primitive member of the family. Its zooids communicated only through proximal and distal communication canals; the zooecial wall is perforated by rare, large pseudopores (Pl. 119, figs. 1, 4, 5). Early populations of *C. primaeva* contain specimens without pseudopores. They are morphologically intermediate between the genera *Clonopora* and *Wolinella*. Similar structure of the zooecial wall with scarce pseudopores is shown by the Silurian *Sagenella consimilis* (Lonsdale) (see Brood 1975). It can be anticipated that the initial encrusting parts of *Clonopora* zoaria are similar to that of *Sagenella*. Brood (1975: pl. 5, figs. 1–2, text-fig. 15) has



TEXT-FIG. 6. Species of the genera *Corynotrypa* and *Lagenosypho* from erratic boulder E-090, Ashgill, Zgierz, Poland. *a. Corynotrypa bassleri* Kiepura, ZPAL Br V/270, × 60. *b. C.* sp., ZPAL Br V/261, × 100. *c. C.* sp. ex gr. *schucherti* Bassler, ZPAL Br V/284, × 100. *d. Lagenosypho gibbosus* (Kiepura), ZPAL Br V/214, × 100.
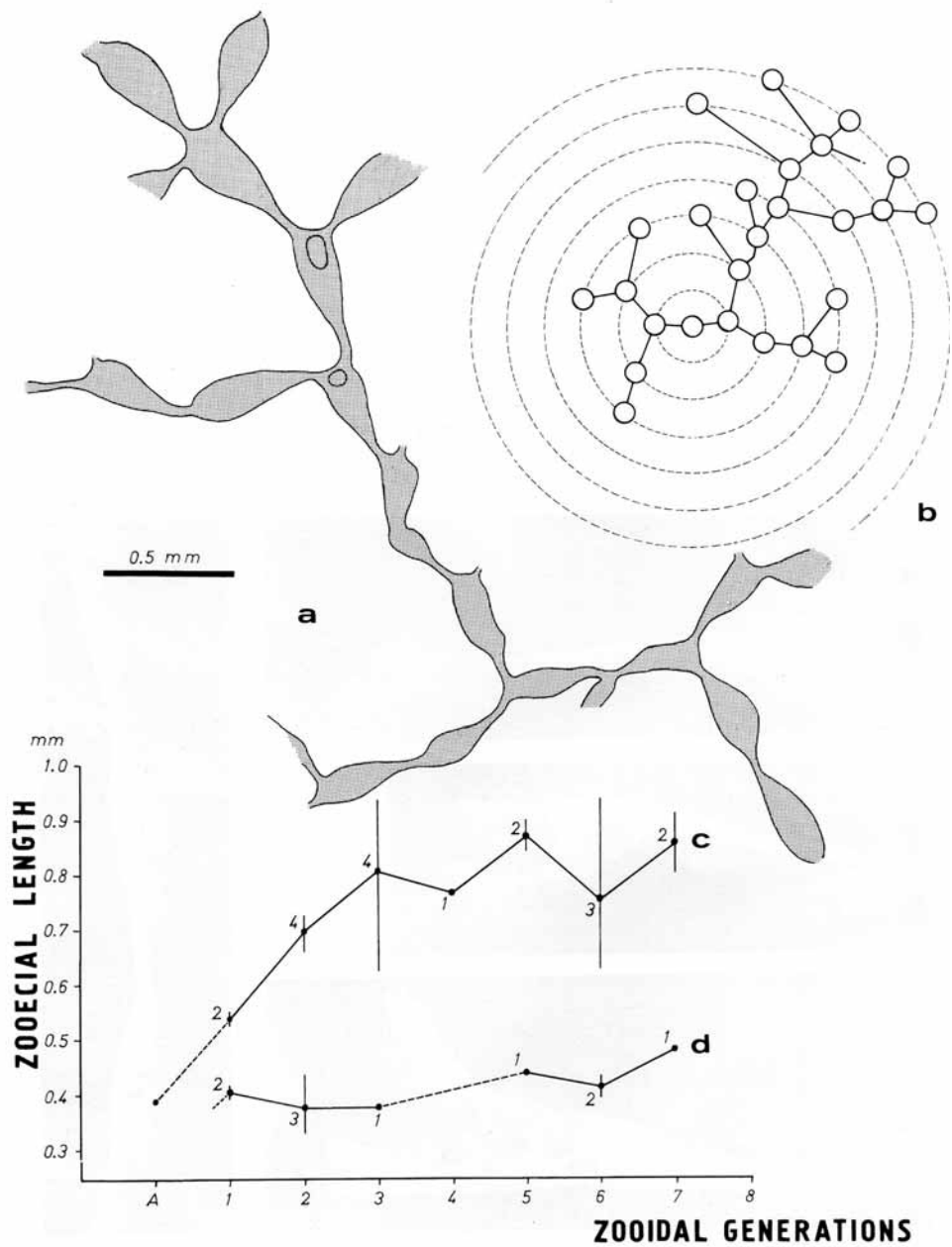
TEXT-FIG. 7. *Corynotrypa* cf. *schucherti* Bassler, Ordovician of Baltic erratic boulders. *a.* contour of the colony growing on trilobite carapace, seen from basal side, erratic boulder E-085, *Eoplacognathus lindstroemi* Zone, Uhaku stage, Mochty, Poland, specimen ZPAL Br V/8. *b.* Harmer's diagram of the same colony. *c.* Changes in zooecial length during astogeny, same colony. *d. Corynotrypa* sp., specimen ZPAL Br V/9, erratic boulder E-107, Middle Caradoc, Zgierz, Poland.

described some structures on colonies of *S. consimilis* which he interpreted as gonozooecia. I have examined original specimens in the Naturhistoriska Riksmuseet, Stockholm, and in my opinion the lack of any modification in the distribution of zooecial apertures in the vicinity of these structures, as well as the infilling of their interior with sparry calcite (instead of micrite occurring inside autozooecia of the same colonies), and different coloration indicate that they were produced by foreign organisms encrusting the surface of the zoaria. Rhizoidal holdfasts of crinoids occurring in vicinity of *Sagenella* colonies show identical shape, coloration and fracture with these 'gonozooecia'. The genus *Clonopora* is known up to the Givetian (Brood 1975).

*Kukersella* Toots occurs in the Baltic province from the Uhaku stage (Llandeilo). Its oldest species, *K. erratica* sp. n. does not show any diaphragms in the adult parts of zooecia, which are typical of the later species *K. bassleri* Toots from the Kukruse stage (lowest Caradoc; Toots 1952; Brood 1975), *K. boreale* (Bassler) from Oandu and Rakvere stages of Estonia (Upper Caradoc; Bassler 1911*b*; Brood 1975), and *K. singularis* (Ross) from North American Trenton (Upper Caradoc; Ross 1967). Zooids of *K. erratica* communicated distally and proximally by wide communication canals and laterally by numerous, small communication pores (Pl. 119, figs. 2, 3). The frontal wall of each zooecium is perforated by numerous pseudopores. Encrusting parts of zoaria are not known, but they were supposedly similar to '*Proboscina*' *auloporoides* Nicholson from the Ashgill of Ohio (Brood 1975). The genus *Kukersella* is regarded as closely related to unknown 'cyclostomes' which were ancestral to post-Palaeozoic 'cyclostomes' even though it is known only from Ordovician rocks. Lack of any reports on porous Cyclostomata from younger Palaeozoic rocks is surprising in view of the extensive work on Carboniferous and Permian Bryozoa in the U.S.A. and Soviet Union. They were presumably a subordinate element of bryozoan faunas during this time. This view is strongly supported by the finding of a double-walled erect cyclostome in the lower Permian of Spitsbergen (Pl. 120). This species (not yet named) shows well-developed distal-proximal communication canals and lateral communication pores (Pl. 120, fig. 3). The mode of budding was probably the same as in Crownoporidae. The double-walled habit of this species is suggested by the presence of mesopore-like interzooidal tissue (Pl. 120, fig. 2). Its 'kenozooecia' are not polymorphs in the very strict sense, understood as non-continuous variability in morphology of zooecia (see Boardman *et al.* 1969; Silén 1977), because continuous morphological series connect them with normally developed autozooecia. It may be that the permeability of a common coelom for free diffusion of morphogenetic 'hormones' does not allow the development of abrupt morphological boundaries between groups of zooids (see Pachut and Anstey 1979; Podell and Anstey 1979; Ryland 1979).

*Ceramoporidae*

Ceramoporidae were double-walled. They differed from contemporaneous Palaeozoic trepostomes and cryptostomes in the presence of well-developed communication pores. The morphology of ceramoporid zooecia and zooecial walls has been described in detail in many papers (Bassler 1911; Utgaard 1968, 1969, 1973; Boardman and Cheetham 1973, and others) and there is no reason to repeat it here. Chamosite internal moulds from the Ordovician of Mójcza (Holy Cross Mts., Poland) and from Baltic erratic boulders show that some zooids communicated only laterally through small communication pores. There are no wide canals similar to those of Crownoporidae, joining zooids of different generations in the zone of astogenetic repetition.

