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POSSIBLE SOLITARY BRYOZOAN ANCESTORS FROM THE EARLY PALAEOZOIC AND THE AFFINITIES OF THE TENTACULITA

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ABSTRACT. – A cemented hemispherical initial part identified in Ordovician *Cornulites*-like minute calcitic tubes is proposed as a homologue of the bryozoan protoecium. These possible cornulitids are thus interpreted as primitive solitary relatives of the Bryozoa, which may mean that the calcareous skeleton preceded coloniality in bryozoan evolution. *Cornulitozoon collare* gen. et sp. nov. from the Baltic Ordovician and *Opatozoon echinatum* gen. et sp. nov. from the Silurian of the Holy Cross Mts., Poland, are described;

KEY-WORDS. – Bryozoa, evolution, Ordovician, Silurian, Cornulitids, Tentaculita.

RÉSUMÉ. – Une partie initiale hémisphérique fixée, qui a été identifiée dans de petits tubes calcitiques comme ceux de *Cornulites*, est considérée comme homologue de la protoécie chez les Bryozoaires. Ces Cornulitides éventuels sont donc interprétés comme des parents solitaires primitifs des Bryozoaires. Cela peut signifier que le squelette calcaire a précédé la colonialité dans l'évolution des Bryozoaires. *Cornulitozoon collare* gen. et sp. nov., provenant de l'Ordovicien de la Baltique et *Opatozoon echinatum* gen. et sp. nov., provenant des Monts Sainte-Croix (Pologne) sont décrits.

MOTS-CLÉS. – Bryozoa, évolution, Ordovicien, Silurien, Cornulitides, Tentaculita.

INTRODUCTION

The distribution of character states and, at least to some degree, stratigraphical order of their appearance, suggests that wall pseudoporosity, the common bud, and hypostegal coelom are advanced features in the Bryozoa. Probably the most primitive bryozoans were those that had tubular zooecia creeping over the substrate with zooids budding separately and connected only by proximal and distal communication pores (or rather canals) (BROOD, 1976; LARWOOD & TAYLOR, 1979; DZIK, 1981). Their first zooid (ancestrula) developed from a dome-shaped skeletal structure produced by the metamorphosing larva after it settled on the substrate. The presence of this protoecium is a primitive feature that has been proposed as a basic synapomorphy of the stenolaemates (TAYLOR, 1985: p. 365). The only other group of colonial organisms in which a structure analogous to the protoecium develops in early astogeny are the pterobranchs, but these differ greatly in the mode of secretion of the postlarval skeleton (DILLY, 1985). Organisms with similar to the bryozoans way of which secrete organic and calcareous skeleton either develop larval skeleton at the planktonic or embryonic stage, like the molluscs and brachiopods, or start secretion of calcareous tubes well after the larval stage, like the polychaetes and coelenterates. The presence of a hemispherical protoecium, which is followed by a calcareous tube, seems thus to be a unique feature of primitive bryozoans.

It is therefore of special interest that some minute tubular calcareous fossil of the Early Paleozoic possess adnate hemispherical initial parts, followed by creeping, aperturally secreted tubes. In the present paper an attempt is made to interpret the morphology of these fossils and possible evolutionary implications are discussed.

THE EVIDENCE

Application of dilute and/or buffered acetic acid allows recovery of calcitic fossils from limestones if there is enough difference between the sparitic fossils and the micritic rock matrix. The fossils described below have been extracted from Late Caradoc pure, light coloured pelitic limestones which occur widely among glacial erratic boulders of Baltic origin in northern Poland (so called Ostseekalk of German students), and from dark red, marly, very fossiliferous limestones of Late Ludlow age from the Holy Cross Mts., Poland.

