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The reconstruction of “*Hyolithes kingi*” as annelid worm from the Cambrian of Jordan

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With 10 plates and 24 text-figures

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Abstract

Hyolithes kingi from limestones of the Lower Cambrian exposed at the NE-shore of the Dead Sea in Jordan is a characteristic hyolith that produces a *Salterella* as apical fill structure of its tube. In its systematic position, *Hyolithes kingi* can be placed between the genera *Circotheca* and *Orthotheca* of the hyolith family Orthothecidae, but produces fossils that have received the name of *Salterella* when reworked. *Volborthella* and *Salterella* have been placed together in an own phylum separate from hyoliths which were considered a class of molluscs or also an own phylum. The data assembled here indicate that hyoliths like *Hyolithes kingi* were no molluscs, no separate phyla, but can be connected with Annelida. Possible life cycle and soft-body reconstruction are provided, based on observations carried out on a number of different living tube-forming polychaetes. Hyoliths are here considered as own, extinct group of the Annelida Sedentaria.

Zusammenfassung

Hyolithes kingi aus unterkambrischem Kalk des Nordostufers des Toten Meeres (Jordanien) erweist sich als typischer Hyolith, der allerdings im hinteren Teil seiner Wohnröhre eine Füllstruktur erzeugt, die bei Abrollung und Umlagerung der Röhre als *Salterella* übrigbleibt. *Hyolithes kingi* kann im System zwischen den Gattungen *Circotheca* und *Orthotheca* der Hyolithenfamilie Orthothecidae eingeordnet werden. Ihr Umlagerungsprodukt *Salterella* ist zusammen mit *Volborthella* allerdings zu einem eigenen Stamm der Invertebraten erhoben worden, der von den Hyolithen getrennt gesehen wird, wobei letztere teils als eigene Klasse der Mollusken, teils als eigener Stamm angesehen werden. Es werden hier Argumente zusammengetragen, mit deren Hilfe belegt werden kann, daß Hyolithen wie *Hyolithes kingi* keine Mollusken waren. Der Vergleich mit einer Anzahl heutiger Röhrenwürmer ergibt, daß Hyolithen sowie Volborthellen und Salterellen keine getrennten Stämme der Invertebraten darstellen und am ehesten den Anneliden angegliedert werden können. Unter der Ausnutzung verschiedener Eigenarten der röhrenbildenden Polychäten lassen sich der Lebenszyklus und die Weichkörperorganisation von *Hyolithes kingi* rekonstruieren. Hyolithen werden als eigene, ausgestorbene Einheit der Annelida Sedentaria angesehen.

1. Introduction and Geological Frame

Deposits containing abundant remains of organisms that had produced conical tube-like conches with or without internal apical fill structures formed in many places of the world during Lower Cambrian times. The fossils have been described under a number of names based on the three factors of:

1. original composition
2. preservation and degree of completeness when embedded in the sediment; mode of deposition
3. diagenetic history and that of the rocks containing them.

Names like *Volborthella*, *Salterella*, *Hyolithes*, *Orthotheca*, *Circotheca*, *Biconulites*, *Coniconchia* and others are used and more are to be found in literature.

Geologists and paleontologists concerned with representatives of this group of Lower Cambrian fossils have placed them in a group with members of very different parts of the invertebrate section of the animal kingdom. *Salterella* and *Volborthella* have long been considered to represent ancestral forms of cephalopods (CLARK 1925; SCHINDEWOLF 1928, 1934; POULSEN 1932). HANAI (1957) thought that rostra of Cretaceous belemnites contained a *Salterella*-stage as recapitulation of phylogenetic precursors of these cephalopods.

NAEF (1924, 1926) considered *Hyolithes*, *Salterella* and *Volborthella* to belong to the extinct mollusc class Odontomorpha. He had revived ideas of NEUMAYR (1879) and had worked them out in greater detail, which resulted in a hypothetical reconstruction (NAEF, 1924, fig. 12 c-d). MAREK & YOCHELSON

(1976), without consulting NAEF's work, also reached the conclusion that hyoliths are molluscs but that *Salterella* and *Volborthella* should be excluded. YOCHELSON (1977) presumed that the latter genera represented members of an extinct phylum which was given the name Agmata. GLAESSNER (1976), in contrast, reconstructed *Volborthella* as an agglutinated tube of a sessile annelid. RUNNEGAR (1980) thought that hyoliths represented organisms which were organized in a similar manner to siphunculoid worms. Forms of some of the members of the phylum Hyolitha of RUNNEGAR appear in the ancestorship of the cephalopods in DZIK's scheme (1981). DZIK called his hyoliths with chambered tubes "Conicochia". However, according to LYASHENKO (1957), this was the term for a group of fossils which included hyolithids and tentaculites and represented a class of molluscs. FISHER (1962), moreover, considered this to be an unfortunate placement and subsequently created the tongue-twister "Calypptomatida", a term which was to encompass hyoliths. He regarded hyoliths as a molluscan class distinct from all others. It can therefore be concluded that hyoliths and related forms have found almost as many names and places in the natural system as people have worked with them.

Beds with well preserved fossil remains of a representative of this controverse group of Upper Lower Cambrian organisms were found at the shore of the NE end of the Dead Sea (Jordan). They provided a welcome opportunity to tackle the problem of classification. In regard to the question of the evolution and phylogeny of conchiferan molluscs (BANDEL, 1982), hyoliths and related forms are puzzling. Organisms that produce these charakteristic fossils appear in the geological records earlier than undisputed conchiferan molluscs, such as bivalves, gastropods and cephalopods. Hyolithes were found as early as in pre-trilobite faunas at the very base of the Cambrian (RUNNEGAR et al, 1976) while undisputed conchiferans appear higher up in the Lower Cambrian (RUNNEGAR, 1985).

In the field, *Hyolithes kingi* closely resemble molluscan fossils such as Silurian orthoceratids; but their chronological appearance preceeds that of unquestionable conchiferans by several tenths of million years.

A closer look at the well preserved fossils from the shore of the Dead Sea provided much data that did not fit into the old idea of molluscan relationship as expressed in literature from relatively early times (BARRANDE, 1867) up to the present day (DZIK, 1982). In a more recent approach, molluscs and worms that produce features similar to those found in *Hyolithes kingi* were studied: in the Mediterranean region at the Laboratoire Arago (Banyuls-Sur-Mer), from the Atlantic Ocean (Bretagne, Bermuda), the Caribbean Sea (Columbia, Santa Marta) and the North Sea (Belgium). It soon became evident that annelid worms provide a better model for the reconstruction of *Hyolithes kingi* than molluscs can and that the model can also provide a means of connecting many of the different conical fossils of the Lower Cambrian within the same group of organisms.

Geology

Cambrian rocks are extensively exposed in southern Jordan and along the fault line which represent the eastern border of the Dead Sea/Wadi Araba depression. The northernmost outcrops lie just to the north of the mouth of the Zarka Máin River, at the shore of the Dead Sea.

Cambrian deposits mainly consist of sandstone with intercalated siltbeds. Carbonate rocks are to be found only in the outcrops near the eastern shore of the Dead Sea whereas they disappear further to the south due to change of

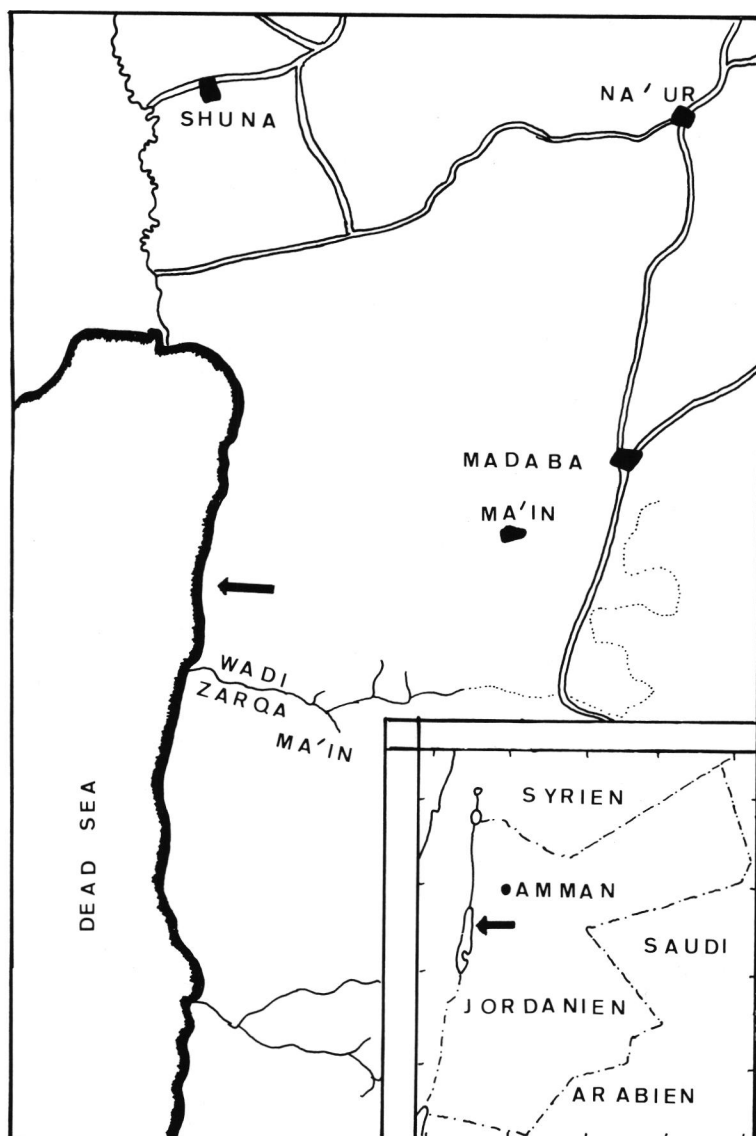


Fig. 1: Index Map. Arrow indicates the outcrop with the section shown in Fig. 2.

facies. The limestone unit was discovered by HULL in 1886. He called it the Wadi Nasb Limestone. In it, CAMPBELL found a fauna and gave it to KING (1923) to be described. The latter author noted that some of the rocks consisted predominantly of hyolith shells. Later BLANKENHORN (1930) collected fossiliferous samples which must have come from about the same locality as is featured in this study. BLANKENHORN gave his fossils to R. & E. RICHTER (1941) who described the fauna. WETZEL (1947) and QUENNELL (1951) changed the name of the unit to Burj-Limestone because of its outcrop at the SE end of the Dead Sea near the town of Ghor Safi. The outcrop at El Burj was also visited by BLANKENHORN (1912, 1914); R. & E. RICHTER (1941) also studied the fossils he collected there. According to these authors and to PICARD (1942), the limestone unit of the Wadi Nasb (Burj) Limestone is of Late Lower Cambrian age.