Early astogeny of ceramoporids has been studied in two zoaria from Llanvirn erratic boulders (text-fig. 8). Single-walled non-porous ancestrula gemmated from a large hemispherical protoecium. The first zooids germinating from the ancestrula communicated with it through wide proximal canals. The colony-wide hypostegal coelom developed at the stage of second or third generation of zooids, probably slightly later than in early Trepostomata (see Boardman and McKinney 1976; McKinney 1977). Growing in a fanwise manner the zoarium surrounded the ancestrula up to its upper side, so the whole surface of the colony was covered by soft tissue (see text-fig. 9a).

The mode of evolutionary development of colony-wide hypostegal coelom in Ceramoporidae is exemplified by the astogeny of *Flabellotrypa* Bassler. This genus is known from Ashgill of Baltic region (Kiepura 1962) and from

Gedinnian of North America (Brood 1975); it is morphologically intermediate between the families Corynotrypidae and Ceramoporidae. Since these families appear in the lower Ordovician, the presence of a *Flabellotrypa*-like intermediate link in lower Ordovician beds can be expected. Zoaria of *Flabellotrypa* developed according to the common bud principle (Kiepura 1962), in a similar fashion to some modern Cyclostomata. The single-walled ancestrula developed a front of soft tissue which secreted a common external cuticle and calcareous skeleton for the whole zoarium. The ancestrula did not develop its own, single-walled aperture but was merged into the common cover of the hypostegal coelom. The upper surface of the colony does not show any distinct boundaries between zooecia—they all have a common external skeleton (epitheca) and growth lines run across all zooecia (see Kiepura 1962; Brood 1975). This means that the separation of zooecia was performed by the secretion of internal walls of a secondary lamellar layer (Brood 1975), in the same manner as separation of zooecia and canals in *Wolinella*. Only the marginal part of the zoarium, bearing apertures of zooecia, was covered by the hypostegal coelom (text-fig. 9b).

The oldest known ceramoporid species is *Ceramopora? unapensis* Ross from the late Canadian of Oklahoma (Ross 1966). In the Baltic region ceramoporids appeared in the Kundan stage (Lowermost Llanvirn)—*Anolotichia revalensis* is the oldest known representative of this group. Utgaard (1968) has postulated exclusion of *A. revalensis* from the genus *Anolotichia* but he has not indicated any other place for it. *A. revalensis* stratigraphically precedes several other Baltic species which do not have mesopores or cystopores; these were placed by Bassler (1911b) into the genera *Ceramopora* and *Anolotichia*. All these species are closely related to one another and may be all derivatives of *A. revalensis*. For convenience I will treat this cluster of species as belonging to the genus *Ceramopora* s.l. Utgaard (1969) excluded all Baltic species described by Bassler (1911b) from the genus *Ceramopora*, but the generic concept adopted by this author seems to be slightly too narrow.

Species of *Ceramopora* s.l. are characterized by the presence of numerous communication pores between zooecia and by the lack of any interzooecial coenosteum-like tissue. They have closely packed, cylindrical zooecia. Development of a looser distribution of polypides needs the space
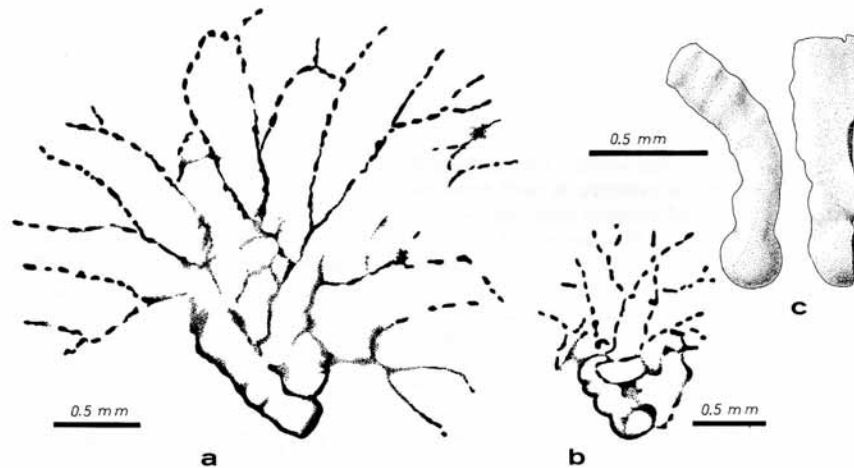


TEXT-FIG. 8. Early astogeny of *Ceramopora* sp. from Upper Llanvirn, Baltic erratic boulders. *a, b.* young colonies growing on trilobite carapaces, seen from basal side, erratic boulder E-085, *Eoplacognathus lindstroemi* Zone, Uhaku stage, Mochty, Poland, specimen ZPAL Br V/7 and 8, respectively. *c.* Chamosite internal mould of ancestrula, erratic boulder E-149, *Eoplacognathus reclinatus* Zone, Lasnamägi stage, Międzyzdroje, Poland, specimen ZPAL Br V/579.

between zooecial apertures to be widened. Soft tissue between zooecia in flat, double-walled bryozoans can secrete a layer of compact calcareous tissue, but the growth of the zoarium vertically, or the formation of high hemispherical colonies, is less 'expensive' in calcareous tissue: dissepiment-like cystopores or tubular mesopores. Strong development of interzooecial tissue in massive ceramoporoids can be interpreted as a result of enlargement of an area of lophophore operation.
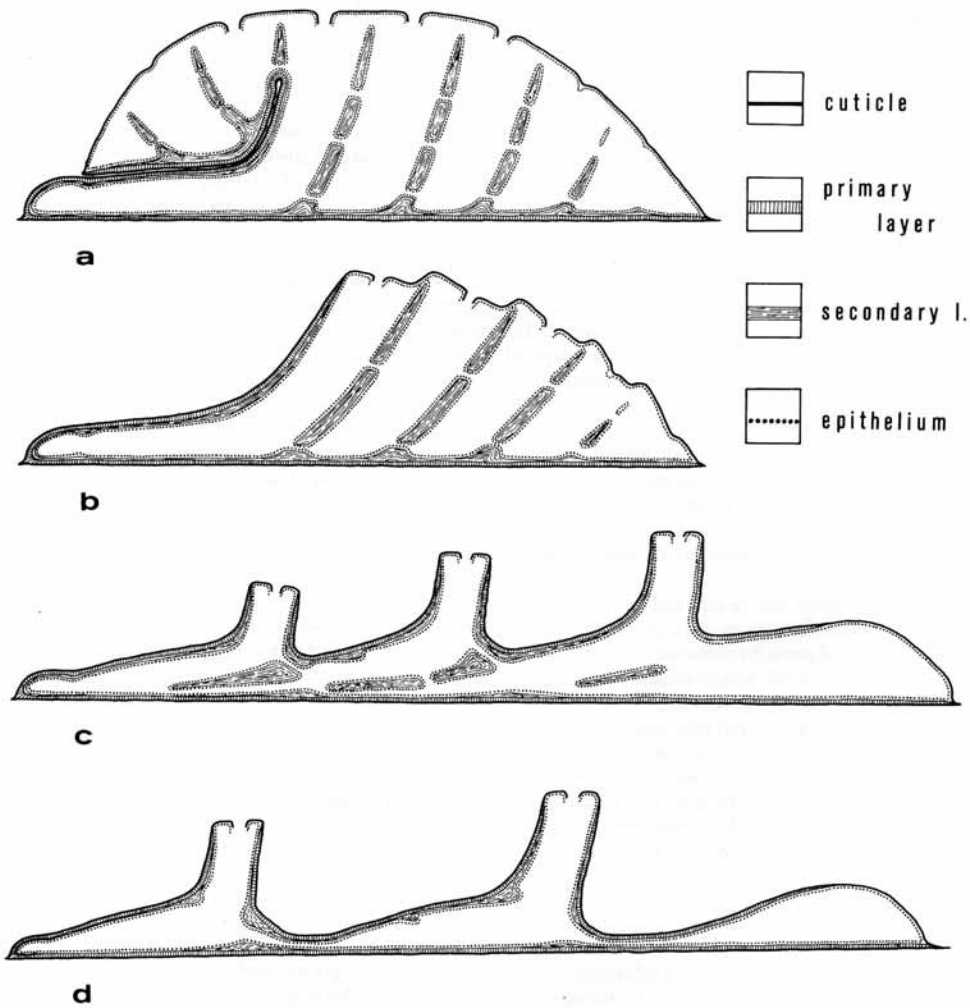


TEXT-FIG. 9. Diagrams illustrating mode of budding in particular groups of Palaeozoic cyclostomes, medial sections of initial parts of zoaria. *a. Ceramopora* s.l. *b. Flabellotrypa. c. Wolinella* and *Diploclema. d. Corynotrypa.*

## RELATIONSHIPS WITHIN EARLY PALAEOZOIC 'CYCLOSTOMATOUS' BRYOZOA

Relations between some genera of Palaeozoic cyclostomes have been discussed above. They form clusters of genera for which the familial level is considered appropriate. Relations between these clusters are much more difficult to determine. It is only possible to propose some models of evolutionary transformations between families.