The Ordovician species *Cornulitozoon collare* gen. nov., sp. nov. co-occurs with a diverse assemblage of corynotrypid bryozoans (see Pl. 1, Fig. 1; also DZIK, 1981) that show exactly the same mode of preservation and thus, presumably, closely similar original microstructure. They are similar to one another in size, shape, structure of the non-porous wall, and in the presence of funnel-like apertural collars. The only significant morphological difference is that these collars are serially arranged along the tubes of *Cornulitozoon* while being singular in associated specimens of *Dentalitrypa* and *Corynotrypa* where the collar developed after termination of growth of the zooecium (DZIK, 1981). Well preserved specimens of *Cornulitozoon* show initial parts which are virtually identical with those of corynotrypid ancestrulae (compare Pl. 1, Fig. 4 and Pl. 1, Fig. 5 with Text-Fig. 4 *in* DZIK, 1981); they have a hemispherical "protoecium" basally attached to the

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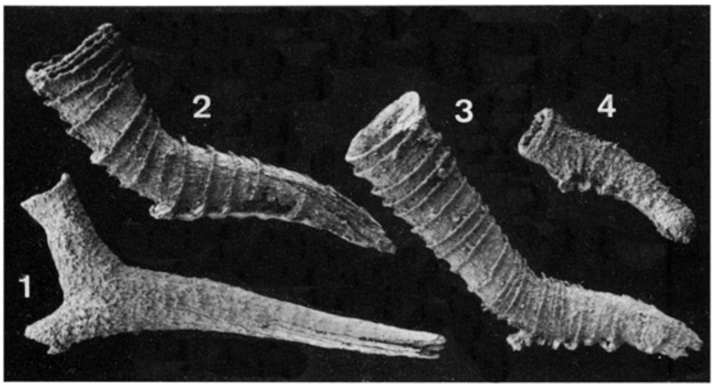
PLATE 1

Fig. 1-4. Small calcitic tubular fossils extracted from the Late Caradoc erratic boulder E-329, Rozewie, Baltic coast of Poland. All X 50. **1**, *Corynotrypa bassleri* KIEPURA, 1962 (specimen ZPAL Br V/848). **2-4**, *Cornulitozoon collare* gen. nov., sp. nov. (specimens ZPAL Br V/849-851) ; note presence of swollen initial part (**2**). **Figs. 5-7.** *Cornulitozoon collare* gen. nov., sp. nov., Late Caradoc, erratic boulder E-329, Rozewie, Baltic coast of Poland. Holotype ZPAL BrV/852 in dorsolateral (**5**), ventrolateral (**7**) views, and close-up of the initial bulbous part (**6**). Note extent of the attachment area and longitudinal orientation of calcite crystals in the wall (**5**, **7**, X 100; **6**, X 200).

PLANCHE 1

Figs. 1-4. Petits fossiles tubulaires calcitiques extraits du bloc erratique E-329, Caradoc supérieur, Rozewie, Pologne (Côte de la Baltique), X 50. **1**, *Corynotrypa bassleri* KIEPURA, 1962 (spécimen ZPAL Br V/848). 2-4, *Cornulitozoon collare* gen. nov., sp. nov. (spécimens ZPAL Br V/849-851) ; remarquer l'existence de la partie initiale renflée (**2**). Figs 5-7. *Cornulitozoon collare* gen. nov., sp. nov. ; bloc erratique E-329, Caradoc supérieur, Rozewie, Pologne (Côte de la Baltique). Holotype ZPAL BrV/852 en vues dorso-latérale (5), ventro-latérale (**7**) et vue agrandie de la partie initiale bulbeuse (**6**). Remarquer l'extension de la zone de fixation et l'orientation longitudinale des cristaux de calcite dans la paroi (**5**, **7** X 100 ; **6**, X 200).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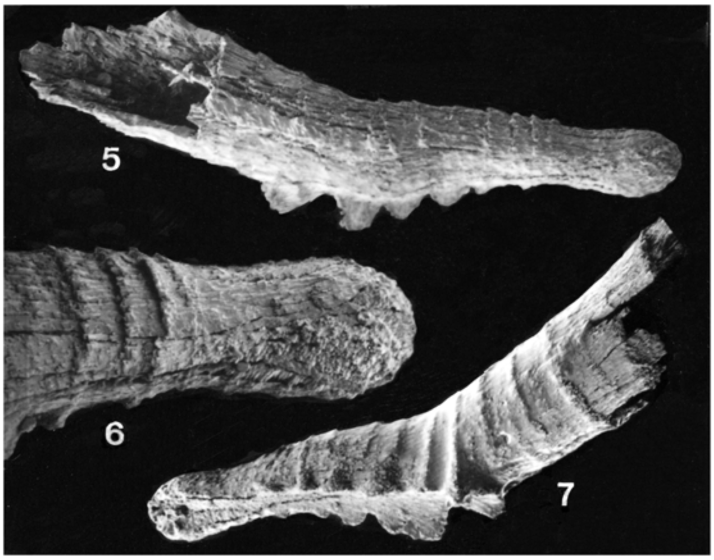
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substrate and subsequent ontogenetic stages with prominent growth lines and rugae. Despite these similarities the new fossil genus differs from bryozoans in being solitary.

