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NOTES ON  
*HYOLITHELLUS* BILLINGS, 1871,  
CLASS *POGONOPHORA*  
JOHANNSON, 1937

BY  
VALDEMAR POULSEN



København 1963  
kommission hos Ejnar Munksgaard

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## Synopsis

The genus *Hyolithellus* BILLINGS, 1871 is discussed, and it is demonstrated that the much disputed "operculum" (*Discinella* HALL, 1871) must be excluded from *Hyolithellus*. The "operculum" has possibly monoplacophoran affinity. Evidence indicates that *Hyolithellus* may well be referred to the class Pogonophora JOHANSSON, 1937. The structure of the tubular skeleton in members of the Pogonophora is strikingly similar to that of *Hyolithellus*. X-ray fluorescence analysis of the tubes apparently also confirms the pogonophoran relationship and the exclusion of *Discinella* and its allies from *Hyolithellus*. Considering the early appearance of representatives of the Hemichordata (Lower Ordovician), it does not seem unreasonable to regard the Lower- and Middle Cambrian *Hyolithellus* as a close relative of the Hemichordata.

## Introduction

Classification of several Cambrian animal groups presents many difficulties. *Hyalithellus* has lately (FISHER, 1962) been referred to an order Hyolithelminthes, the affinities of which supposedly are quite unknown. At present the author is studying a Lower Cambrian fauna from the island of Bornholm containing numerous specimens of *Hyalithellus*. A revision of this genus has long been needed on account of the error made by many authors, in assigning an operculum to it. As will be shown, the "operculum" was correctly established as a molluscan genus by HALL, 1871.

Mr. J. B. KIRKEGAARD, M. Sc., of the Zoological Museum of the University of Copenhagen, called the author's attention to certain hemichordate relatives, class Pogonophora, the members of which mostly belong to the benthonic environment of the deep sea. Their tubular skeleton bears much resemblance to *Hyalithellus* tubes. Mr. KIRKEGAARD kindly placed a specimen of the tube of *Galathealinum bruuni* at the author's disposal for study.

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Class **POGONOPHORA** JOHANNSON, 1937

Order **HYOLITHELLIDA** SYSSOIEV, 1957, (partim)

Family HYOLITHELLIDAE WALCOTT, 1886, (partim)

Genus *Hyolithellus* BILLINGS, 1871

Type species: *Hyolithes micans* BILLINGS

The type species is the most widely distributed of the species referred to *Hyolithellus*, and the discussion mainly concerns this species.

The "operculum": BILLINGS (1871), when describing *Hyolithellus*, assigned an operculum to the tubular fossil, both occurring in the Lower Cambrian of Troy, New York. From the same beds HALL described specimens of *Discinella*. His paper should have been published in 1871, but the whole edition was destroyed by fire, and his results were not published until 1873. In any case, HALL as the first differentiated *Discinella* under a special name. He concluded that, on account of the peculiar muscle scars, the fossil could hardly be recognized as a brachiopod, but rather as a gastropod. The general character of the shell, he further concluded, is such as to ally it with the Discinidae, and, accordingly, the name *Discinella* was proposed. WALCOTT (1886, p. 142) called attention to the fact that the supposed operculum of *Hyolithellus* was the same form, as the one called *Discinella* by HALL. Since then, practically all American paleontologists have followed BILLINGS and WALCOTT in regarding *Discinella* as the operculum of *Hyolithellus*. In this connection it must be noted that they usually occur in the same beds. KNIGHT and YOCHELSON (1960, p. 324) rejected *Hyolithellus* and its "operculum" from the Gastropoda and Monoplacophora. FISHER

(1962) regarded *Barella*, *Discinella*, and *Mobergella* as hyolithelminth opercula.

MOBERG (1892) pointed out that in Swedish sediments, in which *Discinella* may cover almost entire bedding planes, no tubular fossils to match the "opercula" are found. At the same time *Discinella* is absent in beds rich in tubular fossils.

HOLM (1893), when discussing the Hyolithidae refused to recognize any relationship between *Hyolithes* and *Hyolithellus*. With regard to *Hyolithellus* he stated that the tube was difficult to assign to any class, and the "operculum" should be removed from the genus.