The bryozoan nature of Hederellida is not certain. They differ from auloporid corals only in size and in the more cylindrical shape of their zooecia (possibly also in microstructure but more detailed SEM studies are needed). The notion of hederellid-coelenterate relationship is supported by occurrence of medial septa in *Hederopsis* Bassler; they are very similar to septa of *Alveolites*. Only finding older, Ordovician hederellids can help to resolve question of their affinities with other 'cyclostomes'. The families Hederellidae and Reptariidae are undoubtedly closely related. It cannot be stated on the basis of their stratigraphical distribution which of them is ancestral because both appear as late as the Silurian. Possibly the Reptariidae, which do not show any specialization in the budding pattern, are more primitive. The little-known genus *Hernodia* Hall may be ancestral to all Hederellida. The origin of this genus from Ordovician *Wolinella*-like cyclostomes cannot be excluded, though it is not very probable. Hederellids differ from *Wolinella* in very irregular early astogeny, short apertural parts of zooecia and in stronger morphological separation of zooecia. In these characters they resemble the genus *Sagenella* but differ in the lack of wall pseudoporosity. Hederellids supposedly have a zooecial wall without an internal lamellar layer. Hederellids seem to be more primitive than all representatives of the families Corynotrypidae and Crownoporidae.

All genera of Corynotrypidae can be derived from *Wolinella*. The oldest species of this genus, *W. baltica* (Arenig), shows some primitive features (cylindrical shape of zooecia, weakly developed internal walls, etc.) but it is still relatively advanced. No older bryozoan is known which can be an ancestor of *Wolinella*.

I presume that the most primitive genus of Crownoporidae is *Sagenella*. Though it is known only from the Silurian, incrusting parts of *Clonopora* known from the Llanvirn, probably have an identical morphology. The primitiveness of these forms is manifest in scarcity of wall pseudopores and communication pores and canals. They can be derived from encrusting tubular corynotrypids of *Wolinella* type by development of wall porosity. This transformation had taken place not later than in the early Llanvirn.

Ceramoporidae can be derived from *Flabellotrypa*-like forms. More detailed reconstruction of the origin of *Flabellotrypa* is difficult. It can be derived from the *Wolinella–Diploclema* complex but introduction of some hypothetical connecting link is necessary. Transformation of the common bud, producing separated, single-walled zooecial apertures into the colony-wide hypostegal coelom with permanently unfinished development of the adapertural skeleton (text-fig. 9a, b) needs to be introduced. It may be that intermediate forms had colonies with some zones with different modes of maturation of zooids: a zone with single-walled apertures of zooecia, and marginal(?) zone with unfinished separation of zooids from a common bud. Expansion of the latter zone in astogeny during evolution may have resulted in the origin of *Flabellotrypa*-like double-walled bryozoans. Development of *Flabellotrypa*-like forms must have taken place before the middle Arenig; if Trepostomata are derivatives of Ceramoporidae, much earlier.

## AFFINITIES OF PALAEOZOIC 'CYCLOSTOMES'

Palaeozoic 'cyclostomes' form a relatively compact, monophyletic group, with the possible exception of Hederellida. Several evolutionary lineages, which led to diverse large groups of Bryozoa, have their roots here. The central position of single-walled forms in the phylogeny of Bryozoa is also supported by the stratigraphical sequence of appearance of particular groups. Hederellidae may be ancestors of Recent phylactolaemates, Corynotrypidae-ctenostomes and cheilostomes, Crownoporidae-

cyclostomes, and Ceramoporidae may be close to the roots of terepostomes and cryptostomes. Models for the derivation of particular bryozoan orders from Early Palaeozoic 'cyclostomes' are discussed below.

### Plumatellida

Recent freshwater Phylactolaemata are a group of Bryozoa which shows very wide diversity in the degree of colony integration. There is the loosely encrusting, *Plumatella repens*-type with tubular zooecia, which contrasts with the highly integrated, compact *Cristatella mucedo*-type, which is capable of locomotion (see Brien 1960; Wood 1973). It seems doubtful if the low degree of colony integration is a result of secondary simplification, as postulated by Jebram (1973a). It is difficult to find a reason for such a reversal of the predominating direction of evolution in Bryozoa. It seems more probable that *Plumatella*-like reptant Phylactolaemata are the most primitive ones (Toriumi 1956). The similarity of morphology of zooecia and mode of budding ('stolozooids') between Palaeozoic Hederellidae and Recent Plumatellida is worth noting (see text-figs. 1, 2, 10a). Differences in the lack of calcification of phylactolaemate zooecia do not seem significant because it is a typical feature of fresh-water animals.
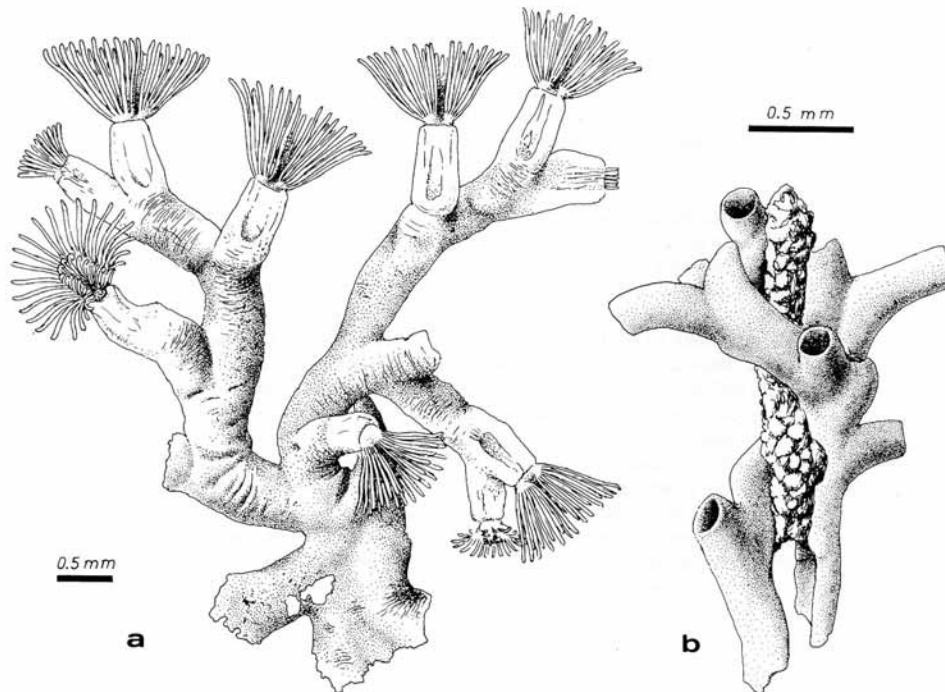


TEXT-FIG. 10. *a*. *Plumatella* sp., Recent, old river-bed of Vistula, Czersk, Poland, young statoblastic colony ZPAL Br V/10. *b*. *Wolinella polonica* sp. n., erratic boulder E-138, *Eoplacognathus foliaceus* Zone, Lasnamägi stage, Llanvirn, Międzyzdroje, Poland; two branches of zoarium growing around a calcite rod (remnant of algal thallus ?), specimen ZPAL Br V/504.

The idea of hederellid-plumatellid evolutionary connections, based on morphological similarity, is however, in contradiction with the widely accepted view of the stenolaemate nature of Hederellida. Basic differences in the anatomical organization between Phylactolaemata and the remaining Bryozoa have been stated by some authors (Lemche 1963; Jebram 1973a). The main difference, most important from the phylogenetic point of view, is that of the orientation of zooids in the colony: zooids of Phylactolaemata bud orally but zooids of Gymnolaemata bud in the anal direction. Jebram (1973a, b) has proposed the former existence of a hypothetical intermediate form with erect branches of the colony. Reptant zoaria of Gymnolaemata are, according to this theory, 'laying on their dorsal sides' by contrast with reptant phylactolaemates. Unfortunately, the morphology of zooecia of fossil bryozoans does not supply any information on the promorphology of soft parts. The functional significance of the medial septa of *Hederepsis* still remains unknown. They indicate only non-radial organization of the hederellid animals. The difference in the mechanism of eversion of polypide between bryozoan groups with calcified and uncalcified zooecial walls is another problem. Larwood and Taylor (1979) discussed the theoretical possibility of deriving forms with a restricted, apertural flexible wall from forms with an entirely flexible body wall. A reverse course of the evolution seems to be equally possible.