A closely related form of slightly larger size and a little more conical in shape, found in a Silurian erratic boulder, links these Ordovician fossils with another problematic taxon, *Opatozoon echinatum* gen. nov., sp. nov. from the Silurian of the Holy Cross Mts., Poland. Its calcitic tubes, a few millimetres in length, occur in a fossil assemblage almost devoid of bryozoans despite a high diversity of associated brachiopods, trilobites, rostroconchs, ostracodes, tentaculites, and corals. The collars on the surface of these tubes are more-or-less undulose distally, and at later ontogenetic stages they form empty spines, giving the fossils an unusual appearance (Pl. 2, Fig. 3).

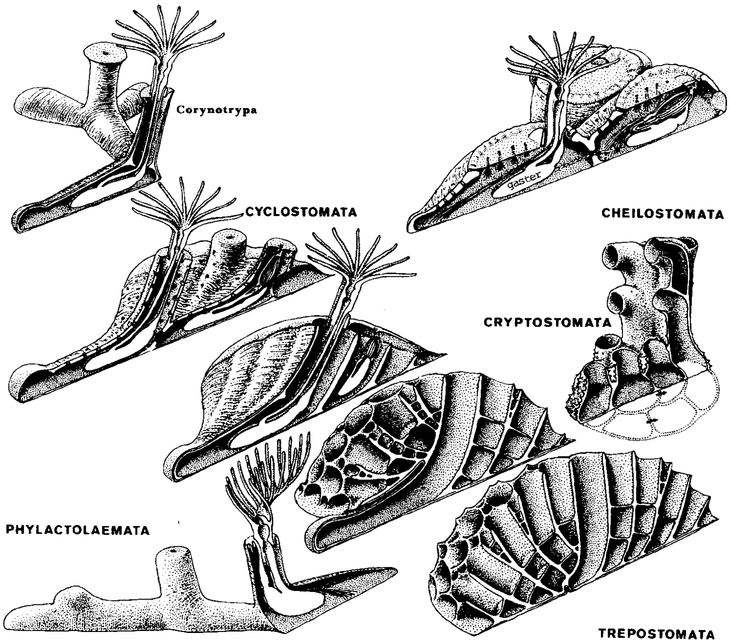
EVOLUTIONARY IMPLICATIONS

The early evolution of the Bryozoa is poorly documented by the fossil record. The oldest, Tremadoc and Early Arenig faunas of unequivocal bryozoans (TAYLOR & CURRY, 1985; TAYLOR & COPE, 1987; HU & SPJELDNAES, this volume) were already composed of evolutionarily advanced forms. Even if a bryozoan affinity is accepted of the controversial Tremadoc fossil *Marcusodictyon* (see TAYLOR, 1984), which may represent the phosphatized basal parts of densely-packed zooecia, this would hardly introduce any change into the generally pessimistic picture. Much room in thus left to speculation.

The zoological evidence suggests that the earliest bryozoans resembled asexually budding colonial phoronids. This is usually interpreted in such a way that the origin of coloniality preceded that of a mineralized skeleton in the evolution of the Bryozoa (FARMER *& al.*, 1973; LARWOOD & TAYLOR, 1979).

It is possible to indicate among fossil bryozoans the ancestral skeletonized forms. The domination of massive colonies of the trepostomes and cryptostomes is definitely a preservational feature. To find delicate encrusting colonies requires different methods of collection and processing. By the Arenig a wide spectrum of colony organizations was represented in the Bryozoa, ranging from single-walled corynotrypids with tubular creeping zooecia to double-walled ceramoporids, trepostomes, and cryptostomes with densely packed zooecia (Text-Fig. 1). The most reasonable way to transform the observed pattern of morphological transition into an evolutionary tree seems to be with the corynotrypids representing its roots (LARWOOD & TAYLOR, 1979; DZIK, 1981). The apparent similarity between *Corynotrypa*, with a mineral skeleton, and the ctenostome *Arachnidium*, devoid of any mineralization, led to the conclusion that the acquisition of the skeleton took place at the transition between the Ctenostomata and the Corynotrypidae (LARWOOD & TAYLOR, 1979). This view may be challenged by the discovery of an apparent protoecium in the *Cornulites*-like Early Paleozoic fossils.