The fossils in this study were collected from a succession of limestone beds of the Wadi Nasb Limestone exposed at the beach of the Dead Sea, about 1 km to the north of the mouth of the Wadi Zarka-Ma'in (Fig. 1). The base of the outcrop exposed in the beach gravel of the Dead Sea consists of silty crossbedded fine sandstone. It is overlain by less than 2 m of sandy limestone which ends in a laminated sparitic limestone Fig. 2 (a). The following, strongly bioturbated nodular limestone is overlain by a 40 cm thick shaly marl. 4 to 5 limestone beds are intercalated into the marl and have provided the fossils described here (Plate 1, fig. 1). The unit is covered by 50 cm thick limestone of coarsely crossbedded structure which contains numerous remains of trilobites. A crossbedded sandstone follows which is overlain by sandy flaser beds with layers of clay pebbles and crossbed inclination in various directions. Bedded and crossbed-

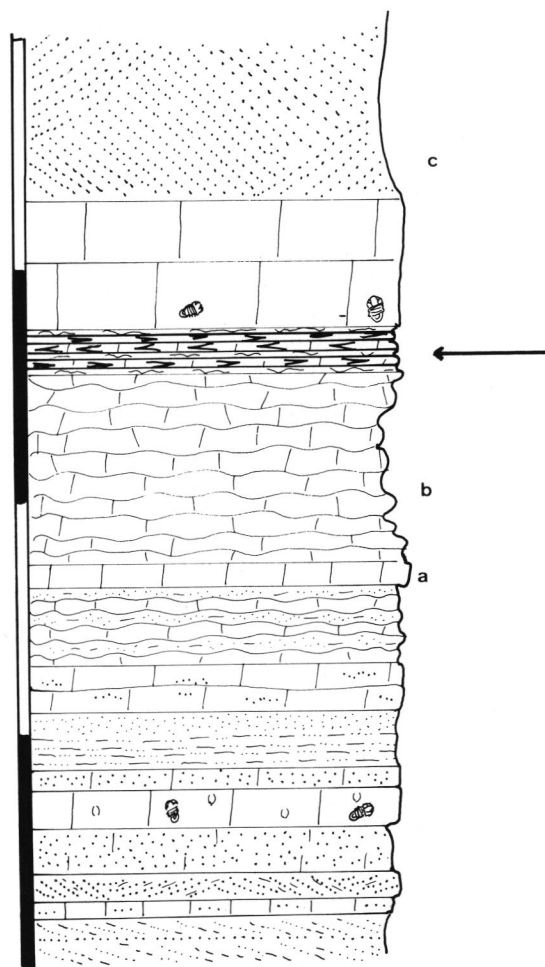


Fig. 2: Section of Lower Cambrian strata exposed just to the north of Wadi Zarqa Ma'in along the shore of the Dead Sea. The base is formed by crossbedded sandstone, bioturbated sandy and fossiliferous limestone and a hard limestone bed (a). Above lies a totally bioturbated nodular limestone (b). The beds that contain *Hyolithes kingi* are indicated by the arrow. Crossbedded limestone with abundant trilobite remains follow above, overlain by sandstone (c). On its surfaces, trilobite trails and meandering trails are common. Each bar (left) represents one metre.

ded sandstone with many trace fossils follow. Above the 10 m thick sandy series there is another crossbedded, coarse-grained, fossiliferous limestone unit. Above it, only massive sandstones are exposed which reach up to the truncation surface formed during the Late Paleozoic and are covered by Permian-Triassic sediments (BANDEL & KHOURY, 1981).

Paleoecology and sedimentology of hyolith beds

Thin sections of limestones containing hyoliths consist of coquina of tubes which lie in a matrix of fine carbonate in which some angular sand grains and silt-sized terrigenous particles are intermixed. While the majority of larger hyolith tubes are oriented in only one direction, smaller biogenes and sediment particles between them have been rearranged in a random pattern by bioturbation. Bioturbation was also strong in the rock-units below hyolith beds. The hyolith limestone beds themselves are interbedded with shale and marl. The unit above consists of crossbedded biogenic calcareous sand in which the primary sedimentary structure has not been destroyed by burrowing endobenthos.

The vertical sequence represents a shift of the depositional environment from the shallow sublittoral sea and a total turnover of the bottom substrate by bioturbation to intertidal deposits, in which the benthos affected only fine sediment particles, to crossbedded supratidal beach deposits without bioturbation.

The totally marine nature of the hyolith limestones is documented by their fossil content. Apart from the dominant *Hyolithes kingi*, remains of skeletal elements of trilobites, mainly exuvia, are very common. Other biogenes consist of fairly large spicules of sponges and tabular fragments of echinoderm skeletons (Plate 1, fig. 4). Faecal pellets and some cellular skeletal calcareous particles of problematic derivation are also common (Pl. 1, fig. 3). The original porous structure of the echinoderm fragments is commonly preserved because the pores had been filled with a fine non-calcareous mud (Pl. 1, fig. 4). Calcareous fossils were recrystallized during diagenesis, while phosphatic trilobite remains retained their original structure. Many of the latter were marginally affected by microboring organisms such as endolithic algae or fungi.

The tubes of *Hyolithes kingi* can be found in quite different states of preservation. This reflects variations in their predepositional history until they were finally buried in the sediment. Many tubes are well preserved, some still have the operculum near to its original place within the tube (Pl. 1, fig. 2). The animals died at the place of their deposition. Death and sedimentation of *Hyolithes kingi* are connected. The presence of tubes and opercula of all sizes indicate that living place of animals of all ontogenetic stages and the place of their burial in the sediment were close.

It is common for several tubes to have been pushed into each other and transported together as composite units of 2 to 6 individual shells (Pl. 2, figs. 7 and 8). The tubes must have been empty when they were washed together and when moving about with the currents. Other tubes were eroded and fractured, in some cases to such a degree that only apical, more solid parts survived while most of the actual walls were destroyed prior to emplacement in the sediment.

Other tubes and tube composites are totally, partly or locally filled with sediment particles cemented by a ferruginous matrix. This material is more resistant to etching with acidic acid than normal rock matrix and may produce steinkerns (internal moulds) in the process. Internal moulds of this kind with hardly any shell connected to them were sometimes embedded in the limestone.

Sediments with hyoliths within them were eroded and hyoliths redeposited. Within this sediment a reducing condition resulted in the deposition of originally pyritic ferruginous cements in the tubes or in parts of them. This matrix was later altered to oxides during redeposition of the hyoliths or during later diagenesis.

A present-day model for the deposition of *Hyolithes kingi* coquinas in the Lower Cambrian Sea on the Northern shore of the African (Arabian-Nubian) continent exists in the shores of the North Sea on the Belgian coast. *Hyolithes* is replaced by *Pectinaria*, a vagile tube-worm. Large numbers of these individuals periodically dwell within the sediment in the lower intertidal and in the sublittoral area.

During storms or incoming tides with extended periods of unusual current directions, these worms are exposed, washed out from the bottom substrate and transported shorewards. Tubes which have been washed out of the sediment but do not contain any animals unite until up to 6 move together by getting pushed into each other. They roll from one ripple valley to the next during their slow migration.

Tubes with animals inside, on the other hand, move alone. All of them may be piled up to form a bed consisting predominantly of *Pectinaria* tubes.

All tubes are orientated parallel to the shore and vertical to the direction of the current. They thus migrate across the tidal flats until they are rolled onto the beach in the uppermost eulittoral. Live animals usually die within the coquina and the whole deposit can be covered by sand when the next tide comes in or by wind. When the tide is in, the fine particles are churned around due to the bioturbation created by small animals such as worms and crabs, while the larger tubes remain unaffected. Below the sediment surface oxygen is consumed rapidly; the sediment itself then turns black due to the deposition of minute crystallites (framboids) of pyrite. A later incoming tide may uncover pyrite encrusted black tubes and tubes filled with unconsolidated sediment and redeposit them along with fresh tubes. The final deposit of *Pectinaria* coquina contains tubes that still hold remnants of the animal, others that were pushed into each other, also tubes that have been eroded by the current while others were redeposited. On a shore with calcareous sand, deposition of this kind would result in rocks similar to those containing *Hyolithes* instead of *Pectinaria*.

2. *Hyolithes kingi*

Historical account

PICARD (1942) determined a *Hyolithes fuchonensis* var. *moabiticus* from the Cambrian limestone of the Dead Sea, the same specimens that were described as *Hyolithes (Orthotheca) kingi* by R. & E. RICHTER (1941), a year earlier. The description and diagnosis according to R. & E. RICHTER (1941) translated from German is as follows: "It is a species of *Hyolithes (Orthotheca)* with a round diameter, straight sides and an apical angle of about 10 degrees. A collar-like thickening of the shell is found within, and the apical end is bluntly rounded."

R. & E. RICHTER, also noted that the outer surface of the shell is smooth, that larger individuals measure about 10 mm in length, and that a spherical "initial chamber" may exist. They found that there was no operculum and that the apertural edge of the shell had always been broken. The hyolith from the Dead Sea was grouped with *Orthotheca* because it is round in diameter. It could be differentiated from other species of this genus by characteristic points: 1) straight shell sides; 2) absence of septa; 3) apical angle. As will be shown below,

only the latter point may apply, and only to a certain extent. It is thus possible and even quite likely the *Hyolithes kingi* is only a synonym for another older species name given to individuals found at another locality. For reasons of convenience the name *Hyolithes kingi* will be used through this study for the hyoliths from the Cambrian of the Dead Sea.

R. & E. RICHTER noted and illustrated that shells of several individuals are often preserved with their shells pushed into each other. The figures on plate 1 leave no doubt that the fossils to be described below in detail and *Hyolithes kingi* were produced by the same type of organisms which also belonged to the same species. From Wadi Saramudsh (SE of the Dead Sea) R. & E. RICHTER described another hyolith of 2.5 cm length with 3 septa. They noted that the only difference between this *Hyolithes* sp. and a *Salterella* was the absence of the central tube ("Sipho"). It is quite likely that *Hyolithes* sp. represents a more completely preserved specimen of *Hyolithes kingi*.

External shape

Smallest conchs encountered in the fossil material consist of tubes with a well rounded apex of 0.1 to 0.2 mm width (Fig. 3). The 1 to 1.2 mm long conch shows an apical angle of about 10 to 12 degrees (adapical of the rounded end).