Simplicity of zooecial morphology and irregular mode of budding does not allow more than the suggestion of a relationship between Hederellida and Plumatellida, especially because there is a gap between known time distributions of these groups between Upper Carboniferous and Cretaceous. Such similarities may only express the primitiveness of both groups in colony organization. The specifity of colony structures in Hederellida is too small even to be sure that they are bryozoans. It is not known if the similarity of some hederellid genera (*Hederepsis*, *Hernodia*) to such tabulate genera as *Aulopora* and *Alveolites*, expressed as the presence of medial septa and non-pseudoporous wall, are effects of convergence or if it is evidence of the coelenterate nature of Hederellida. But taking into account all the scanty data on their construction it seems more probable that they are relatives of the Plumatellida than cyclostomes or tabulate corals.
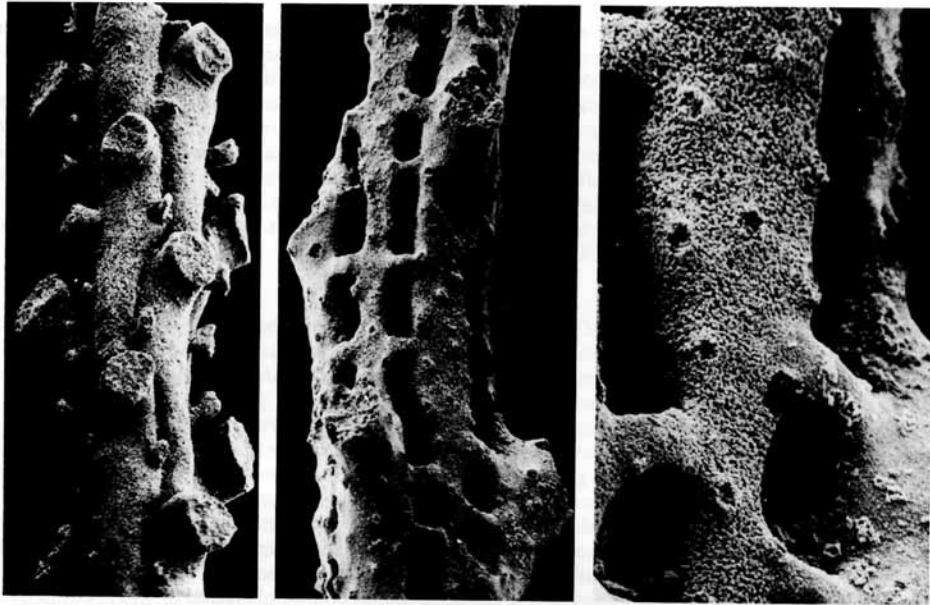
### Cyclostomata

The oldest proven cyclostomes are known from the Upper Triassic (Prantl 1938a; Flügel 1963). The genus *Stomatopora* Bronn seems to be the ancestral one (Walter 1969). Development of complexity of gonozooecia (Walter 1969) and origin, independently in several groups, of colony-wide hypostegal coelom (Brood 1976; Larwood and Taylor 1979) are the principal changes in the evolution of the order Cyclostomata. Even most primitive post-Palaeozoic cyclostomes have well-developed and numerous pseudopores (Illies 1971, 1976). All massive forms show the presence of communication pores between zooids (Boardman and Cheetham 1969, 1973; Brood 1976; Nye 1976). Presence of communication pores differentiates most Cyclostomata from Palaeozoic and Triassic Trepostomata, and together with development of specialized incubating chambers argues against direct relationships between these groups of Bryozoa (Brood 1976).

Trends in development of gonozooecia in the evolution of post-Palaeozoic Cyclostomata have been presented by Walter (1969) and Harmelin (1976; also Illies 1968). If one extrapolates them backward, then the ancestor of modern cyclostomes should be found among Triassic and Palaeozoic forms, similar to *Stomatopora*. They should be characterized by the lack of specialization of gonozooecia which perform the function of incubating chambers (Harmelin 1974). The Upper

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EXPLANATION OF PLATE 119

Figs. 1, 4, 5. *Clonopora primaeva* sp. n., erratic boulder E-112, *Prioniodus variabilis* Zone, Kukruse stage, Lower-most Caradoc, Zgierz, Poland, chamosite internal moulds: 1. holotype ZPAL Br V/354, × 72, 4. specimen ZPAL Br V/355, × 72, 5. same specimen, × 500.

Figs. 2, 3. *Kukersella erratica* sp. n., same erratic boulder, holotype ZPAL Br V/366: 2. × 120, 3. × 360.

PLATE 119



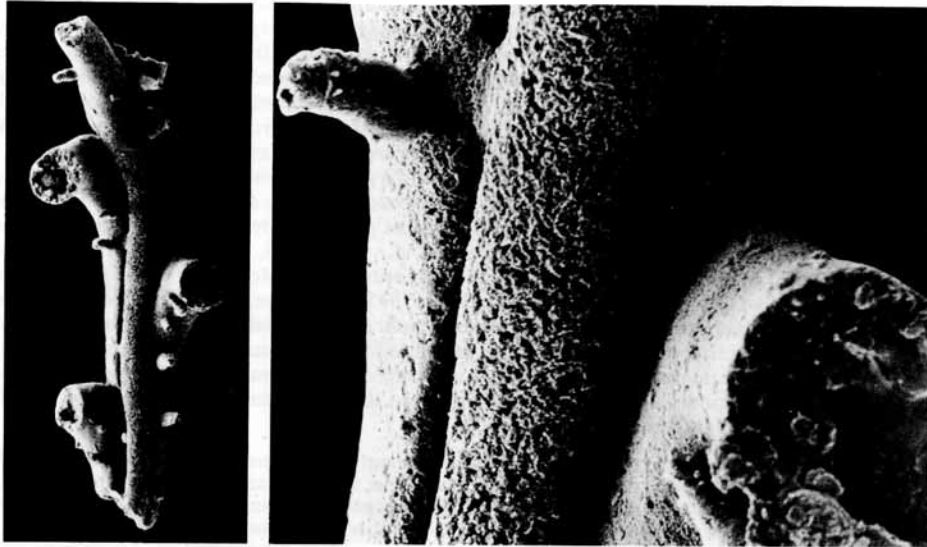1          2          3

4          5

DZIK, *Clonopora, Kukersella*

Ordovician '*Proboscina*' *auloporoides* seems to be most closely-related in colony and zooecial characteristics to post-Palaeozoic Cyclostomata among known Palaeozoic bryozoans. It has a highly pseudoporous zooecial wall and much narrower adapertural parts of the zooecia than their bases— a feature typical for the genus *Stomatopora*. The supposedly related, erect-branched genus *Kukersella* has a similar wall structure and numerous communication pores between zooecia. There are however, some difficulties in accepting the concept of Crownoporidae-*Stomatopora* connection because there is a large stratigraphical gap between Ordovician *Kukersella*-like forms and undoubted *Stomatopora* (Jurassic). This gap may be an artifact because of scant attention to Late Palaeozoic encrusting cyclostomes. Such a view is supported by finding of a rather specialized cyclostome in the Early Permian of Spitsbergen (Pl. 120).

*Trepostomata*

Unequivocal fossil documentation of trepostome evolution begins in the Middle Arenig (Volkhovian Stage) of Baltic region (Bassler 1911*b*) and Upper Cassinian of Arkansas (McLeod 1978). In the Baltic palaeozoogeographical province typical massive trepostomes (*Dianulites petropolitana* Dybowski, *D. fastigiatus* Eichwald, *Nicholsonella gibbosa* Bassler, *Diplotrypa petropolitana* Nicholson, *D. bicornis* (Eichwald)), and hemiphragm-bearing ones (*Hemiphragma rotundatum* Bassler, *Esthonio-pora communis* Bassler, *Dittopora clavaeformis* Dybowski, *D. annulata* (Eichwald)) appear together. Typical representatives of these two groups of the oldest Trepostomate genera such as *Esthoniopora* and *Dianulites* differ mostly in intrazooecial structures. Zooids of *Dianulites*, like most of the early trepostomes (see Bassler 1911*b*; Hinds 1970; McLeod 1978) formed complete diaphragms separating sequential parts of the zooecium. Zooids of *Esthoniopora* formed hemiphragms with the central hole allowing communicating between all the compartments of the zooecium. The three-dimensional morphology of the zooecia is well shown by phosphatic linings commonly found in acid residues from limestones (Martinsson 1965). Linings of hemiphragm-bearing trepostomes have been described by Górka (1969) under the generic names *Phosphotesta* (= *Esthoniopora*) and *Labyrinthotuba* (= *Hemi-phragma*). The morphological complexity of sinusoidally winged *Hemiphragma* linings is not in agreement with the interpretation of hemiphragms as structures constricting the interior of the zooid around the introverted polypide. More probably hemiphragms, similarly to cystiphragms, separated non-functional parts of the zooecia, and the polypide was situated in front of the last hemiphragm or cystiphragm. It is possible that tubes and sacks, commonly found between hemiphragms or cystiphragms (McKinney 1969; Boardman and McKinney, 1976; Boardman 1971) are not polypide remnants but pouches containing excreted products of metabolism (brown bodies) which were lost during growth of the zooecium (may be in degeneration–regeneration cycles).