There is a trend towards a more sophisticated ornamentation of the tubes in cornulitozooids as shown by the transformation of collars into peculiar spines in the Silurian *Opatozoon echinatum*. The oldest cornulitozooid, *C. collare*, is still of younger age than the oldest known corynotrypids and if this trend in ornamentation is extrapolated back from the Late to Early Ordovician one might expect a much simpler ancestral form. It thus seems probable that the corynotrypid *Wolinella* and the cornulitozooid *Cornulitozoon* had a common ancestor as simple morphologically as *Wolinella* but unable to proliferate asexually. The possibility that *Cornulitozoon* is a secondarily solitary derivative of *Wolinella*, analogous to the Recent ctenostomate *Monobryozoon* (BERGE *& al.*, 1985) cannot be excluded. However, to propose such an early reversal would be against the general trend in



Text-Fig. 1. Schematic presentation of early astogenetic stages in the major groups of the Bryozoa, showing transition from single-walled corynotrypids to more integrated and sophisticated colonies of stenolaemates and gymnolaemates. Note presence of pseudoporosity and conical ancestrulae in both early cyclostomes and cheilostomes.

Texte-Fig. 1. Représentation schématique des stades astogénétiques précoces chez les groupes principaux de Bryozoaires. Elle montre la transition depuis les Corynotrypides à paroi simple aux colonies plus intégrées et plus complexes de Sténolémates et Gymnolémates. Remarquer l'existence de pseudopores et d'ancestrulae coniques à la fois chez les Cyclostomes primitifs et les Cheilostomes.

the early evolution of the Bryozoa towards the development of coloniality and increasing integration and specialization of zooids. In any case this still would mean that coloniality was not an immanent feature of the earliest Bryozoa. The possible origin of *Cornulitozoon* by secondary loss of the ability of asexual propagation might imply that its probable relatives, the cornulitids, attained the relatively large size of their tubes secondarily.

Representatives of both these groups co-occur in the Baltic Ordovician, phosphatic steinkerns of *Cornulites* being known as early as the Llanvirn (HYNDA, 1986). In addition to their larger size, cornulitid tubes also differ from cornulitozooids in the presence of longitudinal striations and peculiar internal constrictions which are directed adaperturally (see SCHALLREUTER, 1981). The early ontogeny of the cornulitids is rather inadequately known, but it is clear that in both Late Ordovician *Ancientia* (see ROSS, 1967) and a Silurian cornulitid (misidentified as a nowakiid tentaculite by TUNNICLIFF: 1983,1989) the apex is hemispherical. Except for cementation to the substrate at an early stage, which is shared only by the cornulitids and cornulitozooids, the other features of cornulitids are common also to the tentaculites. This may mean that the tentaculites were cornulitid derivatives, with free living although still benthic early stages (passively lying on the mud?). One may wonder whether this is not part of a general trend that culminated in the Gedinnian with the development of planktonic mode of life of the nowakiids and led later to highly advanced, spirally coiled pelagic forms. The embryonic shells were subconical in *Tentaculites* and subspherical (with mucro) in *Nowakia* and *Styliolina* (see ALBERTI, 1972), which makes them morphologically indistinguishable from embryonic shells of planktotrophic molluscs. There is thus a transition series from the minute cementing cornulitozooids through their larger relatives the cornulitids and free benthic tentaculites up to the planktonic styliolinids. It is tempting to transform this morphoseries into an evolutionary tree rooted at the cornulitids. Class rank can be given to the whole group for which there is a name available, the Tentaculita BOUČEK, 1964.