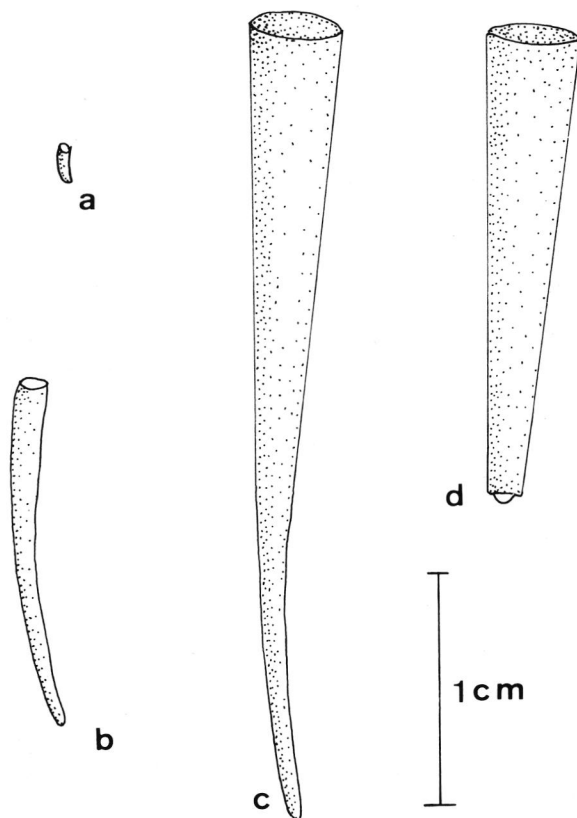


Fig. 3: Outer morphology of the shell of *Hyolithes kingi* in a sketch with earliest ontogenetic stage (a), juvenile (b), exceptionally completely preserved adult tube (c) and usual adult tube with apical portion broken off during life (d).

Larger conchs often show regular light curvature up to a length of about 15 mm and apertural width of about 1 mm (Fig. 3 and 4). The angle of expansion of the walls of the conch (apical angle) is very low here and the walls are almost parallel to each other. Other conchs with the same dimensions may be straight or almost straight, the curved ones are however more common (Fig. 4).

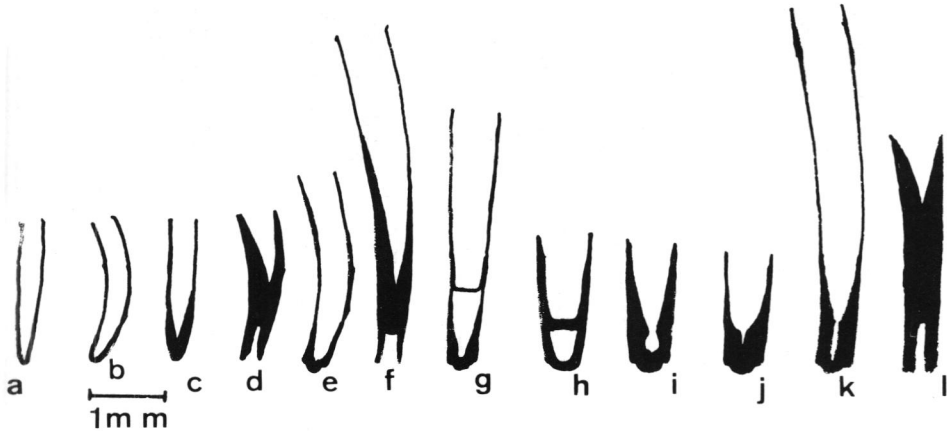


Fig. 4: Redrawn sections of *Hypolithes kingi* that demonstrate the internal fills of apical tube portions at different stages of ontogeny (a-c). Tubes of young individuals (c), show the beginning formation of a constriction due to internal shell deposition. Such deposits characterize d to l. In case d, f and l, the tube was broken off apically to a septum, while in e, g, i, j, k, the tube fractured just posterior of the last-formed septum, which is the usual case. g and h represent cases with an additional septum.

Larger conchs with a diameter of more than 1 mm usually turned into straight cylinders with an apical angle of 10 to 12 degrees (Fig. 5). Although some conchs retained the curvature until fully grown, the more common type is straight. Conchs can be up to 37 mm long and 5 mm wide. Their outer surface shows only indistinct and simple growth lines.

The aperture thus retains its simple and oval to round shape throughout ontogeny. Irregularly oval shapes predominate and one of the longer sides is usually less curved, perhaps representing the venter (pl. 2, figs. 7 and 8). In most cases the outgrown conch lost portions formed during earlier life when it became deposited (pl. 2, figs. 1-6). Breakage occurred when the animal was still alive and produced a new apical morphology of which the most common is a straight fracture just apical to the last septum formed within the conch (Fig. 5). The smallest apices to have such a typical step-like margin between the fractured wall and the watch-glass-like convex septum measure 0.3 mm, the largest 1 mm. Often the sharp breakage edge was worn off and rounded. This probably occurred while the animal was still alive and moving in or on the sediment. A less common type of apex is less than 1 mm wide and consists of a fracture which is usually within the curving portion of the conch, apical to the next septum. A pit extending into a short tube characterizes this apex (Fig. 4 d, f, l, pl. 2, fig. 2). Grown individuals measure 20 to 22 mm in length and the 15 mm of curving early portion of the shell is broken off up to a tube width of 1-2 mm.

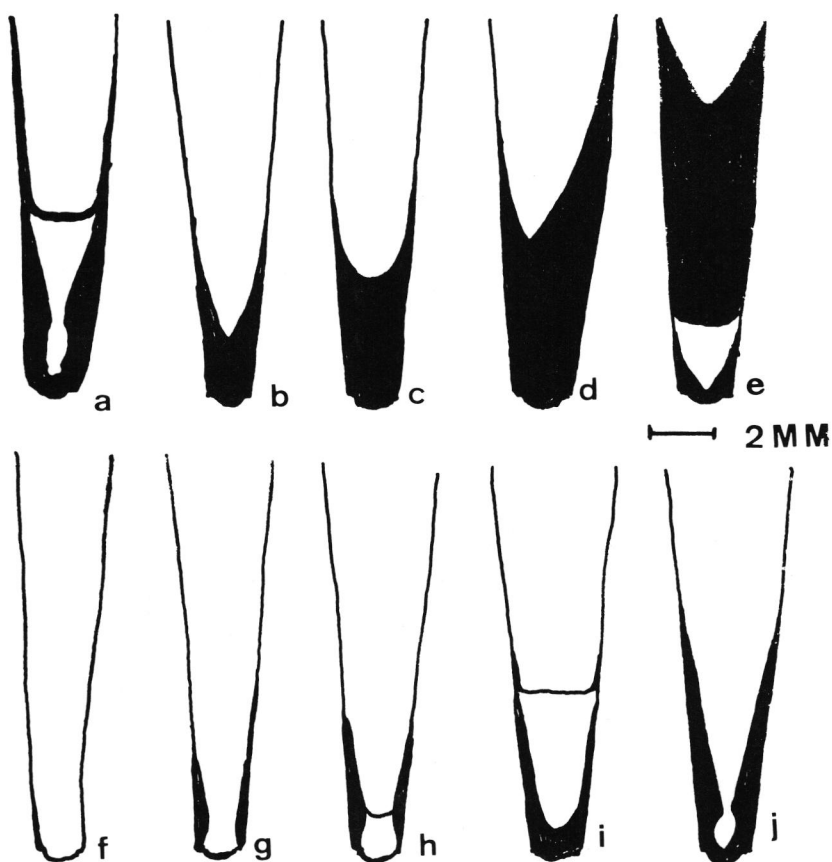


Fig. 5: A) Different stages of internal apical shell additions in redrawn, thin-sectioned tubes of *Hyolithes kingi*. f). No shell additions after septum formation; d) large apical shell refill; b, c, g, j) increasing amount of internal shell additions; a, e, h, i) with additional septum that became covered by shell additions in a and e.

B)

a) A tube with one mm wide aperture is filled by internal shell additions leaving only a 0.2 mm wide central canal filled by sediment and closed with several septa.

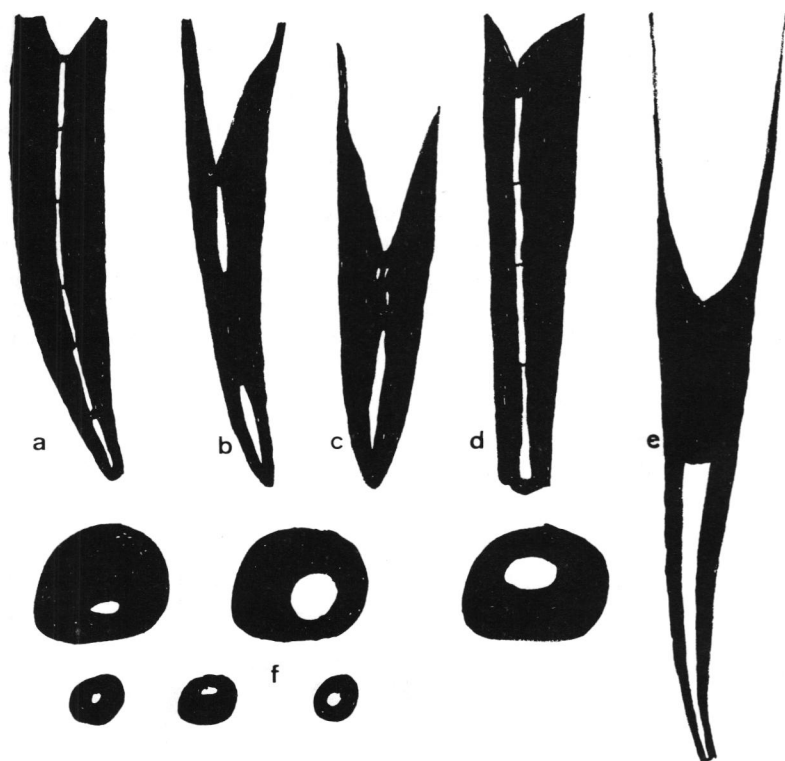
b) The spar cone of this tube is 0.8 mm wide at apertural end and 0.3 mm at apical end. A central tube is partly filled with fine sediment, and here remained visible in thin section.

c) Only sediment-filled central tubes show up from the background of the spar cone. Where sediment had not entered prior to closure with a septum, the cement fill merged with the spar cone during diagenetic recrystallisation of the tube.

d) Central tube preserved in a long spar cone.

e) Tube of 0.6 to 3 mm width and a spar plug covering an upper septum and preserving no central tube, while the cavity of the spar plug covering the lower septum was filled with sediment and thus preserved.

f) Sections vertical to tube axis through apical internal fills show the position of the central canal at variable locations. Smallest 0.5 mm and largest 1.8 mm in diameter.



Internal structure

The apical portion of the tube shows a variety of fill-structures. The most common structure consists of spar cones, but the simplest type of inner shell surface is in unfilled tubes (pl. 3, fig. 2). The smallest shells with up to 1 mm length and an evenly rounded apex 0.1–0.2 mm wide and about the same shell thickness throughout usually remained free of fill structures. Another less common type without apical fills consists of tube ends of more than 0.3 mm in diameter and a broken-off apex. In this case, the new apical end is closed by an evenly curving septum (pl. 2, figs. 5 and 6). It is more common for the apical regions of such conchs to be increasingly filled with calcareous layers until an up to 15 mm long calcareous cone has been formed (pl. 3, fig. 1). The first thickening of the apical wall consists of material added to the inner side of the septum and to the apical sides of the conch. The latter form cones composed of a single mineral calcareous layer with a narrow apical and a wide adapical opening (pl. 2, fig. 1, pl. 3, fig. 2). The thickness of the layers is therefore small at its adapical end and largest (up to 0.2 mm) near the apex, but ends before reaching the septum. The angle formed by the layers of the filling cones increases from about 12 degrees until it then remains between 20 and 30 degrees. Layers piled on top of each other form the apical filling which is therefore of almost radially symmetrical shape, usually 2–15 mm long, and reflects the shape of the external conch. The central apical hole in consecutive layers of the cone decreases in diameter until with about 3–4 layers, it measures one third to one fifth of the conch diameter. The central tube is at first round, later oval with an adapical narrowing until it finally becomes an even cylinder (pl. 3, figs 1–6; Fig. 4 and 5). The deposition of apical filling in all stages of its growth may have

become arrested and conserved due to the adapical construction of a septum that sealed off smaller or larger portions of the apical conch (pl. 2, fig. 3; Fig. 4 and 5). The central tube only rarely lies in the exact centre of the conch, more often its position is subcentral or submarginal. In more apical parts the central tube itself is usually sealed off by septa which may have closed off very fine grained sediments within the shut tube section (pl. 3, fig. 4).