   There are no features in the skeletal morphology of Trepostomata which are not known among fossil Cyclostomata. Corynotrypidae lack any wall pseudoporosity, as do all trepostomes. The morphology of ancestrula and early astogeny of the most primitive Trepostomata (Boardman and McKinney 1976; McKinney 1977) are closely related, if not identical, to these of Ceramoporidae (text-fig. 8) and Recent Lichenoporidae (Borg 1926; Boardman and McKinney 1976). Diaphragms commonly occur in Crownoporidae (Ross 1967; Brood 1975). Therefore, the origin of double-walled Trepostomata from either double-walled Ceramoporidae or single-walled Corynotrypidae is possible. An origin from the ceramoporids seems to be the more probable, because development of inter-zooecial tissue may be interpreted as the reason for disappearance of communication pores between zooids. Lack of mesopores and communication pores in the early genus *Orbipora* may eventually be explained as secondary feature.

It is difficult to estimate when the trepostomes originated from early 'cyclostomes' but several fossils similar to trepostomes have been described from the Tremadoc and Upper Cambrian and assigned to other groups of colonial animals (*inter alia* see McLeod 1979). One of the most conspicuous findings is *Palaeobotryllus taylori* Müller from the Upper Cambrian of Nevada (Müller 1977). It is a secondarily(?) phosphatized fossil of a colonial(?) organism bearing at least an analogue of the colony-wide hypostegal coelom. All 'zooecia' were secreted by a continuous epithelial cover and between particular zooids acanthopore-like spines occur. Lack of any developmental separation of chambers (the whole upper surface of 'zooecial walls' is smooth) speaks against

the interpretation of this fossil as an ascidian skeleton (Müller 1977). If one accepts secondary phosphatization of this fossil, *Palaeobotryllus* does not differ from young colonies of trepostome *Orbipora* (see Kiepura 1962) or some cryptostomes (see McKinney 1978). If this is true, the first lineage of trepostomes which lacks separated single-walled ancestrula must have appeared before the Upper Cambrian. Appearance of trepostomes with single-walled ancestrula should be even earlier.

### Cryptostomata

The oldest known cryptostomes are *Stictoporellina gracilis* (Eichwald) from the Volkhov stage, *Phyllodictya flabellum* Bassler and '*Coscinium*' *praenuntium* Bassler from the Kundan stage of the Baltic region (Bassler 1911b). Presence of well-developed lunaria in some of them, together with the frequent presence of cystopore-like interzooecial tissue, suggests that fistuliporids were ancestors of Cryptostomata. The oldest cryptostomes show a wide, encrusting base to the colony and massive, irregularly anastomozing branches. Later evolution of Cryptostomata is expressed mainly in the more regular arrangement of branches and the more gracile colony shape. The first zooids, together with ancestrula, were double-walled in advanced forms (McKinney 1978). The degree of colony integration in some cryptostomes was very high. Some supporting structures present through the whole colony were developed in many cryptostomes (Tavener-Smith 1973; McKinney 1978). The possibility cannot be excluded that some groups of Cryptostomata, e.g. Rhabdomesonidae, developed from Trepostomata independently (Tavener-Smith 1975) but there is still little evidence for reconstructing details of such derivation.

### Ctenostomata

Lack of continuous calcareous skeleton is a diagnostic feature of the order Ctenostomata. Therefore numerous calcareous encrusting structures like *Allonema*, *Marcusodictyon*, etc., which have been described as ctenostomes cannot be assigned to this order (Dzik 1975; Larwood and Taylor 1979). Their relation to Bryozoa is doubtful. *Ropalonaria* Ulrich, from the Upper Ordovician is the first undoubted ctenostome (Pohovsky 1978). It gave rise to several lineages of boring forms which continued during the Palaeozoic, Mesozoic and Tertiary to the Recent without strong changes in biology and morphology (see Pohovsky 1978; here text-fig. 11). In the shape of zooids and mode of budding (commonly on triads) the genera *Ropalonaria* and *Corynotrypa* are closely similar to each other (compare text-figs. 11 and 7). The early astogeny with gemmation of the first two zooids at an angle of 180° is identical in both genera. Stratigraphical sequence indicates the derivation of *Ropalonaria* from *Corynotrypa*. *Ropalonaria* probably evolved as a form which became progressively boring by an increased ability to dissolve calcareous substrata. Concurrently, the ability to secrete a calcareous skeleton was progressively lost. If the encrusting *Arachnidium* is a descendant of
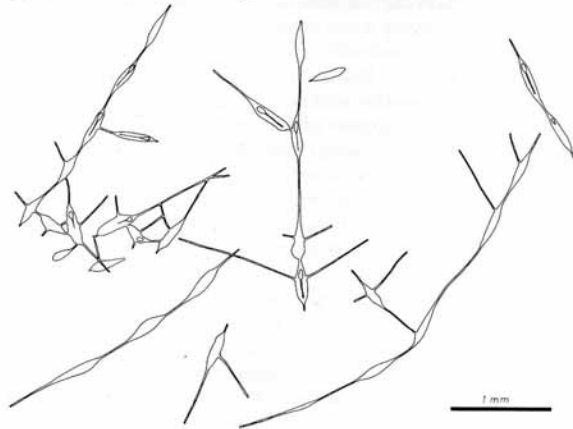


TEXT-FIG. 11. *Ropalonaria* sp., erratic boulder, Přidolian, Rozewie, Poland, colony boring nautiloid shell.

*Ropalonaria*-like, boring forms, this explains its lack of calcareous skeleton. On the other hand, *Arachnidium* is externally almost identical with *Corynotrypa schucherti* and may be a direct successor of *Corynotrypa* by loss of calcification for some other reason. In this case, *Arachnidium*-like forms perhaps existed in the Palaeozoic, although the earliest known fossil occurrence is of Middle Jurassic age (Voigt 1977; Taylor 1978). Erect ctenostomes are known from the Upper Cretaceous (Voigt 1966). It is thus possible to order the stratigraphical sequence of forms from calcareous *Corynotrypa* through boring *Ropalonaria*, non-mineralized *Arachnidium* to erect typical Ctenostomata.

### Cheilostomata

Close relationship between Ctenostomata and Cheilostomata was widely accepted (see Banta 1976 for discussion on anatomical grounds). It has been considered that erect *Labiostomella*-like ctenostomes were ancestral to Cheilostomata and that during development of cheilostomes trans-formation of erect colony branches into polymorphs (avicularia, vibracularia, apertural spines) took place (Silén 1942). However, polymorphism in the cheilostome colony is a secondary feature, and the earliest Cheilostomata lack apertural spines, avicularia, and ovicells (Dzik 1975; Banta 1976), although in the Jurassic *Pyriporopsis* pore chambers occur, which have been interpreted as polymorphs (Pohovsky 1973). Non-sexual cheilostome polymorphism basically differs in character from that of stenolaemate Bryozoa (Silén and Harmelin 1974; Hinds 1975; Silén 1977). It is expressed in high anatomical complexity of polymorphs, and gradual transformation of normal autozooecia into polymorphs does not occur within a single colony of primitive single-walled Cheilostomata. This is a case of polymorphism in the very strict sense (Boardman *et al.* 1969; Silén 1977). Development of polymorphism in early cheilostomes has been explained as independent evolution of duplicate gene sets responsible for the last stages of organogenesis of zooids (Dzik 1975). This type of polymorphism was permitted because of the relatively low degree of interzooidal integration in early Cheilostomata (Cook 1979). It could not have developed in double-walled (or at least strongly-integrated) stenolaemate Bryozoa with a common bud, because every physiological factor produced by a single zooid also influences neighbouring zooids (Pachut and Anstey 1979; Podell and Anstey 1979; Ryland 1979; Cook 1979). Little is known about factors inducing realization of particular programmes of organogeny in cheilostomes. In some advanced forms polymorphic zooids have a stable position in the colony (Powell and Cook 1966) but in early cheilostomes polymorphs appear randomly (Dzik 1975). According to Silén (1977) polymorphs developed from 'dwarfed' zooids, which do not attain normal size. The oldest known avicularia are not smaller than associated autozooids (Boardman and Cheetham 1973; Cheetham 1976; Dzik 1975). For the appearance of non-feeding heterozooids, the energy stock gained by autozooids must be sufficient for their nourishment (Schopf 1973; Silén 1977). This may explain the frequent lack of heterozooids in the early zone of astogenetic change, where the paramount necessity is the rapid budding of more feeding zooids (Dzik 1975).