HEDSTRÖM (1923), after including *Discinella* in a new genus, *Mobergella*, referred the univalve fossil to the Gastropoda, as already tentatively suggested by HALL. In 1930 HEDSTRÖM realized that the name *Discinella* could not be suppressed, as the action was contrary to the rules of international zoological nomenclature. On the other hand, a differential analysis showed that important differences in number and arrangement of the muscle scars occur, and, accordingly, HEDSTRÖM concluded that the name *Mobergella* might be applied to specimens, which differ clearly from *Discinella*.

C. POULSEN (1932) described *Hyolithellus micans* and *Discinella micans* from the Lower Cambrian of East Greenland. He referred *Discinella* to the family Patellidae. POULSEN'S material clearly demonstrates that a disparity exists with regard to the diameter of the specimens of *Discinella* and that of the tubular *Hyolithellus* shells. The diameter of *Discinella* is up to twice the diameter of the tubes. The same disparity is quite evident in specimens figured by LOCHMAN (1956). In the author's opinion an eventual operculum should be expected to fit in with the tubes or to be slightly smaller.

COBBOLD, who in several papers described occurrences of *Hyolithellus* in England, never found an operculum, which could be assigned to the genus. In Sweden the "opercula" and the tubes occur at definitely separate levels. The author may add that *Hyolithellus micans* occurs abundantly in a Middle Cambrian clay on the island of Bornholm. In this deposit *Discinella* and *Mobergella* are totally absent. The absence cannot be explained as an effect of separation during transportation, as the hyolithellid



tubes in the clay are associated with thousands of inarticulate brachiopod shells, which from point of view of transportation dynamics are very similar to the shell of *Discinella*.

The author believes that the above mentioned objections clearly demonstrate that the "operculum" of *Hyolithellus* must be excluded from the genus. At the same time the muscle scars seen in *Discinella*, *Mobergella*, and *Barella* in some respects are very similar to those found in the Monoplacophora (text fig. 1 d). In the Lower Cambrian faunas only members of the order Tryblidioidea bear any resemblance to *Discinella* and its allies, which possibly should be regarded as close relatives of the Monoplacophora.

### **Previous classification of *Hyolithellus***

Since BILLINGS established *Hyolithellus* in 1871, the genus has been assigned to various classes and phyla. Originally *Hyolithellus* was believed to be closely related to *Hyolithes*, and naturally the presence of a hyolithellid operculum was essential in this connection.

As late as in 1959 SYSSOIEV grouped the order Hyolithellida (comprising *Hyolithellus*, *Coleoloides*, and *Coleolus*) and the order Hyolithida in a superorder Hyolithoidea of the phylum Mollusca.

Also a relationship to some worm phylum like the phoronids has been suggested, and this viewpoint is favoured by several paleontologists. FISHER (1962) established an order Hyolithelminthes, comprising the families Hyolithellidae and Torelledidae. He cautiously regarded class and phylum as uncertain, but the entoproctid or phoronid relationship was suggested on account of the phosphatic shell composition.

As mentioned earlier the author's attention has been called to the class Pogonophora, the tubes of which strikingly resemble that of *Hyolithellus*. The resemblance even included the concentrations in the tubes of certain elements.

### ***Hyolithellus* and class Pogonophora JOHANNSSON, 1937**

The following analysis of structures in *Hyolithellus* and the Pogonophora is based mainly on specimens of *Hyolithellus micans*, obtained by elutriation of a Middle Cambrian clay from the island

of Bornholm, and on a 30 centimetres long tube of the pogonophore *Galathealinum bruuni* KIRKEGAARD, kindly furnished by Mr. J. B. KIRKEGAARD.

**Tubular structure:** It is a characteristic feature in *Hyalithellus* that the tubular shell is curved and irregular near the apical end but straightening toward the aperture. The growth angle in the adult section varies from one to four degrees. The cross section is circular, and the diameter may rise to about three millimetres.

This description also perfectly covers *Galathealinum*.

Tubes of *Hyalithellus* show characteristic surface markings consisting of an irregular annulation and transverse striation, considered to be growth lines. The annulations and striae are usually diminutive, but irregularly spaced, coarser markings occur, possibly indicating major changes of growth conditions (text fig. 1b). Interior surface of tube is smooth, devoid of septa or any other structure. The tube is thin-walled at the apical end, but thickens progressively toward the aperture (text fig. 1c).