Operculum

Opercula of all growth stages from 0.4 to 4 mm width are common. Several opercula were found within the conch, more or less in their natural position (pl. 1, fig. 2; Fig. 6). The operculum consists of two parts, the outer round to oval lid and two inner tooth-like processes, one the reflected image of the other. The



Fig. 6: Sketch of thin sections of *Hyolithes kingi* tubes with operculum still present at the inner filling.

smallest opercula (0.4–0.5 mm in diameter) have smooth symmetrically outward bulging lids. (Fig. 7a; pl. 4, fig. 3). Larger opercula retain the round lid-shape but show growth increments of different thickness. On the side of the lid on which growth increments are narrow, the rim becomes successively thickened from within and added surface is straight or slightly concave. On the opposite margin the lid shows the widest increments of growth. The lid is thin at this place and its edge is bent upwards. At lateral margins, growth increments are of intermediate width, the lid is moderately thickened from within and straight or slightly bent up. A fold thus crosses the lid from right to left, separating a lower from an upper part of the operculum.

The teeth-like projections are placed so that their longaxis follows the symmetrical axis (pl. 4, fig. 1, 3). Both processes consist of two thickened prongs connected to each other by thin walls. Prongs near the slow growing margin of the lid are almost vertical and form an angle of 50 to 70 degrees. They do not change their position during growth of the operculum, but become thickened and wider. At first they are of round shape and about as long as the lid is wide. During enlargement the width remains stable in relation to the operculum diameter, but the projecting ends are widened and form flattened sides which

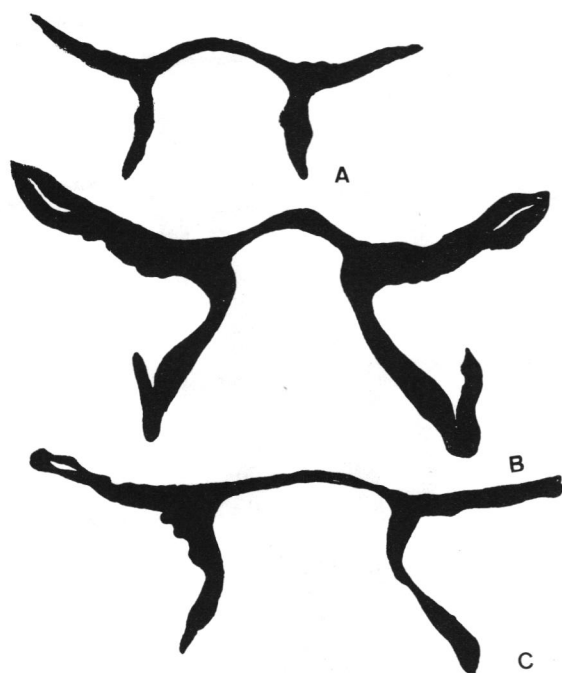


Fig. 7: Sections of opercula of *Hyolithes kingi* redrawn. All have been cut vertically to the lid surface such a way that teeth-like projections remain symmetrical. A) simplest and youngest operculum; B and C) larger opercula with more complex and thickened structure of the projections.

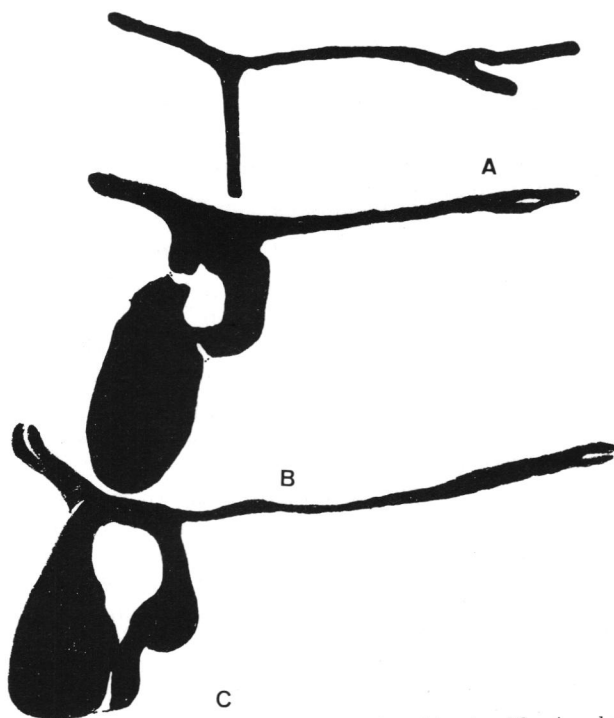


Fig. 8: Transversal sections of opercula of *Hyolithes kingi* with simple projections in young individuals (A) and more complex ones in older individuals (B to C).

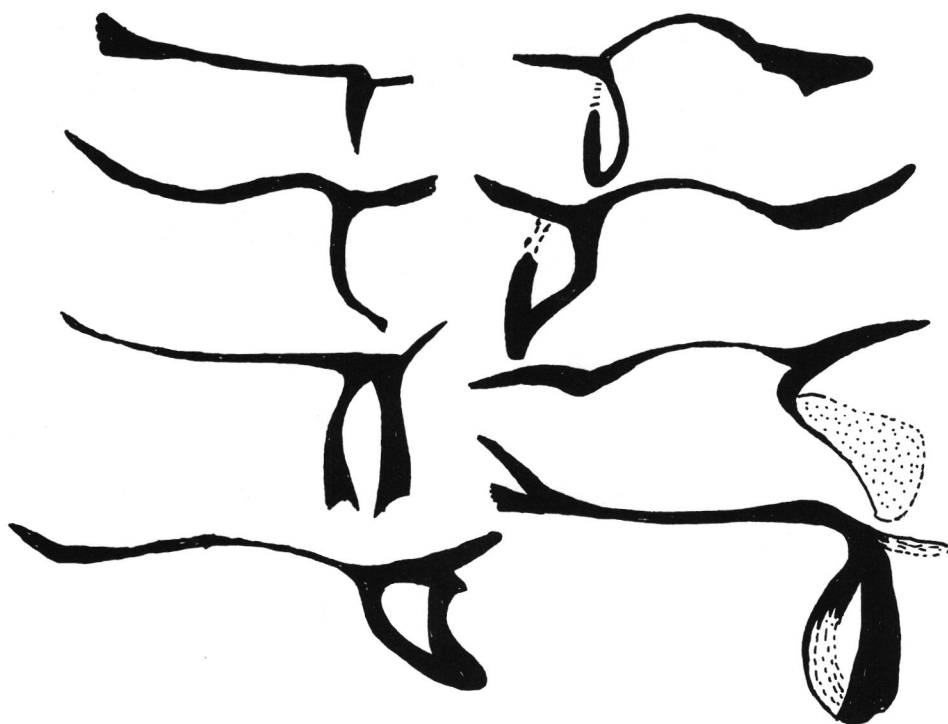


Fig. 9: A series of sections through opercula of *Hyolithes kingi* redrawn to demonstrate the variations of the lid margins and curvature of lid rims with complexity and variability increasing with size.

develop into concave depressions. The opposite prongs grow with the fast growing side of the lid and thus change their location on the operculum. They incline forwards and outwards. Both prongs and lid become thickened by added calcareous layers and only in the space between the projections, little or no shell is added (Figs. 6-9; pl. 4, fig. 1-3).

Ontogeny of the tube

When benthic life begins a blind-ending tube is secreted. This narrow conical conch of 1 - 1.2 mm length, 0.2 to 0.4 mm width and well rounded closed apical end is consolidated by the secretion of an evenly thick calcareous layer.

The head portion of the animal produced an umbrella-like lid with solid stalks. The tissue is connected to this operculum along the rim of the lid and surrounds the stalk, so that growth can develop along lid margins and lower sides as well as on the projections of the stalk.

The mobile animal can now close its aperture by withdrawing into its tube and shutting it with the operculum at the aperture or somewhat behind it. It starts feeding. The shell is enlarged and at the same time shell material is deposited on the inside near the apical end of the shell. Walls are secreted at this point which eventually decrease the diameter of the shell lumen to a third or a fifth of its original width. Into this central or subcentral to marginal apical tube the thin posterior end of the soft body of the animal can be extended and anchored, thus providing the maneuverability of the creature in the anterior portion of its body. The thin tube holding the thin posterior end of the creature is about as long as a fourth to a third of the extended animal. The conch is

enlarged in relation to the growth of the soft tissue of the animal living within. When the shell growth at the aperture is more rapid than apical shell filling, a septum is produced to seal superfluous apical room. Septa are usually secreted where the apical fill structure ends. The conch is predestined to fracture at this point when the animal is washed about by the currents or when it moves through the sediment. Breakage can also be due to borings of shell-penetrating organisms (algae, fungi, etc.) that can no longer be sealed off from the tube behind the septa. Septa also close other portions of the apical lumen and often shut off detrital material or fine particles. During conch growth the operculum also increases in diameter and thickness. Shell additions change the outer shape from bulging symmetrical to straight with an upper fold. The lower side of the operculum stays stable in its position on the tissue, whereas the upper side increases more strongly in width. Both tissue and operculum increase in length. Ventral and dorsal position of the tube is also indicated by less strongly bent sides that probably lay on the sediment. When the animals reached maturity they produced a 3.5 cm long conch of a maximum thickness of about 5 mm. In this conch only the anterior 1.5 cm of tube are open and provide shelter and a living chamber for the animal. The abdominal portion of the animal extends into the thin tube produced due to secondary internal shell thickening. Most animals live in about 2 to 2.5 mm long shells. Their posterior portions were broken off during the course of ontogeny. Others may have had to carry their whole shell in which all apical portions were sealed by consecutive septa except the actual living tube as in other individuals. Living environments consists of carbonate sand in agitated, sublittoral shallow water in fully marine conditions.

3. Comparisons with other Groups of Invertebrates

Salterella and *Volborthella*

Salterella and *Volborthella* are to be found in rocks of the same age as *Hyolithes kingi* and have been classified as conical macrofossils. Their sizes range from between 1 to 7 mm in length and 0.5 to 1.5 mm in width. Their construction is quite uniform, their composition, however differs. Whereas the typical *Salterella* consists mainly of calcium carbonate, *Volborthella* is mainly made up of non carbonate silt- and sand-sized grains. Both are of simple conical shape and consist of internal layers diverging from a narrow central to subcentral tube.