*Arachnidium* is probably the generalized form of ctenostome from which Cheilostomata can be derived (Dzik 1975; Banta 1976). Many characters of *Arachnidium* support its relationship with *Pyriporopsis* Pohovsky, and are in common with *Corynotrypa*. It has been suggested that the genus *Arachnidium* is a successor of *Corynotrypa* (Dzik 1975; Banta 1976). Derivation of *Pyriporopsis* and related genera (Wawaliidae) from *Arachnidium* (Banta 1976) would require evolutionary 'reversals': reduction of calcareous skeleton (*Corynotrypa-Arachnidium* transformation discussed above), and next its secondary development (*Arachnidium-Pyriporopsis* transformation). The similarity of skeletal microstructure between stenolaemate and cheilostomate Bryozoa argue against such an interpretation. For the same reason independent origin of calcareous skeleton in *Corynotrypa* and Cheilostomata (Larwood and Taylor 1979) seems doubtful. Derivation of Cheilostomata from *Corynotrypa*-like 'cyclostomes' needs the development of a wide opesium and non-radial distribution of hydrostatic muscles (Dzik 1975). Until more data on the pre-Jurassic single-walled bryozoans is available it is impossible to say whether the direct ancestor of cheilostomes was similar to *Coryno-trypa* or to some '*Proboscina' auloporoides*-like form (presence of pseudopores in the gymnocyste of early cheilostome *Wawalia* (Dzik 1975) suggests the second possibility), or whether secondary development of the skeleton occurred.

Similarities in larval development and early astogeny support the thesis of cheilostome-ctenostome proximity (Banta 1976) and their separation from Cyclostomata. Some primitive Recent Ctenostomata and Cheilostomata have larvae of the 'Cyphonautes' type, which show a much more complex anatomy than stenolaemate larvae (Nielsen 1970; Zimmer and Woollacott 1977a). Cyclostome larva form a hemispherical, relatively large primary disc, after attachment to the substrate, with a calcifying cuticle. A tubular ancestrula germinates from the centre or side of the primary disc (Nielsen 1970; Zimmer and Woollacott 1977b). In typical cheilostomes an ancestrula is derived from total metamorphosis of larval tissue after settlement. In more advanced forms an ancestrular complex of several zooids is either successively differentiated from the larval tissue, or simultaneously differentiated (Cook 1968, 1973). It is noteworthy that one of the simplest Recent cheilostomes—*Membranipora*
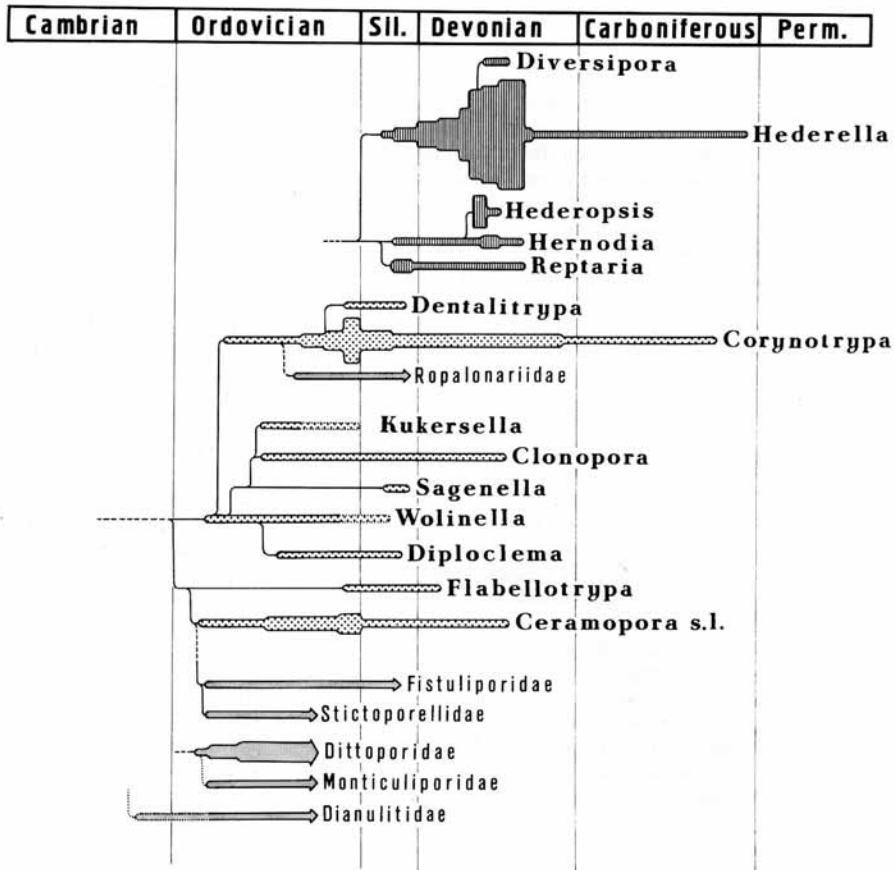


TEXT-FIG. 12. Age distribution and proposed relationships of Palaeozoic 'cyclostomes' Phylactolaemate(?) Hederellida are lined, Cyclostomata stippled, ctenostomes (*Ropalonaria*), cryptostomes (Fistuliporidae, Stictoporellidae), and trepostomes (Dittoporidae incl. Estonioporidae, Monticuliporidae, Dianulitidae) grey.

*membranacea*—has an abbreviated early astogeny: from the larva ancestrular twins develop (Lutaud 1961). This indicates that morphological simplicity of this species (see Ristedt 1977) is rather a secondary feature than the effect of primitiveness. The oldest known cheilostome ancestrula from Valanginian of Poland (Dzik 1975) is distinctly separated from subsequent generations of zooids, and has a cone shaped, long gymnocyste. A similar shape is shown by the ancestrulae of Albian *Wilbertopora mutabilis* Cheetham (Boardman and Cheetham 1973; Cheetham 1976). Ancestrulae of both species are similar in shape to the ancestrula of *Corynotrypa* and related Early Palaeozoic genera (text-figs. 4*b*, 7*a*). It seems therefore that the larval development and early astogeny of the oldest Cheilostomata, primitive Ctenostomata and corynotrypids may have been similar, and more primitive than that of Recent Cyclostomata. Anatomical similarities between larvae of Cheilostomata and Ctenostomata can be explained as common characteristics inherited after their common ancestors: *Corynotrypa*-like Palaeozoic forms.

## TAXONOMIC CONCLUSIONS

Brood (1975) has shown that single-walled Palaeozoic cyclostomes (with the exception of Hederellida) form a compact monophyletic group, and that they should be classified separately from post-Palaeozoic Cyclostomata in the suborder Palaeotubuliporina Brood, 1972. Lack of specialized gonozooecia is the most important feature which characterizes Palaeozoic cyclostomes. The taxonomic significance of communication canals between zooids of different generations is not clear because of scarcity of data on post-Palaeozoic cyclostomes. It seems that at least some kenozooids of Mesozoic cyclostomes had such canals (see Voigt 1978). Identification of such canals in thin section or acetate peels is rarely possible.

The classification of Palaeozoic cyclostomes presented by Brood (1975) may be too complex at the family level. Presence of wall pseudoporosity in *Sagenella* of the same pattern as in the genus *Clonopora* suggests that existence of communication canals may be anticipated, though they have not been found in thin sections. In view of the lack of data on encrusting stages of *Clonopora* and *Kukersella*, it is not possible to indicate any important difference between these three genera which can justify their separation on the familial level. The only unequivocal difference is between genera with non-pseudoporous (*Corynotrypa*, *Wolinella*, *Dentalitrypa*, *Diploclema*) and pseudoporous zoecial walls (*Clonopora*, *Sagenella*, *Kukersella*). The position of *Flabellotrypa* is isolated; this genus may belong to the family Ceramoporidae.

Bassler (1911*b*) postulated a close relationship between Ceramoporidae and Fistuliporidae and has created the suborder Ceramoporoidea for these families, included in the Cyclostomata. Astrova's (1964, 1965) concept of the Cystoporata is apparently identical. The close relationship between the suborders Ceramoporina Bassler, 1911 emend. and Palaeotubuliporina is shown by the presence of communication pores, lack of wall pseudopores, presence of lunaria, and single-walled ancestrula. Ceramoporids can be derived from single-walled Palaeotubuliporina through *Flabellotrypa* as the intermediate link. Known data do not allow exclusion of Ceramoporina from Cyclostomata. They differ from Palaeotubuliporina only in the presence of the colony-wide hypostegal coelome (just as Cerioporina differ from Tubuliporina). The systematic position of fistuliporids is more equivocal, because of little data on the early astogeny and morphology of the earliest representatives of this group. Lack of communication canals and pores between zooecia may be involved in the strong development of interzooecial tissue. The presence of lunaria, the microstructure of zooecial walls and shape of zoaria indicate a close relationship to Ceramoporidae (Bassler 1911*b*; Utgaard 1973).