*Galathealinum* has the same type of surface markings (text fig. 1a), a similar smooth interior surface, and a gradual thickening of the tube wall is also seen. Characteristic in the pogonophore are one to two centimetres long, irregularly spaced sections, in which the annulation is particularly coarse. In the dried specimen of *Galathealinum* the transverse markings on the surface present points of weakness, at which the tube easily breaks. Apart from this, brittle and more soft sections of the tube evidently alternate, at least in some pogonophores. Similar points of weakness are probably also present in *Hyalithellus*, and this may explain, why the fossil fragments rarely exceed five centimetres in length. Fragments of *Hyalithellus* with unusually coarse annulation on the surface have been recorded (WALCOTT, 1890, and LOCHMAN, 1956). WALCOTT thus recognized a variety, *H. micans rugosa*, based on a single tube, which shows coarse transverse ridges and striae, between which are fine longitudinal striae. Similar specimens collected by LOCHMAN show no trace of longitudinal striae, and she was reluctant to refer these specimens to WALCOTT's variety, or to describe them as a new subspecies. The present writer believes that the coarsely annulated hyolithellid fragments may well correspond to the likewise coarsely annulated sections in *Galathealinum*.

LOCHMAN (1956) reported that some thin tubular fragments of *Hyolithellus* show a scattering of oval holes or pores through the lamina of the tube wall. She suggested that this is probably the structure of each individual layer, but superposition of layers in complete tubes gives the appearance normally observed. Despite careful study of the beautifully preserved hyolithellid fragments from Bornholm the author has not been able to find a similar porous structure, and he believes that the pores may possibly be due to imperfect state of preservation, or eventually a result of the method of preparation by etching with acetic acid. Natural pores are not seen in the specimen of *Galathealinum*, but a slightly damaged section of the tube shows mechanically produced holes through the outer lamina.

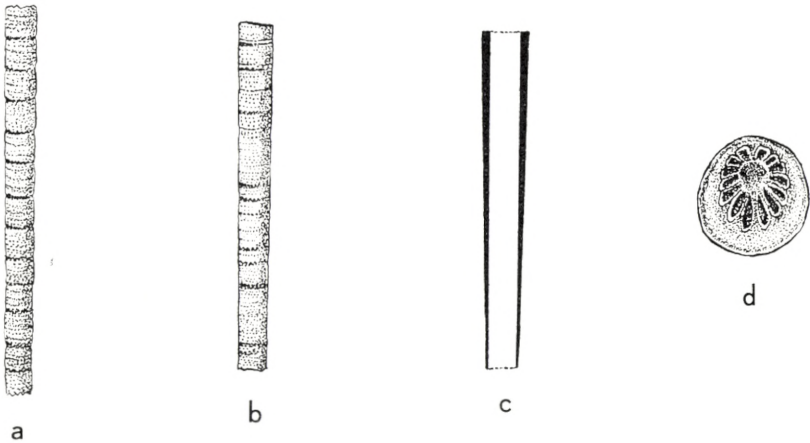


Fig. 1. a: Growth lines on tube-fragment of *Galathealinum bruuni* KIRKEGAARD (2 ×); b: Growth lines on tube-fragment of *Hyolithellus micans* BILLINGS (2 ×); c: *Hyolithellus*, longitudinal section, showing progressive thickening of the tube wall (2 ×); d: *Mobergella holsti* (MOBERG), ventral view, showing muscle scars (4 ×).

The tubular substance: The tube of *Hyolithellus* is composed of many fine laminae, added progressively layer by layer. The thin apical part of the tube thus contains only a few layers. Exactly the same structure is found in *Galathealinum*.

Mr. IB SØRENSEN, cand. polyt., of the Geological Institute of the University of Copenhagen, kindly made X-ray fluorescence analysis on specimens of *Hyolithellus* and the tube of *Galathealinum*. Considering the remarkable results (table 1, p. 12), a

similar analysis of specimens of *Mobergella* was imperative. In order to differentiate the influence of diagenesis in the fossils in the deposit, several specimens of the associated brachiopod: *Acrotreta socialis* were analysed.

The specimens of *Hyalithellus* and *Acrotreta* were collected from the unconsolidated Middle Cambrian clay on the island of Bornholm. Evidently, the deposit, apart from precipitation of some pyrite, can only have been imperceptibly affected by diagenetic processes, and, accordingly, much of the original shell structure of the fossils is preserved. The specimens of *Mobergella holsti* originate from a sample of pure, Lower Cambrian sandstone from the island of Öland.