Carbonaceous *Salterella* BILLINGS, 1861 was described earlier than silicious *Volborthella* SCHMIDT, 1888. Both fossils – independently of each other – were considered to represent early molluscs. CLARK (1925) and POULSEN (1932) interpreted *Salterella* as the remains of primitive cephalopods. SCHINDEWOLF (1928, 1934) classified *Volborthella* as the oldest and most primitive nautiloid cephalopod. KOBAYASHI (1937) united *Salterella* and *Volborthella* as related forms of Cambrian fossils that intermediate between hyoliths and nautiloids, but are to be considered as closer to the latter. TEICHERT (1964) placed both genera into the order Volborthellida. KOBAYASHI (1937) placed them close to the molluscs, but cautiously referred to them as doubtful taxa.

YOCHELSON (1977, 1981) revived the opinion expressed by GÜRICH (1934) in the case of *Volborthella* and considered *Salterella* to stand apart from other Cambrian fossils. YOCHELSON thought that this genus was so different to other fossils that it would be appropriate to designate a new phylum for it; the Agmata. YOCHELSON (1983) proposed that *Volborthella* from the Baltic region and *Salterella* from Scotland may be remains of the same organism which had only been affected differently by diagenesis. The author had noted all degrees of

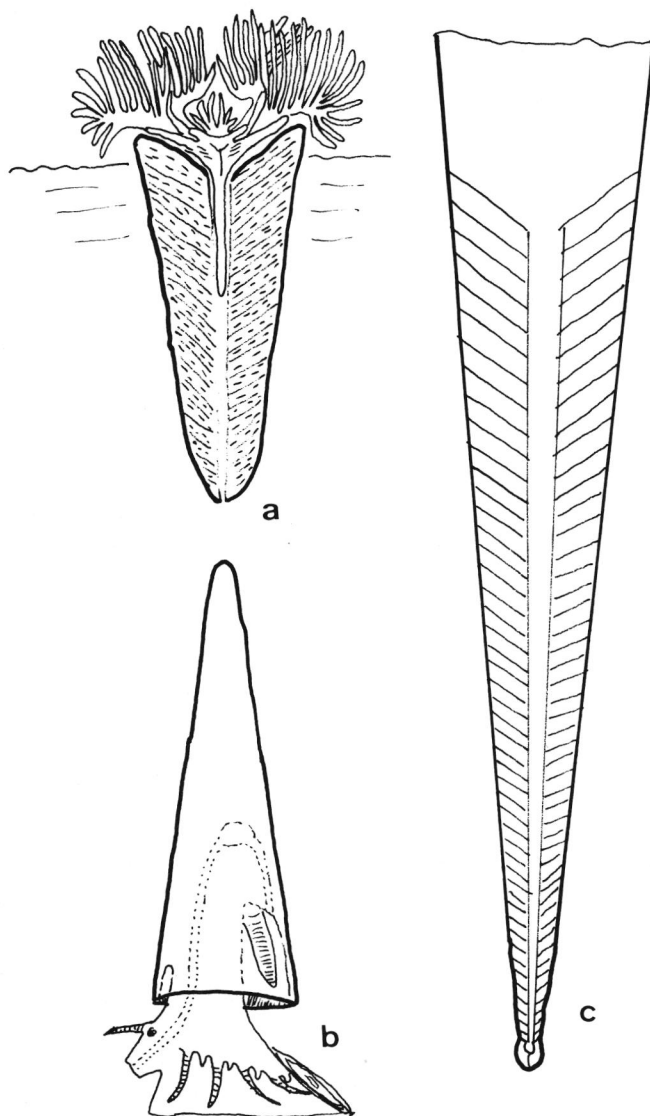


Fig. 10: *Volborthella* (a, c) and *Hyolithes* (b) reconstructed as suspension feeding benthic worm by GLAESSNER (1976) (a), as untorted but otherwise archaeogastropod-like mollusc by NAEF (1913) (b), as buoyant nautiloid cephalopod by SCHINDEWOLF (1934). (Re-rrawn and slightly modified from Figs. 1 A (a); 12 d (b) and Abb. 1 (c) of cited authors).

interrelations between the two fossils with cone in cone structure ranging from purely calcareous to purely non-calcareous composition. In his 1983 paper he therefore withdrew his statement of 1977 that *Volborthella* and *Salterella* might possibly represent two families of the new phylum Agmata, 1981. He then considered them to be congeneric and diagenetic alterations of more or less the same original.

GLAESSNER (1976) in contrast, reconstructed *Volborthella* as a product of annelid worms, following ideas expressed by LIPPS & SILVESTER (1968). GLAESSNER reconstructed *Volborthella* as tube and holdfast of a suspension

feeding polychaete worm that in a general sense is comparable to modern sabellariid worms (Fig. 10a). He thought that the actual *Volborthella* portion of the worm was an anchoring device which helped the worm in its living environment of shifting silts and sands. Only the caudal appendage of the worm was reconstructed as extending into the central tube of the cone.

The different "species" of *Salterella* are based on outer shape; i.e. bullet-shape, slim, curved (YOCHELSON, 1977). Inclination and spacing of the laminae were sometimes also considered to represent specific characters of species, their variability was however noted at a later date (YOCHELSON, 1981, 1983). There is also a wide variation in composition ranging from purely calcareous to purely non-calcareous materials.

It was possible to study *Volborthella* from its original place of description, the Lower Cambrian of Estonia near Reval (Tallinn) in the Baltic Region of the USSR and to prepare thin sections from a material collected by Prof. Dr. E. Voigt (Hamburg) and made available for study by Dr. W. Weitschat (Hamburg) (pl. 5, fig. 2, 4, 5).

Conical fossils are preserved in a silty sandstone with sedimentological features characteristic of intertidal environments such as crossbedding on a minor scale and desiccation cracks. This reinforces SCHINDWOLF's (1934) interpretation of a deposition of the *Volborthella* layers within the realm of the intertidal zone. Here *Volborthella* is concentrated in 1–2 cm thick coquinas composed of 1–7 mm long cones with a maximum width of 1.5 mm. The apical (narrow) end of these cones is always blunt and its apertural (wide) end is concave, occupied either by a wide or by a narrow depression. In the thin section typical laminae as well as a central to subcentral canal is quite visible, as in the illustrations of GÜRICH (1934, pl. 12) and SCHINDEWOLF (1934, pls. 17, 18, 19). In the Baltic material not only lamina filled cones are preserved but also a sediment-filled room apically of these (pl. 5, figs. 2, 4).

Laminae of *Volborthella* are less inclined than those found in *Hyolithes kingi* but otherwise these cones closely resemble apical fragments of the *Hyolithes kingi* tube in structure and size but not in composition. There is a slight possibility that the silt laminae are replacements or fillings of originally calcareous shell material or hollow chambers. However, if this is the case, the diagenetic change would have to have taken place before the final emplacement of the fossils. It is more reasonable to assume a primary composition of aragonitic material agglutinating silt particles.

The *Salterella* studied was kindly provided by Dr. ELLIS YOCHELSON (Washington). Some rock samples containing typically preserved *Salterella rugosea* BILLINGS from the Lower Cambrian of the Appalachian mountains in the USA revealed in thin sections structures just like those described and illustrated by YOCHELSON (1970, 1977, 1981; YOCHELSON et al, 1970; GRIFFIN & YOCHELSON, 1975). *Salterella* is an up to 9 mm long conical fossil with an apical angle of 8–9°. The wide (apertural) end shows a cavity with approximately the same depth as width. Laminae composing the cone are preserved as relicts included in large crystals of calcite. Predominantly apical layers meet with smaller angles than predominantly apertural ones. Thus inclination of the laminae decreases in apertural direction. The central to submarginal tube remains unfilled by laminae (pl. 5, fig. 1, 3). In some specimens laminae have been destroyed by recrystallisation. The structure, size and composition of the fossils closely resembles that of apical fills of *Hyolithes kingi*.

It is now possible to employ YOCHELSON's (1977) statement that a separate phylum for *Volborthella* and *Salterella* is no longer justified when these fossils

can no longer be considered different from others. The filled apical portions of the tube of *Hyolithes kingi* is composed in all essential features as that of *Salterella/Volborthella*. Diagenesis has obliterated individual laminae by recrystallisation, but growth and mode of lamina deposition of the apical tube portions can be reconstructed by comparing different individuals of *Hyolithes kingi*. These fossils, in thin section, leave no doubt that their original internal structure was laminated. If we are also to include *Hyolithes guiraudi* THORAL in this discussion (see chapter 3 b), it should be noted that there are no differences between the "digestive system" of this form and that of *Volborthella/Salterella*. Different "species" of *Salterella/Volborthella* may reflect true differences but might also simply consist of different portions of apical tube fills from slender curved apical tube portions to more apertural and straight ones. The great similarity between *Volborthella* and *Salterella* on one hand and *Hyolithes kingi* tube portions on the other indicates that the *Hyolithes kingi* tube was also of simple structure and that all three fossils belong to the same group of organism.

Hyolitha

RUNNEGAR et al. (1975) and RUNNEGAR (1980) have tried to evaluate characteristics in hyolith morphology and structure as regards their usefulness in determining the place of this group in the animal kingdom. They come to the conclusion that hyoliths should be ranked within a separate phylum Hyolitha. RUNNEGAR put 8 points together which he considered to be "facts" about hyoliths that "everybody agrees on". Let us have a closer look at these 8 points and consider them from the point of view of what we know about *Hyolithes kingi*.

The first of these facts is: „There are two kinds of hyoliths, those with appendages (Hyolithida) and those with no appendages (Orthothecida). "*Hyolithes kingi*" is a representative of the second of these kinds. In shape it intermediates between *Orthotheca* and *Cirotheca*, DZIK (1980) tried to minimize the appendage difference by reconstructing soft and fleshy appendages for Orthothecida. *Hyolithes kingi*, like other orthothecids, shows no features of the shell or the operculum that could be used to demonstrate the presence of such fleshy appendages. DZIK (1981) reconstructed another circothecid/orthothecida precephalopod, thus providing us with two hypotheses to choose from. MAREK & YOCHELSON's description (1976) is still useful for differentiating between Hyolithida and Orthothecida. It points to the significance of the presence or absence of a ligula.

The second point of general agreement according to RUNNEGAR (1980) concerns the structure of the shell of hyoliths. RUNNEGAR et al. (1976, figs. 5 and 6) and DZIK (1979, fig. 8) illustrated shell structures. The former noted features resembling the crossed lamellar structure of the molluscs. YOCHELSON (1979) found the data convincing and considered it a good reason for placing hyoliths in the phylum of Mollusca. Crossed lamellar structure is found only among molluscs in recent invertebrate skeletons. This evidence however is not as conclusive as YOCHELSON believed. The "crossed lamellar structure" of the illustrated hyolith is calcitic, whereas that of recent molluscs is aragonitic. The connection between biocrystallites of the molluscan crossed lamellar structure has been shown in great detail (BANDEL, 1979). It has also been shown that this structure becomes completely destroyed when aragonite is transferred into calcite during diagenesis (BANDEL, 1981; DULLO, 1983; BANDEL & WEITSCHAT, 1984, DULLO & BANDEL, 1987). Not a single case is known to date in which the crossed lamellar structure was preserved when recrystallized into calcite. In the data presented by DZIK (1979) the shell is replaced by non calcareous material.