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EXPLANATION OF PLATE 120

Figs. 1–4. Unnamed double-walled(?) cyclostome from Kapp Starostin Formation (lower Permian) of Polakkfjellet, Spitsbergen: 1, 2. random thin sections of zoarial branches, sample M, × 40, 3, 4. siliceous internal mould of the zoarial branch, interzooecial communication pores and canals seen, 3. × 50, 4. × 150.

PLATE 120



1

2

3

4
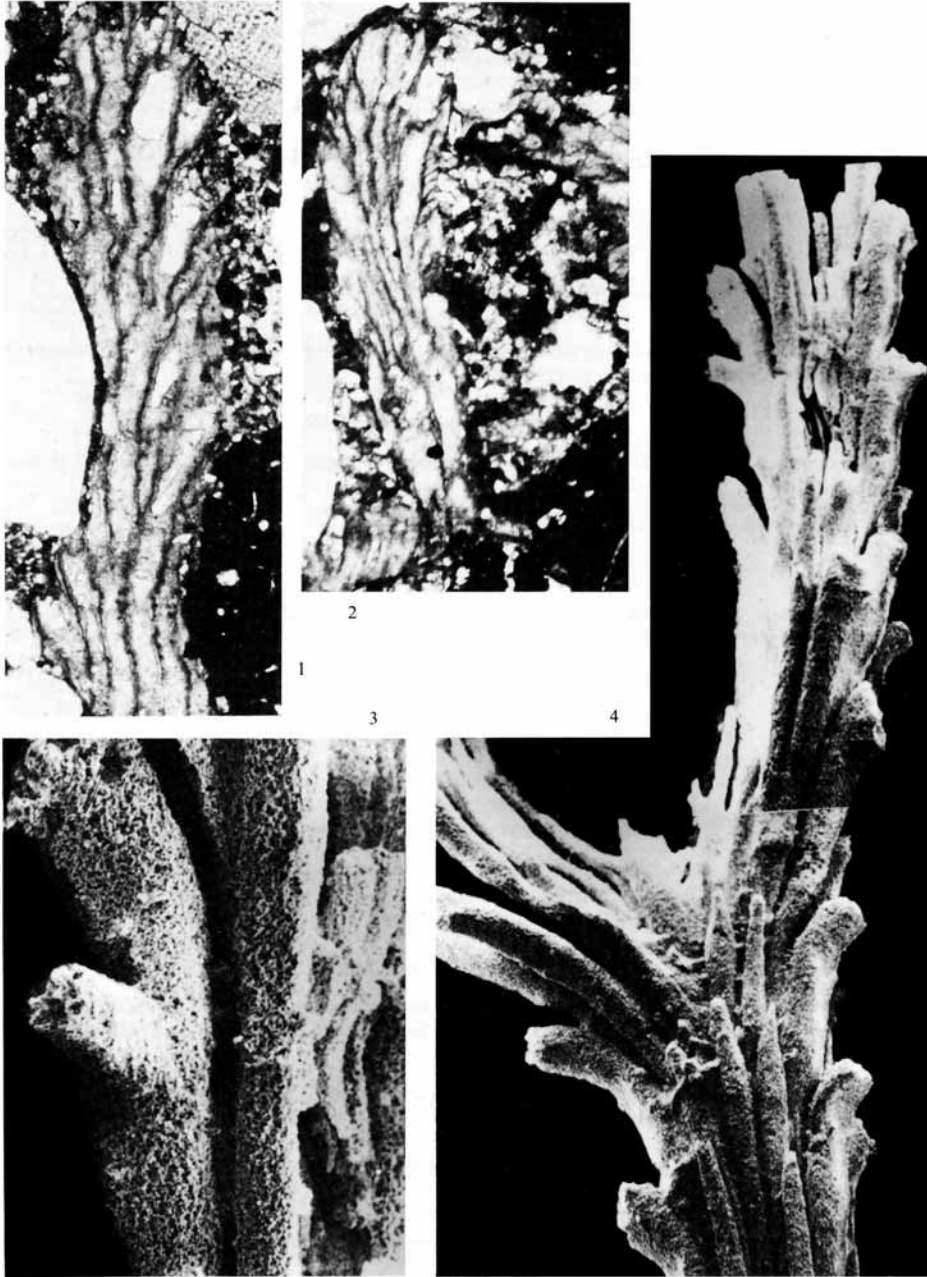
DZIK, Permian Bryozoan

A connection with the Cyclostomata is also supported by presence of gonozooecia of primitive stomatoporid shape (Utgaard 1973). The supposed relationship between fistuliporids and Crypto-stomata is of systematic interest. The earliest known fistuliporid, *Fistulipora primaeva* Bassler, from the Volkhov stage, occurs together with the oldest cryptostomes and seems to be closely related to them morphologically. Primitive cryptostomes differ from primitive fistuliporids only in their branched, erect colonies; in both groups lunaria and cystopores occur (see Bassler 1911*b*). It is more convenient to include fistuliporids in the order Cryptostomata than in the Ceramoporina (= Cystoporata).

*Diagnoses of new and emended taxa*

### ? subclass PHYLACTOLAEMATA Allman, 1856
### Order HEDERELLIDA Bassler, 1939

*Emended diagnosis.* Single-walled bryozoans with strongly calcified, tubular, non-pseudoporous zooecia. Zooids gemmated laterally or frontally.

### Family REPTARIIDAE Simpson, 1897

*Emended diagnosis.* All zooids of similar shape, gemmating laterally from the proximal parts of parent zooids.

Genera included: *Reptaria* Rolle, 1851; *Hernodia* Hall, 1883.

### Family HEDERELLIDAE Kiepura, 1973

*Emended diagnosis.* Some zooids, permanently non-maturating, undertake the function of stolons from which laterally or frontally numerous autozooids gemmate.

Genera included: *Hederella* Hall, 1883; *Diversipora* Kiepura, 1973.

## SYSTEMATIC DESCRIPTIONS

### Subclass GYMNOLAEMATA Allman, 1856
### Order CYCLOSTOMATA Busk, 1852
### Suborder PALAEOTUBULIPORINA Brood, 1973

*Emended diagnosis.* Single-walled bryozoans lacking specialized gonozooecia or with *Stomatopora*-like ones. Zooids of different generations communicated through wide communication canals. Adapertural parts of zooecia long, erect, thinner than remaining parts of zooecia.

### Family CORYNOTRYPIDAE fam. n.

*Diagnosis.* Non-pseudoporous zooecial walls; more or less fosiform shape of zooecia. Interior of adult zooecia frequently constricted by adapertural hemiphragms or longitudinal ribs separating longitudinal canals.

Genera included: *Corynotrypa* Bassler, 1911; *Diploclema* Ulrich, 1889; *Dentalitrypa* Kiepura, 1962; *Wolinella* gen. n., *Lagenosypho* Spandel, 1898.

### Genus WOLINELLA gen. n.

*Type species. W. polonica* sp. n.

*Diagnosis.* Erect uniserial colony branches with encrusting early portions. Subcylindrical zooecia with long apertural parts.

*Remarks. Wolinella* gen. n. differs from other Corynotrypidae fam. n. in erect colonies and almost cylindrical zooecia. All three species known can be treated as temporal subspecies within monospecifica evolutionary line (see Dzik and Trammer 1980).

Species included. *W. polonica* sp. n.; *W. baltica* sp. n.; *W. brevis* sp. n.; *Mitoclemella kullsbergiana* Brood, 1974; *Corynotrypa hennigi* Brood, 1975 (? = *Clonopora gotlandica* Brood, 1975).

Distribution. Arenigian to Wenlock of Baltic region; Llanvirnian to Caradocian of the Holy Cross Mts., Poland.

### *Wolinella baltica* sp. n.

(Plate 117, fig. 4; text-fig. 3*a*)

*Holotype.* ZPAL Br V/196; Pl. 117, fig. 4.

*Diagnosis.* Long, slender zooecia. Below the central part of each zooecium runs a longitudinal canal, separated by a calcareous wall.

*Remarks. W. baltica* sp. n. differs from *W. polonica* sp. n. in the usual presence of only a single longitudinal canal, and from *W. brevis* sp. n. in longer zooecia and distinct separation of the canal. Only fragmentary, erect branches of colonies are known. Variability in their shape is rather small: it is expressed mostly in the development of longitudinal septa. Young zooecia have these septa weakly developed, adult ones have a strongly constricted interior of zooecia. Rarely a few parallel longitudinal canals are developed.