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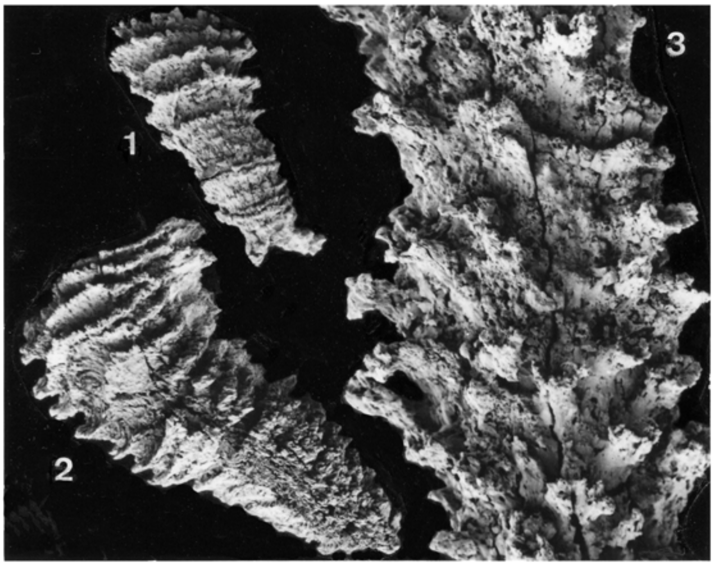
PLATE 2

Figs. 1-3. *Opatozoon echinatum* gen. nov., sp. nov.; Late Ludlow, Lower Rzepin Beds, Belcz near Opatow, Holy Cross Mts, Poland. **1**, juvenile specimen ZPAL Br V/853 with adnate initial part partially preserved, X 100; **2**, holotype ZPAL Br V/854, X 100. **3**, wall fragment of adult specimen ZPAL Br V/855, X 300. **Figs 4-6.** Silurian cornulitids. **4**, a tube of *Cornulites* sp. with *Ancientia*-like adult sculpture, specimen MB W 39 (possibly the Wenlock of Dudley, England), X 3. **5-6**, *Cornulites serpularius* SCHLOTHEIM, 1820; Pridoli of the Baltic area, Beyrichienkalk erratic boulders. 5, specimen MB W38 with partially preserved ornamentation of the wall ; Hiddensee, NE Germany. Note also imprints of vesicular inner surface of the wall at later stages of the ontogeny, X 3. **6**, longitudinal section of the tube, Orlowo, Poland, X 10.

PLANCHE 2

Figs. 1-3. *Opatozoon echinatum* gen. nov., sp. nov. ; Ludlow supérieur, Lower Rzepin Beds, Belcz près d'Opatow, Monts Sainte-Croix (Pologne). **1**, spécimen juvénile ZPAL Br V/853 avec la région initiale adnée partiellement conservée, X 100. **2**, holotype ZPAL Br V/854, X 100. **3**, fragment de paroi du spécimen adulte ZPAL Br V/855, X 300. **Figs. 4-6.** Cornulitides siluriens. **4**, tube de *Cornulites* sp. avec une ornementation adulte comme celle d'*Ancientia*, spécimen MB W 39 (provenant peut-être du Wenlock de Dudley, Angleterre), X 3. **5-6,** *Cornulites serpularius* SCHLOTHEIM, 1820 ; Pridoli de la Baltique, blocs erratiques du Beyrichienkalk. **5**, spécimen MB W 38 avec l'ornementation partiellement conservée de la paroi ; Hiddensee, NE de l'Allemagne. Remarquer aussi les empreintes de la surface interne vésiculaire de la paroi aux stades tardifs de l'ontogénie, X 3. **6**, section longitudinale du tube, Orlowo (Pologne), X 10.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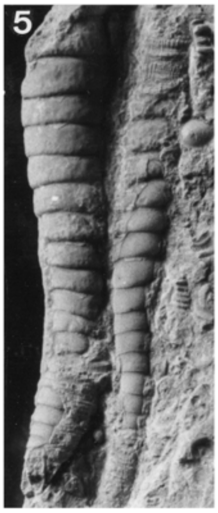
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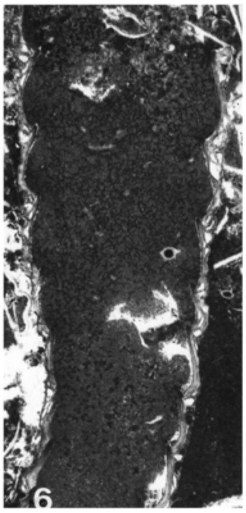
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The zoological affinities of the Tentaculita are difficult to infer because of an almost complete lack of data concerning anatomical organization of the soft parts of the animals which secreted these widely distributed calcareous tubes (LARDEUX, 1969). The proposed homology between the apical swollen part of *Cornulitozoon* tubes and the bryozoan protoecium may be the clue. If this interpretation is correct, the Tentaculita are lophophorates close to the extinct ancestors of the Bryozoa. The evidence for this relationship is rather weak it is dependent on a few characters that can easily originate through adaptation to a similar mode of life (the apparent similarity between the styliolinids and pteropod gastropods is a good example). *Cornulitozoon* may possibly belong to an extinct group very distantly related to the extant phyla.