DZIK's suggestion that in this case something like the helical structure of the pteropods resembles his figure can be rejected once his figures have been compared with figures from the studies on pteropod shells by BE et al. (1972), BANDEL (1977), RAMPAL (1972). There is no similarity whatsoever.

The structure of fossil hyolith shells (RUNNEGAR et al., 1976) can easily be compared with that of the tube of the recent annelid worm *Ditrupa* (see chapter 4, i) (pl. 10, figs. 1 and 2). Here, a high Mg-Calcite shell shows a structure that has a superficial resemblance to an aragonitic crossed lamellar structure and could have easily been transformed into stable low Mg-Calcite with preservation of the primary morphology during diagenesis.

RUNNEGAR's (1980) third point of "mutual agreement" was that hyoliths had a ventral and a dorsal side and a ventral mouth. Evidence of the location of the mouth was seen in fossils that had presumably preserved their digestive system. Such cases were believed to have occurred in *Hyolithes* (*Orthotheca*) *guiraudi* THORAL (1935, pl. 14) from the Lower Ordovician of the Montagne Noire (France). THORAL described external and internal moulds of hyoliths which, like *Hyolithes kingi*, reached a length of 3.5 cm and show an apical angle of about 12° and a similar operculum. But in contrast to the latter, they had a more strongly flattened ventral side. THORAL (1935) noted that an 8 mm long, weathered section of the apical portion of a tube of *Hyolithes guiraudi* showed a 0.4 mm wide central canal and that below, 20 laminae filled the ventral side of the tube. The fossil is preserved as a secondary replacement of the original material by quartz. THORAL interpreted laminae and tube as remains of the tissue of the original organism that had inhabited the tube. He hypothesized that the central tube might represent part of the digestive system and laminae ventral of it part of the genital system. THORAL did not note the similarity of his fossil to sectioned or weathered *Volborthella* which at that time had been well illustrated by GÜRICH (1934) and SCHINDEWOLF (1934).

RUNNEGAR et al. (1976) also disregarded this data when reinterpreting THORAL's figures. In their interpretation of the preserved features organs changed their location. The laminae were now interpreted as part of the digestive system and the central tube as intestine (hind gut). Similar fossils from the Middle Cambrian of Antarctica (RUNNEGAR et al., 1975, fig. 3 C-E) in shape and size closely resemble weathered *Volborthella* or silicified and weathered *Salterella*. But they were also considered to represent fossilized digestive systems of hyoliths. It is quite likely that these features represent diagenetically altered remnants of apical internal shell fills as in *Hyolithes kingi* and similar to those from *Salterella* and *Volborthella*. It is most probable that they have nothing to do with digestive systems and are without value for phylogenetic considerations. MESHKOVA & SYSSOJEV (1981) also described such fossils.

RUNNEGAR's (1980) fourth statement considers the morphology of the operculum which is presumed to have been connected to the tissue of the organism by two muscles and opened by hydrostatic pressure. According to RUNNEGAR et al. (1975) processes on the inner surface of the operculum were used as levers to open the operculum. This may or may not have been so, and would in any case be based purely on a hypothetical reconstruction of the organism. The operculum could also have functioned in a manner comparable to that of recent serpulid worms as proposed here (see chapter 4 c). In this case the projecting processes would extend into the fleshy stalk and "muscle impressions" as seen by MAREK (1963) may represent tissue operculum connections. The operculum of hyoliths is a linking factor between circothecids with round to oval tubes like *Hyolithes kingi* and hyolithids with flattened ventral sides.

The fifth argument of RUNNEGAR (1980) concerns helens, calcareous appendages that set orthothecids without such a structure apart from hyolithids which should have them. In most cases of hyolithid species they have not been found. Their function remains a puzzle.

Points 6 to 8 are not facts about Hyolitha, but interpretations according to which the animals were nearly sessile unspecialized detritivorous creatures that generally occupied low energy environments. They are assumed to have had an annelid-siphunculoid-molluscan grade of organization but so different from any of these invertebrate phyla that they are best placed in a phylum by themselves. All these points are speculative, and the only characteristic that can be reconstructed from the rocks: "preference of low energy environments" is not valid of *Hyolithes kingi* (see chapter 1 c).

Only the first 4 points on RUNNEGAR's list are related to the acutal construction of a conch like that of *Hyolithes kingi*, but even here there is only a very limited agreement. Runnegar's diagnosis of the phylum Hyolitha: "bilaterally symmetrical coelomate metazoa with a recurved gut, longitudinal, circular, probably dorsoventral body muscles, and well organized, probably aragonitic exoskeleton formed by additive deposition from an enclosing mantle", cannot be accepted. RUNNEGAR et al. (1975) even thought that forms like *Hyolithes kingi* with a chambered apical portion of the tube may have had "gas filled chambers ... (that) may have made the apex buoyant enough to keep it above the sediment-water interface". How the creature managed to fill gas into these chambers remains a mystery. The opinion expressed by these authors that an exoskeleton would be useful to an animal of this type and was therefore developed by hyoliths which formerly had no shell and were of siphunculoid appearance is LYSSENKOISM at its best.

From Lower Cambrian limestones, exposed at the small road leading from Ferrals-les Montagnes to Favayroles in the Montagne Noire in Southern France, one bed holds a coquina of hyoliths. This thin limestone bed connected to massive archaeocyathid limestones has been recrystallized and slightly deformed during late diagenesis, but the hyoliths are preserved well enough (pl. 7, figs. 1-6) to be compared with *Hyolithes kingi* from Jordan. The opercula (pl. 7, figs. 1 and 2) are like those of *Hyolithes kingi*, as well as the apical fill structures and the fractured tube ends (pl. 7, figs. 4 and 5).

Tubes have commonly been pushed into each other to form bundles when transported (pl. 7, figs. 3 and 6), again as seen in the Dead Sea area. This occurrence in Southern France demonstrates that *Hyolithes kingi* had a geographically wide distribution at Lower Cambrian time.

Similar hyoliths, but without the characteristic apical fills of *Hyolithes kingi*, could be studied on an *Orthotheca* from the Lower Cambrian of Australia, kindly provided by Prof. Dr. WERNER BUGGISCH (University of Erlangen), and another *Orthotheca* from the Lower Cambrian of Sweden collected by Dr. D. ANDRES (Freie Universität Berlin) that I could prepare for thin-sectioning. The individuals from Australia are phosphatized and have septa with different thickness rather well developed (pl. 6, Fig. 1), which have been added to the inner tube wall. The *Orthotheca* from Sweden has very well preserved wall structures where inclined additions of calcareous layers to the tube from inside are seen (pl. 6, fig. 4). The operculum of this *Orthotheca* can also be found within the tube (pl. 6, fig. 5) and closely resembles that of *Hyolithes kingi* in thin-section. The section vertical to the tube axis (pl. 6, fig. 2) reveals that the Swedish hyolith is more clearly an orthothecid than *Hyolithes kingi*, where the ventral side is less well developed and more rounded. The septa are of different thickness (pl. 6, fig. 3), but apical fill structures like those of *Hyolithes kingi* are

not present in this species. With exception of this last feature, both orthothecids from Australia and Sweden are closely similar to *Hyolithes kingi* from Jordan as well as from the Montagne Noire.

Tentaculites

Hyoliths have often been associated with tentaculites when their place in the system of invertebrates was being considered. NAEF (1924, 1926) placed them in their own order Odontomorpha along with styliolined tentaculites. LYASHENKO (1957) followed this line of thought and united hyolithids and tentaculites in the class Coniconchia. YOCHELSON (1961), in contrast, stated that hyoliths differ from tentaculites in a number of ways. He thought tentaculites had a large apical chamber, a smaller average size, a circular cross section throughout; external annulations of the tube, and no operculum, in all of which points they would differ from hyoliths.

Tentaculites themselves are, however, not very homogeneous, they have to be split into at least two independent large groups. One consists of tentaculites in a narrow sense with the type genus *Tentaculites*, the other contains styliolinids with characteristic types such as *Nowakia* and *Styliolina*. While *Tentaculites* and *Volynites* from the Wenlock and Ludlow beds of Sweden, on which BLIND (1969) based an extensive study, represent benthic organisms, styliolinids swam freely in the Plankton during their lifetime. Benthic tentaculites are larger and of more solid construction than the styliolinids BOUČEK (1964) refers to.

Let us first consider the benthic *Tentaculites-Volynites* types. BLIND (1969) showed that the first primordial shell to be formed consists of a conical tube with an evenly rounded apex similar to that of *Hyolithes kingi* in both shape and size. As in the latter, this early ontogenetic part of the tube is usually lost in larger fossils.

The wall of *Tentaculites* is calcareous and composed of thin calcitic lamellae which are very well preserved in the specimens studied by BLIND (1969, pl. 13, figs. 2, 3). The wall may have become thickened in apical portions of the tube, in the process of which some of these internal additions reach a character of *Salterella* structure (BLIND, 1969, pl. 17, fig. 3; pl. 18, fig. 3). Septa of variable thickness and in variable sequence are present, some of them pierced by a somewhat irregular hole. These tube features resemble those seen in *Hyolithes kingi* and similar hyolithes (pl. 6, figs. 1, 3, 4).

BLIND (1969, fig. 1) also noted an operculum that consisted of a cupola-like, round structure with an independent hinge. This "operculum", however, which was found only in one individual of *Tentaculites*, is part of the glabella of a trilobite as demonstrated by SCHRANK (1970) and had accidentally fallen into the aperture of the tube. It is part of the species *Calymene tentaculata*.

BLIND thought *Tentaculites* and *Volynites* represented members of a new subclass of the cephalopoda and that these creatures, in contrast to other members of this class, lived with their apex attached to the bottom substrate. BLIND thought that the shell had originally been aragonitic in composition as is the case in cephalopods and that the nacre lamellae are still preserved after having been recrystallized into calcite.

There is no known nacreous shell that has been diagenetically altered to calcite, preserving its lamellar structure (DULLO, 1983, DULLO & BANDEL, 1987). Good shell preservation of *Tentaculites* and *Volynites* are indicators of originally calcitic composition. Here we know of numerous examples of good preservation of lamellar calcitic structure through diagenesis (BANDEL & WEITSCHAT, 1984). The irregular hole which is present in some of the septa cannot be taken as

evidence of the presence of a siphuncle as is found in recent and fossil cephalopods. It is far more similar to septa present in the tubes of many recent serpulid worms (pl. 9, figs. 3 and 4) and in some fossil hyoliths. Camerae of tentaculites probably did not function hydrostatically as assumed by FISHER (1962) and BLIND (1969).