The tubes of *Hyalithellus* consist mainly of an organic substance and some calciumcarbonate. X-ray analysis shows that no phosphorus is present. A control analysis of a minimal amount of pure phosphate indicates that even extremely poor concentrations or traces of phosphorus will show up. The absence of this element is most unexpected. The specimens of *Acrotreta* and internal molds of hyolithellid tubes from the same deposit show a "normal" concentration of phosphorus. These conditions have caused the author to believe that the phosphate found in hyolithellid tubes from deposits elsewhere is mainly secondary, having replaced the calciumcarbonate, and probably to some extent dependant upon the phosphorus originally contained in the soft parts of the animal, and now preserved in the internal molds of the tubes. The replacement of calciumcarbonate by phosphatic material is a common phenomenon in sediments.

Most probably the tube of *Hyalithellus* consists primarily of thin laminae of organic substance, separated by films of calciumcarbonate. Such texture is found in the pogonophore *Galathea-linum*. The X-ray fluorescence analysis of the pogonophore shows a relatively high content of calcium, but no phosphorus. According to IVANOV (1960, p. 93), the organic substance of the pogonophore tubes is a polysaccharid (tunicin). It is commonly believed that the organic substance in *Hyalithellus* is chitinous, but this cannot be ascertained.

The distribution of other elements needs some comments. *Galathea-linum* contains a small amount of vanadium, iron, and manganese. In the three fossil genera analysed, vanadium is

absent, and they further differ in containing titanium and chromium, which are absent in the pogonophore. These elements originate supposedly from precipitation of mostly iron-rich solutions. In the Middle Cambrian clay from Bornholm, containing *Hyolithellus* and *Acrotreta*, the iron is accompanied by a notable amount of manganese. The sediment is seen to contain some pyrite, which also to some extent has affected the fossils, as some of these show a brownish stain or coating originating from iron.

Cerium, which is absent in *Galathealinum*, accompanied calcium, and partly substituted this element, when subsequently precipitated in the fossils. Cerium may have been present in *Mobergella* and *Acrotreta*, but absent in *Hyolithellus*, when the animals were alive.

After burial, the tubes of *Hyolithellus* and the shells of *Acrotreta* and *Mobergella* were further enriched in potassium and silicium. At the same time the eventual amounts of iodine and sulphur were carried away in solution. Vanadium may, or may not, have been present originally, only to be substituted by chromium and titanium.

*Hyolithellus* and *Galathealinum* are both distinguished by the rich concentration of zinc, which is only very poorly represented in *Mobergella* and *Acrotreta*. In the last mentioned genera the poor concentration supposedly balances with the average concentration of this element in the sea water, when the animals were alive. The pogonophore is rich in nickel, and also *Hyolithellus* contains a surplus of this element, as compared to *Mobergella* and *Acrotreta*. Finally, the hyolithellid tube and the pogonophore tube are distinguished by the absence of phosphorus, and deficiency, respectively absence of cerium. In the present writer's opinion the chemical similarities, pointed out above, support the proposed pogonophoran affinity of *Hyolithellus*.

The X-ray analysis also serves to show that *Mobergella* and its allies, probably primarily phosphatic, are to be regarded as distinct genera, which cannot be referred to as hyolithellid opercula.

The shell material of *Mobergella* differs from that of *Hyolithellus* in the content of calciumphosphate, the surplus of cerium, the pronounced deficiency of zinc, and the somewhat smaller content of nickel.

TABLE 1. Concentrations of elements in the specimens of *Galathealinum*, *Hyolithellus*, *Mobergella*, and *Acrotreta* as registered by X-ray fluorescence analysis.

	<i>Galathealinum</i>	<i>Hyolithellus</i>	<i>Mobergella</i>	<i>Acrotreta</i>
CALCIUM . . . . .	+++	++++	+++	++++
CERIUM . . . . .	÷	+	++	+++
CHROMIUM . . . . .	÷	++	++	++
IODINE . . . . .	++	÷	÷	÷
IRON . . . . .	++	++++	++	++++
MANGANESE . . . . .	+	+++	+	++++
NICKEL . . . . .	++++	+++	++	++
PHOSPHORUS . . . . .	÷	÷	++	++
POTASSIUM . . . . .	÷	+	+	++
SILICIUM . . . . .	÷	+	+	+
SULPHUR . . . . .	++	÷	÷	÷
TITANIUM . . . . .	÷	++	++	++
VANADIUM . . . . .	++	÷	÷	÷
ZINC . . . . .	++++	+++	+	+

Relative concentrations indicated by following symbols: ÷ = absent, + = traces or very poor, ++ = poor, +++ = moderate, ++++ = rich. The symbols are only valid for intergeneric comparison. No quantitative distinction between the individual elements is implied.