Nevertheless, there are reasons to believe that the ability to secrete skeleton is a very ancient trait of the lophophorates. Recent discoveries of Cambrian fossils with permineralized soft parts, as well as reinterpetations of earlier findings, have led to the recognition of several extinct forms providing insight into the early diversification of the lophophorate body plan. The best known of these, *Dinomischus* and *Eldonia*, widely distributed in Early and Mid Cambrian seas, had a cup– or disc- shaped skeleton surrounding the lophophore-bearing body (DZIK, *in press*). Another possible lophophorate of the Cambrian may be *Cambrorhytium* from the Burgess Shale of British Columbia (CONWAY MORRIS & ROBISON, 1988). The weakly mineralized or organic tube of conical shape was secreted by accretion (as indicated by distinct growth lines). Soft parts sometimes preserved within these tubes show visceral organs and tentacles well behind the aperture, an indication that the tentacle-bearing part of the body was contractile and, to some degree, separated from a kind of mantle that secreted the tube. This, being unlike the coelenterates whose soft parts are more tightly unified with their skeletons, is reminiscent of the Bryozoa. *Cambrorhytium* may thus be another "solitary bryozoan" which, taking into account its early geological age, seems to be a good candidate as a common ancestor of the cornulitids and the Bryozoa. Regrettably, too little is known about the soft body anatomy in all these possible early lophophorates. Still, they provide strong evidence for high taxonomic diversity of the group in the Early Palaeozoic. The Tentaculita seem to represent one of early, extinct classes of the phylum Lophophorata.

This makes the proposed hypothesis that the mineral skeleton preceded coloniality in the Bryozoa easier to accept. On morphological and (taking into account incompleteness of the fossil record of reptant bryozoans) stratigraphical grounds, *Cornulitozoon* represent a suitable connecting link between the skeletonized ancestors of the Bryozoa and their most primitive colonial forms.

Another question requires reconsideration in this context, namely whether the skeleton of the Cheilostomata really developed independently of that of the stenolaemates. New evidence has recently appeared in support of the view that the Cheilostomata developed directly from a skeletal, *Corynotrypa*-like ancestor. The Late Ordovican, operculum-bearing *Schallreuterella*, having a distinctly developed, probably weakly calcified frontal wall in otherwise well-mineralized zooecia of distinctly cheilostomate appearance (HILLMER, 1987), may be close to the stenolaemate-gymnolaemate transition. This makes the time gap between the first Late Ordovician ctenostomes and the oldest known Late Jurassic cheilostomes less significant, evidently being result of generally poor knowledge of Late Palaeozoic and Triassic single-walled bryozoans. Moreover, the presence of pseudopores in the gymnocyst of the early cheilostome *Wawalia* (DZIK, 1975; additional SEM evidence is now available) may suggest derivation of the cheilostomes from palaeotubuliporine stenolaemates somewhat more advanced than *Corynotrypa*.

TAXONOMY

Class ? Tentaculita BOUČEK, 1964

Order Cornulitida BOUČEK, 1964.

COMMENTS: – The cornulitids differ from the tentaculitids in having initial parts of their tubes cemented to the substrate. The similarity in shell morphology is so close that the cornulitids are often misinterpreted as tentaculitids (see, for instance, TUNNICLIFF: 1983, 1989). In adult parts of the cornulitid tube, external layers of the wall tend to be split forming numerous vesicles (Pl. 2, Fig. 6), resulting finally in a vesicular structure of the adaperturally thickened tubes. This feature, being typical only for adult Silurian *Cornulites* does not characterize the group as the whole. Members of the Cornulitida can be distinguished from the tentaculitids only when their cemented initial parts are preserved. Most probably the tentaculitids had free-living (even if they were benthic) larval and early postlarval stages, producing a bulbous or subconical embryonic shell devoid of any transverse ornamentation (but with longitudinal striae present at least in the nowakiids; ALBERTI, 1972) and ornamented tubular postembryonic stages, like the cornulitids, with transverse rugae and longitudinal striation. Early tentaculitids also had internal, adaperturally directed constrictions of the cornulitid type.