*Material.* Thirty-six fragments of zoaria from Baltic erratic boulders E-079, 089, 117, 204; nine from the Mójcza Limestone (sample A-14); five from Sukhrumägi section, Estonia.

*Distribution. W. baltica* sp. n. occurs in the Baltic region since Middle Volkhov stage (Arenig) up to Aseri stage (Llanvirn); in the Holy Cross Mts. occurs in equivalents of Upper Kunda stage (Lowermost Llanvirn). Known from Estonia (Sukhrumägi: B IIβ), erratic boulders from northern Poland, and from the Mójcza, Holy Cross Mts., southern Poland.

### *Wolinella polonica* sp. n.

(Plate 117, figs. 1–3; text-figs. 3*b*, 10*b*)

*Holotype.* ZPAL Br V/496; Pl. 117, fig. 2.

*Diagnosis.* Subcylindrical zooecia with long, curved apertural parts. Several longitudinal canals run along the zooecia which communicate with them by one or two communication pores.

*Remarks. W. polonica* sp. n. differs from the remaining species of this genus in the strong separation of several longitudinal canals in erect branches of the zoarium. A few encrusting zooids and numerous fragmentary erect branches show that *W. polonica* sp. n. is a rather variable species. Variability in external shape is expressed mostly in the elongate and curved apertures. Internally they are strongly variable in the number and shape of longitudinal canals. The number of canals varies from one to six. Development of small, basal communication pores (through which the zooid connected with the stolon) is very variable; sometimes only a thin distal pore is developed. Longitudinal ribs and separating canals are also variably developed; often lateral communication pores between stolons occur.

*Material.* One hundred and twenty-eight fragments of zoaria from Baltic erratic boulders: E-137, 138, 143, 149, 194, 215, 249, 260, 283.

*Distribution. W. polonica* sp. n. occurs in the Baltic region in Lasnamägi stage (Llanvirn). Known from erratic boulders from Poland, and from the Holy Cross Mts.

*Wolinella brevis* sp. n.

(Plate 117, fig. 5; text-fig. 3*c*)

*Holotype.* ZPAL Br V/372; Pl. 117, fig. 5.

*Diagnosis.* Short zooecia with wide apertural parts. The proximal part of adult zooecia is strongly constricted internally with posterodorsal recess.

*Remarks. W. brevis* sp. n. differs from the remaining species of the genus in its short zooecia and in the lack of full separation of longitudinal canals. Only fragments of erect zoarial branches are known. They are variable in zooecial length and in the shape of the aperture, but the range of variation is rather small.

*Material.* Thirty-three fragments of zoaria from Baltic erratic boulders E-085, 112; eight fragments of zoaria from the Mójcza Limestone (sample A-7) may belong to this species.

*Distribution. W. brevis* sp. n. occurs in Uhaku and Kukruse stages (Uppermost Llanvirn—Lowermost Caradoc) of the Baltic region. It is known from erratic boulders from Poland. In equivalents of Kukruse stage of the Mójcza Limestone, Holy Cross Mts., Poland fragmentary zoaria occur which may belong to this species.

Genus DENTALITRYPA Kiepura, 1962

*Type species. Corynotrypa (Dentalitrypa) bidens* Kiepura, 1962.

*Emended diagnosis.* Fusiform zooecia with funnel-like apertural parts, separated from the remaining parts of zooecia by hemiphragm-like constriction.

*Remarks. Dentalitrypa* differs from *Corynotrypa* in the structure of adapertural parts. Lunarium-like structures occur at least in the type species.

*Distribution.* Ashgill to Ludlow(?) of Baltic region. Known from erratic boulders from Poland.

*Dentalitrypa infundibuliformis* sp. n.

(Plate 118, fig. 3; text-fig. 5*d–f*)

*Holotype.* ZPAL Br V/627; Pl. J18, fig. 3.

*Diagnosis.* Funnel-like short zooecia with a very wide aperture.

*Remarks. D. infundibuliformis* sp. n. differs in shape from all known single-walled Bryozoa. Shape of the 'hemiphragm' in the aperture is badly known because of recrystallization of zooecial walls. No remains of spines or lunaria in apertures have been observed. Zooecia of *D. infundibuliformis* sp. n. vary slightly in their length and curvature: sometimes their axes are slightly sinuous vertically.

*Material.* Thirty-six isolated zooecia from two erratic boulders: E-161, 168.

*Distribution. D. infundibuliformis* sp. n. is known only from two erratic boulders of Baltic origin from Poland. Both boulders do not contain stratigraphically important fossils but may be of Wenlock or of Ludlow age.

Family CROWNOPORIDAE Ross, 1967

(Incl. Kukersellidae Brood, 1975; Clonoporidae Brood, 1975; Sagenellidae Brood, 1975.)

*Emended diagnosis.* Tubular zooecia with pseudoporous external walls and communication canals end pores between zooecia. Lack of any specialized gonozooecia.

*Remarks.* Crownoporidae differs from Corynotrypidae in the presence of pseudopores, from Ceramoporidae in single-walled organization, and from all post-Palaeozoic cyclostomes in the lack of gonozooecia.

*Genera included. Sagenella* Hall, 1851; *Clonopora* Hall, 1883 (? = *Mitoclemella* Bassler, 1952); *Kukersella* Toots, 1952.

### Genus CLONOPORA Hall, 1883

*Type species. Clonopora semireducta* Hall, 1883.

*Remarks.* Baltic species are characterized by subcylindrical erect branches with several rows of zooecia, few pseudopores and lack of lateral communication pores.

### *Clonopora primaeva* sp. n.

(Plate 119, figs. 1, 4, 5)

*Holotype.* ZPAL Br V/354; Pl. 119, fig. 1.

*Diagnosis.* Branches of zoaria are dichotomously divided, with varying arrangement of zooecia, radial to oriented to one side. Zooecial walls with rare, large pseudopores; no lateral communication pores between zooecia.

*Remarks. C. primaeva* sp. n. is the earliest species of the genus and family Crownoporidae. Some specimens (from boulder E-113) lack any pseudopores and are morphologically transitional between *Wolinella* gen. n. and *Clonopora. C. primaeva* sp. n. differs from *Kukersella erratica* sp. n., which occurs with it, in the lack of a complex system of communication canals and pores. Frequency of pseudopores is the most variable morphological character of this species; they are never as numerous as in *Kukersella* or Mesozoic cyclostomes. Commonly zooecia are aperturally oriented on the same side of a branch. The 'basal' side is then flat, with a tress-like arrangement of basal parts of zooecia. There is continuous transition to round branches. Dichotomously branching fragments of zoaria are rare.

*Material.* Fifty-eight fragments of zoaria from erratic Baltic boulders E-079, 112, 113, 130, 143, 154, 236; fifteen from the Mójcza limestone, samples A-4, 19, 20, 30.

*Distribution. C. primaeva* sp. n. occurs in the Baltic region since the Upper Kunda stage (Lowermost Llanvirn) up to the Jōhvi stage (Upper Caradoc) and in the Mójcza Limestone, Holy Cross Mts., Poland in equivalents of Kukruse to Jōhvi stages (Caradocian).

### Genus KUKERSELLA Toots, 1952

*Type species. K. boreale* Toots, 1952.

*Emended diagnosis.* Cylindrical branches of zoarium; zooecia with numerous pseudopores and lateral communication pores.

Species included: *K. bassleri* Toots, 1952; *K. boreale* (Bassler, 1911); *K. singularis* (Ross, 1967); *K. erratica* sp. n.

*Distribution. Kukersella* occurs from Llandeilo to Upper Caradoc in the Baltic region and in the Trenton of North America.

### *Kukersella erratica* sp. n.

(Pl. 119, figs. 2, 3)

*Holotype.* ZPAL Br V/366; Pl. 119, figs. 2, 3.

*Diagnosis.* Zooids of different generations communicate through wide communication canals; lack of any diaphragms in zooecia. Zooecial walls with numerous pseudopores and communication pores.

*Remarks. K. erratica* sp. n. differs from *K. bassleri*, which is the closest morphologically and strati-graphically, in the lack of diaphragms in the older parts of zooecia. Other species of the genus differ in the same character, and in having different arrangements of pseudopores. The co-occurring species *Clonopora primaeva* sp. n. differs in the lack of communication pores. Distribution of the apertures of zooecia and the communication canal system is very variable. On some parts of a branch only an irregular net of communication canals is developed.

*Material.* Eleven fragments of zoaria from two erratic boulders: E-112, 140.

*Distribution. K. erratica* sp. n. occurs in the Baltic region in the Uhaku stage and Kukruse stage (Uppermost Llanvirn-Lowermost Caradoc). The species is known only from erratic boulders from Poland.

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