A large apical chamber is only found in styliolinids. These rarely have septae and are of much smaller size (BOUCEK, 1964). FISHER (1962) used the difference in the "embryonic" stage to separate two orders, the Tentaculitida LYASHENKO 1955 with tapering to bluntly pointed conical tube end and the DACRYOCONARIDA FISHER 1962 with tear-drop-like embryonic chamber. BLIND & STÜRMER (1977) studied a styliolinid from the Devonian in x-ray pictures and discovered a siphuncle and remains of the soft parts and opercula. A fresh study of the material revealed that neither of these features were present. The "opercula" are small bivalves (veliger shells) and the "siphuncle" is a result of the flattening of the shell and thus, an artefact of diagenesis. In the case of fig. 3 of BLIND & STÜRMER's study a juvenile cephalopod was mistaken for a styliolinid and here, the presence of a septum is not surprising. This individual was refigured from an original plate by BRASSEL et al (1971) where it had also erroneously been determined as tentaculite.

The thin shell of styliolinids could well have been aragonitic as is documented by their diagenetic history (BANDEL, 1972). Their occurrence in Devonian pelagic limestones of all kinds indicates that they are remains of planktonic organisms. Styliolinids show no close similarity to hyoliths. YOCHELSON (1979) considers them to be representatives of a distinct phylum but connects them to *Tentaculites*. *Tentaculites* differs from *Styliolina* as regards shell size, shell construction and shell composition and has also lived in a different environment, so that it is more likely that *Tentaculites* is related to hyoliths, perhaps representing a separate group of tube-dwelling annelid worms, while *Styliolina* may have been an early branch of planktonic molluscs, related to gastropods or pregastropods, but certainly not related to recent pteropods as assumed by ZITTEL (1881) and many others after him.

Molluscs

Hyoliths have often been considered to belong to the phylum Mollusca. Here they have a class to themselves or are related to one of the classes still in existence today. Connections to the pteropods were assumed by BARRANDE (1867) and many later authors. NAEF (1928) agreed with the placement within the molluscs and united hyoliths and *Salterella/Volborthella* with other conical fossils of problematic affinities in a separate class which he called Odontomorpha. He assumed that odontomorphs were of conchiferan organization and that some of them showed fairly regular chambers in the apical portion of their shells. NAEF considered the latter to represent precursors of cephalopods but rejected the idea that *Volborthella/Salterella* might represent an early *Orthoceras*-like cephalopod. To make his point clear NAEF drew a hypothetical reconstruction of the Odontomorpha (Fig. 12b).

FISHER (1962) also considered hyoliths to be members of an independent molluscan class, but, unfortunately, gave them a new name: "Calypptomatida" and disregarded NAEF's earlier suggestion, which at least had the benefit of being much easier to pronounce and spell. In addition, FISHER suggested that there were two very different ecological types to be found in the orthothecid branch of his Calypptomatida. One lived upright "with the apex thrust in the seabottom", while the other, provided with apical chambers, swam freely in an "assuredly pelagic" way of life.

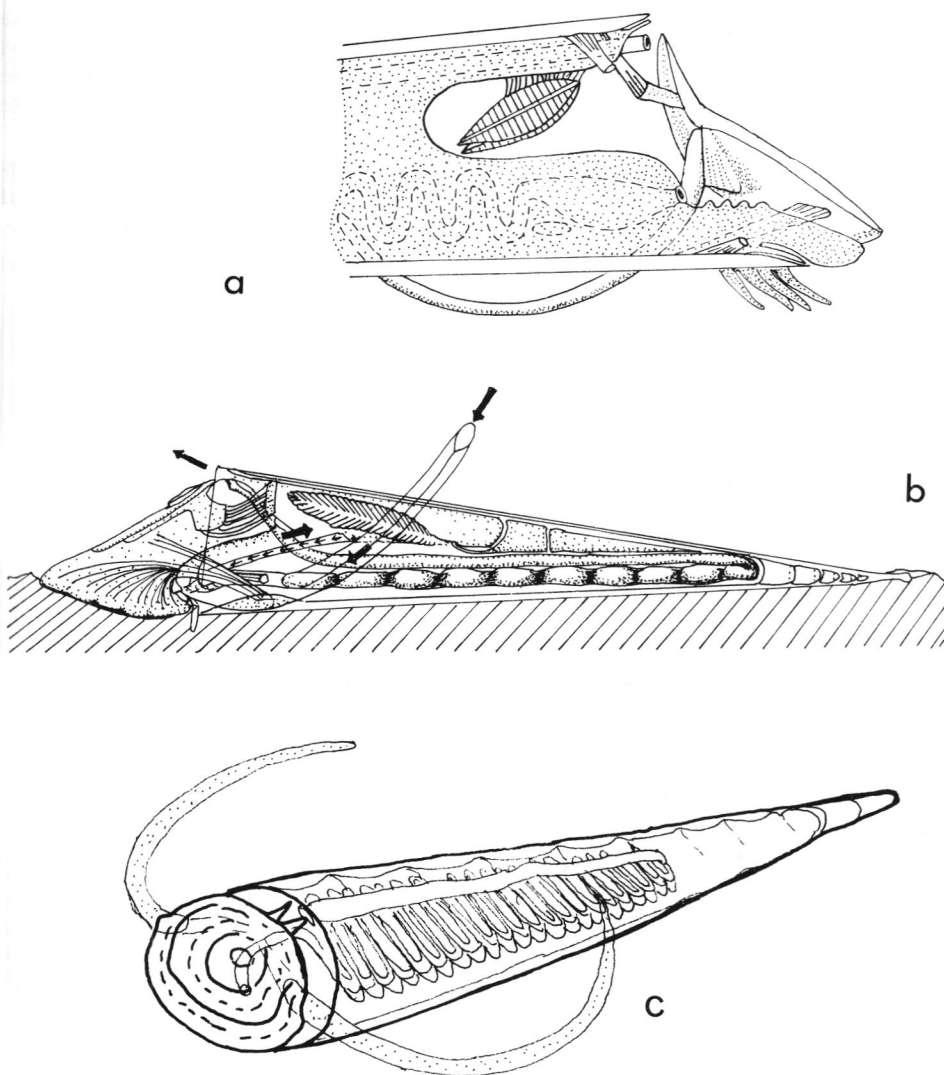


Fig. 11: Reconstructions presented by MAREK & YOCHELSON (1976) (a), DZIK (1980) (b) and RUNNEGAR et al. (1975) (c) of a hypothetical hyolith similar to *Hyolithes kingi*. a) Soft part organisation as own class of molluscs; b) as filter-feeding molluscs; c) as organisms representing a phylum for itself. (Redrawn and slightly modified from cited authors.)

Without referring to NAEF (1924, 1928), MAREK & YOCHELSON (1976) rediscovered the similarity of hyoliths to molluscs and thought them a separate class. They presented a further hypothetical reconstruction of the soft parts of hyoliths that showed a "molluscan" organization far different to anything known to exist in this phylum today. The operculum, for example, was reconstructed as attached to the tissue of the mantle instead of the foot as occurs in gastropods, ammonites and nautiloids (Fig. 11 a).

In one of his publications DZIK (1979) considered hyoliths to represent the Paleozoic ecological analogues of recent Turritellidae. He based his reconstruction partly on the endeavour of MAREK & YOCHELSON, however, placed the operculum on the foot (Fig. 11 b). DZIK suggested that two uncalcified tubular

siphos and a larval and embryonic shell almost identical to those of Pteropoda existed. He compared the operculum to that of recent Neritacea. The shell was considered to show spiral structure as supposedly seen in some pteropods. The outcome is once more a model with little resemblance to any organism alive today.

In a more recent reconstruction of circothecid hyoliths DZIK (1981) produced a very different model to his former model for orthothecids (Fig. 12), but close to that shown by NAEF (1928), to whom however, no reference was made.

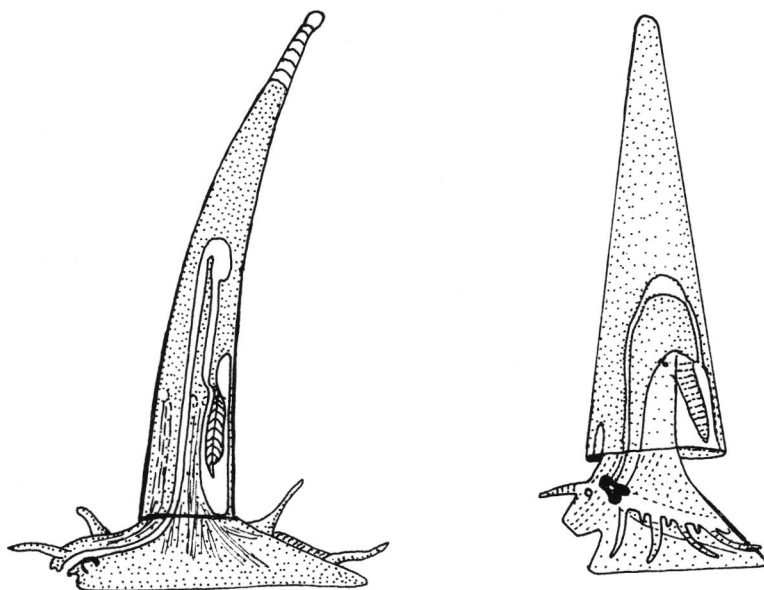


Fig. 12: The hypothetical reconstruction of a circothecid hyolith similar to *Hyolithes kingi* by DZIK (1981) (redrawn from his figure) as precursor of cephalopods resembles and reinvents NAEF's (1913) reconstruction of the hypothetical molluscan group Odontomorpha.

DZIK hypothesized that some Cambrian hyoliths, similar to *Hyolithes kingi* in construction, represent intermediate forms from yolk-poor to yolk-rich embryonic development. While MAREK & YOCHELSON (1976) noted that the initial shape of all hyoliths consisted of a tapering bullet-shaped tube with circular cross section and simple aperture, DZIK found embryonic shells of spherical and fusiform shape and 0.6 to 1.2 mm width. These were chamosite and glauconite moulds derived by dissolution of erratic boulders. The "embryonic" and "larval" shells could well represent internal fills of the lumina of hyolithid tubes of different sizes as assumed by BANDEL (1983, figs. 7, 13) DZIK's statement that "hyoliths are characterized by a high diversity in their larval development" could then be interpreted to be a result of the different size of internal moulds in different sections of filled tubes of the type of *Hyolithes kingi*. DZIK (personal communication) rejects the possibility of these dissolution remnants of erratic boulders from Poland being steinkerns and, therefore, opposes BANDEL's interpretation of 1983.