Family Cornulitozoidae fam. nov.

DIAGNOSIS: Minute cornulitids having tubes externally ornamented with numerous lamellar collars and smooth internally.

COMMENTS: Members of this new family differ from the Cornulitidae FISHER, 1962 and Ancientiidae ROSS, 1967 in lacking internal constrictions in their tubes and having outside lamellar collars instead of thick annuli, and from the former, also in the much smaller adult size.

GENERA INCLUDED: *Cornulitozoon* gen. nov. and *Opatozoon* gen. nov.

Cornulitozoon gen. nov.

TYPE SPECIES: *C. collare* sp. nov.

DERIVATIO NOMINIS: The name is a modification of that of *Cornulites*, with ending that indicates proposed bryozoan affinities.

DIAGNOSIS: Tubes with adnate cemented proximal part comprising approximately one third of the total length, and free distal part ornamented with prominent densely distributed, simple collars.

SPECIES INCLUDED: The type species of Late Ordovician age and an unnamed species found in a boulder with abundant trilobites of the genus *Encrinurus* and other Silurian fossils from Józwin near Konin, Poland.

Cornulitozoon collare sp. nov.

(Pl. 1, Figs 2-7)

HOLOTYPE: ZPAL Br V/852; Pl. 1, Figs 5-7.

DERIVATIO NOMINIS: After collars ornamenting the tubes.

TYPE HORIZON AND LOCALITY: Erratic boulder E-329 of Ostseekalk type, Late Caradoc, Rozewie, Baltic coast of Poland.

DIAGNOSIS: Tubes about 1.5 mm in length, slowly increasing in their diameter, which reaches in adults approximately 0.3 mm.

MATERIAL: 5 specimens from the boulder E-293, Mochty near Zakroczym, Poland, 2 specimens from E-174, Orlowo, Baltic coast of Poland and 97 associated with the holotype in the boulder E-329.

COMMENTS: Close to the apertures of large specimens the collars, which are rather variably distributed, became more densely spaced which suggests termination of tube growth. Such specimens with well preserved apertural margins range in diameter from 0.24 to 0.32 mm, the mean of 19 measurements from sample E-329 being 0.27 mm, standard deviation 0.03 mm. Some of these specimens show close spacing of their collars also at earlier stages, for instance at the junction between the cementing and free parts. Tubes of the Silurian species found in boulder E-331 from Józwin near Konin, Poland are somewhat larger in size and more widely conical in shape but still have uniformly dense collars.

DISTRIBUTION: *C. collare* sp. nov. is a common fossil in boulders of the Ostseekalk type, a light coloured pelitic limestone containing numerous individuals of the receptaculitid *Tetragonis sulcata* EICHWALD, 1840 (boulders E-293 and 329) as well as in a pink coloured variety with abundant examples of the dasycladacean alga *Palaeoporella* (boulder E-174). Both these rock types contain conodonts of North American Midcontinent affinities (*Belodina* and *Icriodella*) which provides additional evidence for relatively warm-water conditions. The age of the boulders is most probably Latest Caradoc.

***Opatozoon* gen. nov.**

TYPE SPECIES: *O. echinatum* sp. nov.

DERIVATIO NOMINIS: After Opatów, a town in the Holy Cross Mts. close to the type locality.

DIAGNOSIS: Widely conical tubes a few millimeters in length with undulating collars at later ontogenetic stages transformed into empty spines.

SPECIES INCLUDED: Only the type species.

***Opatozoon. echinatum* sp. nov.**

(Pl. 2, Figs 1-3).

HOLOTYPE: ZPAL Br V/854 ; Pl. 2, Fig. 2.

DERIVATIO NOMINIS: After spinose appearance of tubes.

TYPE HORIZON AND LOCALITY: Red limestones of the Lower Rzepin Bed, Belcz near Opatów, the Holy Cross Mts., Poland.

DIAGNOSIS: as for the genus.

MATERIAL: 7 specimens from the type locality.

REMARKS: The apical part of the tube is not preserved in any of the studied specimens. Judging from the specimen most complete in this respect (ZPAL Br V/853, Pl. 2, Fig. 1), the cementing part was perhaps very short, with free tubes budding almost directly from the protoecium.

DISTRIBUTION: Known only from the type locality.

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