Summary of conclusions: The occurrence on the island of Bornholm of numerous specimens of *Hyolithellus* in a deposit devoid of discinelloid forms, and the Scanian occurrence of *Mobergella* at stratigraphical levels, definitely separate from levels containing *Hyolithellus* and *Torelrella*, indicates that *Mobergella* and its allies cannot be regarded as hyolithellid opercula. Also the disparity with regard to the diameters of tubes and "opercula", and differences in concentrations of elements in the shells and tubes support a separation.

The genera *Discinella*, *Mobergella*, and *Barella* with regard to pattern of muscle scars show affinities to the Monoplacophora.

In *Hyolithellus* the entire tubular structure is identical to that of recent members of class Pogonophora, which is closely related to the hemichordates. Also the texture of the hyolithellid tube is identical to that of the pogonophore tube. The similarity is further

accentuated by the concentrations of zinc and nickel. In both groups the tubes are believed to consist mainly of organic substance in thin laminae separated by films of calcium carbonate. The available evidence thus favours the reference of *Hyalithellus* to the Pogonophora.

The class Pogonophora is divided into two orders: Athecanephria IVANOV, 1955 and Thecanephria IVANOV, 1955. The orders are classified by differences in the anatomy of the soft parts, and, accordingly, the position of the hyolithellids within the class is open to discussion. The present writer tentatively suggests that a third order: Hyolithellida, comprising the families Hyolithellidae WALCOTT, 1886 (partim) and Torelledidae HOLM, 1893, may be added to the class.

### Biology of the Hyolithellida

It is indeed interesting that the class Pogonophora originated in the Lower Cambrian and has been able to persist up to the present day. Several paleontologists believe that fauna elements living in the deep sea or on the abyssal part of the continental slope may obtain a geologically long life owing to the supposed stable ecology of these habitats. If representatives of animal groups only known as fossils are to be found, they will most likely be inhabitants of the abyssal regions, and evidence at hand shows that these regions do contain relicts. During the Danish Galathea Deep Sea Expedition 1950–1952 the monoplacophore *Neopilina* LEMCHE was found, and this genus belongs to the order Tryblidioidea, which was formerly regarded as a Paleozoic group (Cambrian — Devonian). Also the Pterobranchia (Ordovician–Recent) may be mentioned. The author regards the class Pogonophora as another example. Possibly more relicts are waiting for discovery, and in future work special attention should be directed to the abyssal part of the continental slope.

The majority of the pogonophore species are found between 1500 and 10000 metres of depth, but species of *Siboglinum* are known to range into littoral waters. As the pogonophores are obtained by dredging, mostly at abyssal depths, not too much is known of their habits. They are assuredly benthonic, leading a sedentary life in the bottom ooze, never leaving their tubes,

which apparently have an upright position, with the irregularly curved apical end buried in the ooze. The larval development is known only in a few species. In these the eggs are hatched in the female tube in the section close to the aperture, and also the larval development takes place in the tubes. The larva probably only leads a brief free existence, before starting the building of the tube.

The hyolithellids occur in practically all types of sediments, but are not too common in sandstones or siltstones, unless they are argillaceous, and they are very rare in dolomites and gray-wackes. Like the pogonophores the hyolithellid tubes were most likely anchored in an upright position with the apical end buried in the soft bottom. The uncommonly wide distribution of *Hyolithellus* has been explained by the wide tolerance as to facies, and furthermore a planktonic larval development has been suggested. The present writer is of the opinion that a tolerance also of depth may be assumed, and pathways of migration may have crossed depths, which would present unsurmountable obstacles to the common shallow water fauna.

The hyolithellids may be regarded as the scarce shallow water representatives of the Cambrian pogonophores, predominantly occupying the abyssal regions, which are not represented in the sedimentary record. As stated by LOCHMAN, the nature of *Hyolithellus* is such that several species may be present, but a differentiation has not yet been possible.

Considering the fact that other groups with hemichordate affinity (Pterobranchia) appeared in the early Ordovician, the occurrence of Pogonophora in the Cambrian must be regarded as very probable.



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