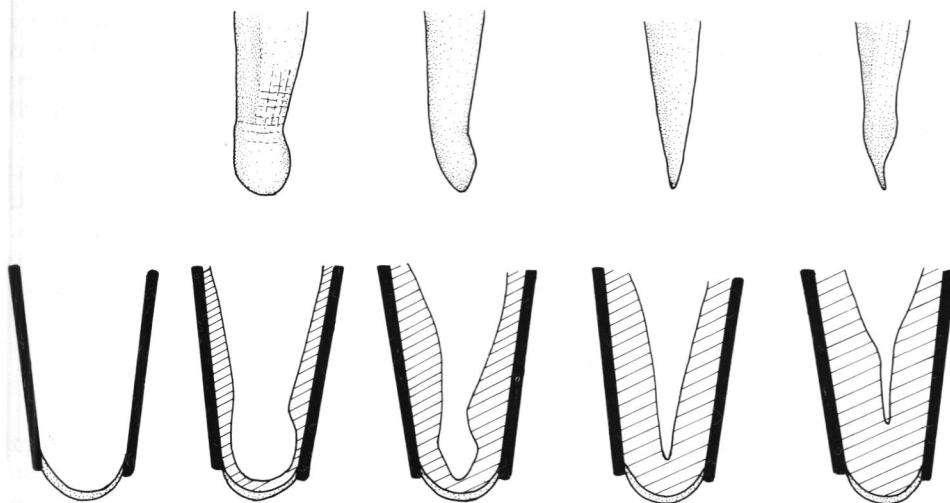


Fig. 13: Apical portions of the shell tube of *Hyolithes kingi* have become filled with cone-like shell additions (lower row). Internal molds of such inner tube ends produce "larval conch" as those illustrated by DŽIK (1978 and 1980) and here redrawn above the *Hyolithes kingi* tubes.

If we compare recent molluscs with a conical shell to *Hyolithes kingi* we can note a number of differences, 10 of which are listed here.

1. The crossed lamellar structure of hyoliths is not comparable with that of molluscs, as is shown in detail in chapter 4 i. Crossed lamellar structure in molluscs is always aragonitic while hyolith shell structures that are known were probably calcitic.
2. The long conical shell shape with a closed apex is rare among molluscs. A conch of this kind is frequent only among representatives of fossil chambered cephalopods. It always consists of aragonite mostly with in nacreous structure.
3. Pteropods with conical shells such as *Cuvierina* or *Hyalocylis* have a much thinner wall. In addition, pteropods appear much later in geological history (Upper Cretaceous) and cannot be connected with hyoliths.
4. *Caecum* and related tusk-like mesogastropods cannot be connected to hyoliths. They always have an early coiled ontogenetic shell which is typical of gastropods in general.
5. The operculum of hyoliths cannot be connected to a foot. The projections would lie within the foot and interfere with the creeping sole. Even if the foot was reconstructed as head-cover, as in ammonites and some nautiloids, the projections would enter the brain capsule.
6. Septa are common among all molluscs with conical shells, but they are also to be found in other groups with shells or tubes like brachiopods, especially in worms. Narrow tube-like constrictions as those at the end of the living chamber as in *Hyolithes kingi* have not been found in any mollusc. Apart from siphuncular tubes in cephalopods a continuation of the apical end into a narrow tube is not known in the molluscan shell. The visceral mass of molluscs is usually rounded.
7. A variability of shell shape and shell thickness to that large degree as is seen in *Hyolithes kingi* would be unusual in molluscs.

8. The presence of sediment particles in areas that have been closed off by septa would be difficult to explain in a mollusc. This material would have to migrate backwards between shell and mantle. Sediment entering the space between mantle and shell is either expelled or covered by shell material (pearls) long before the end of the living chamber is reached.

9. As far as the relation of *Hyolithes kingi* to *Volborthella/Salterella* is concerned, it should be noted that this group of Cambrian organisms contained animals which formed apical shell fillings with agglutinated sediment particles. Such shell formation is unknown in molluscs.

10. Last not least: Hyoliths occur earlier than undisputed conchiferan molluscs.

4. Comparison with extant Annelids

Formation of the primordial tube of *Protula tubularia*

Protula tubularia (Serpulidae, Filograninae) is a sedentary tube worm that constructs a calcareous aragonitic tube which it cannot leave. The tube may be attached to some hard substrate, or may become free from its attachment base and project into the water. In the Mediterranean Sea in spring and early summer, animals produce large gelatinous egg masses containing numerous spherical transparent egg capsules, each of which holds one egg. The soft egg mass is attached to the erect tube end of the mother animal and floats in the water.

Eggs are rich with yolk-reserves and larvae remain free swimming for only 2–6 days after hatching. A double row of cilia (prototroch) surround the anterior part (head) of the trochophora-larva and enable hatchlings to swim in water and

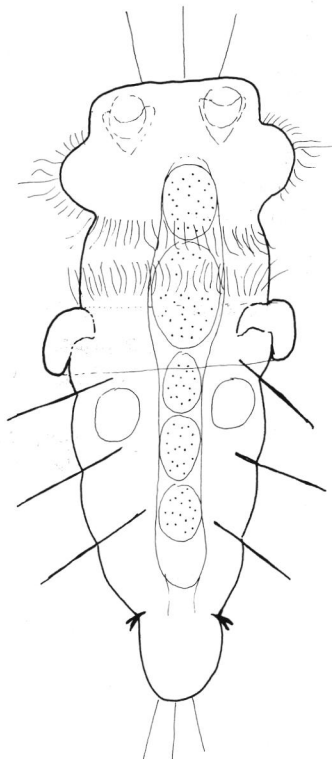


Fig. 14: Sketch of trochophora larva of *Protula tubularia* ready to settle.

be spread by drifting with the currents. Hatchlings of *Protula tubularia*, in contrast to many other related sedentary annelids, do not feed while swimming in the sea. Two simple cup-like eyes are situated on the sides of the head and 3 sensory cilia are present on the head as well as on the abdominal end (Fig. 14).

During transition from free swimming larva to crawling worm the construction of the body is changed. The digestive system opens to the outside with a frontal mouth and a posterior ventral anus. Yolk cells that are concentrated in the larva between the ciliary rings of the head are spread along the middle axis of the body lying in the digestive tract. The three portions of the body: head, thorax and abdomen are present when the larva settles, after which they enlarge. The head develops ciliated outgrowths to the left and right which slowly grow into tentacles with ciliated food grooves (branchial filaments). Below the ciliary rings of the head two short outgrowths develop, which form the collar of the thorax. The latter includes three segments, each with a pair of bristles (setae). These parapodia can be moved in and out and sideways by muscles attached to their base so that they can be used for movement on the bottom substrate when the larva settles. The short abdominal body portion ends with two claw-like bristles. A trochophora-larva ready for settling can postpone benthic life for several days if it comes into an environment not appropriate for tube attachment. During this time the tentacle crown continues in its growth, while the trochophoral ciliary rings remain functional and propel the larva through the water in spiral movements (fig. 15).

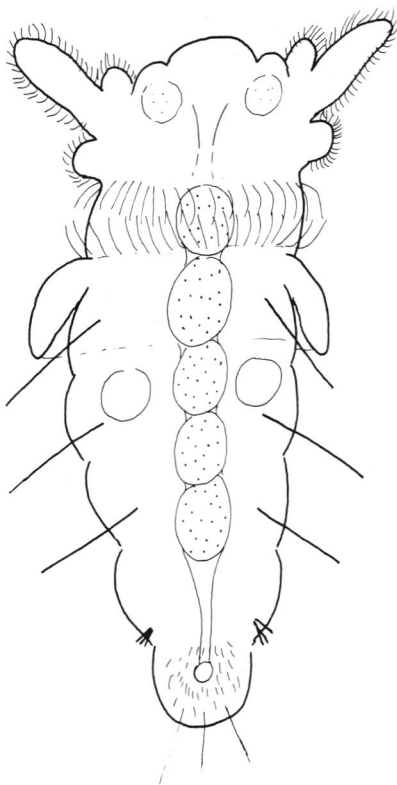


Fig. 15: Sketch of *Protula tubularia* that had been delayed in its settlement, so it unites larval and adult morphological features. The head and the digestive system are ready to function in a tube worm, while ciliation of the larva is still retained and enables the worm to continue swimming and to search for a suitable substrate.

The larva that settles on an agreeable substrate attaches itself to the posterior body by secreting one or several threads. Within hours the whole posterior portion of the body becomes surrounded with an organic tube that is free with exception of the anchoring threads. This primordial tube covers only the posterior portion (thorax and abdomen) of the body and reflects its shape and size. Ciliary rings at the base of the head disappear, while the tentacle crown continues its growth, takes up its function and begins to collect food.

As soon as the tube end comes into contact with the collar of the anterior thorax-segment, enlargement of the tube becomes more rapid. At the same time the tube is calcified along its whole length by aragonitic crystallites. The tube remains free until it has grown to double length of the worm within it (Fig. 16, pl. 8, fig. 5).

In transition from metamorphosing worm to tube-dwelling worm, the posterior portion (abdomen) of the body stretches considerably. The posterior claw-like pair of bristles now anchors the animal within its tube, while the bristle pairs of the thorax are used to climb up and down within the tube. The outside

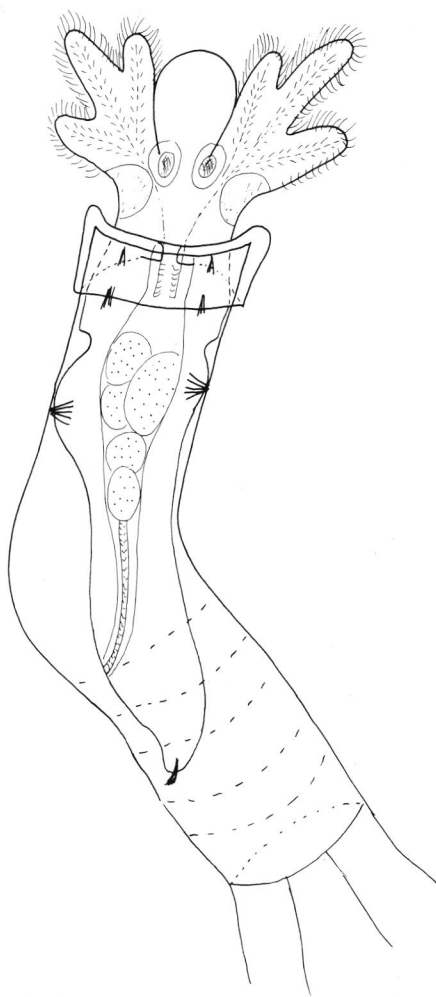


Fig. 16: Sketch of *Protula tubularia* after settlement and first tube calcification with the primordial tube attached only by organic threads.

of the tube is covered with mineral deposits (aragonite crystallites) with the aid of the collar, while the inside of the tube is coated with an organic layer that provides good holdfast for the setae through a succession of grooves and ridges. The worm is usually anchored to its tube with the abdominal claws. During activity the abdominal portion of the body is stretched and can easily be twisted by 180 degrees. When the animal retracts into its tube and into its original untwisted position it withdraws the thoracic setae from their holdfasts on the inner organic cover and contracts the body by muscular action (pl. 9, figs. 1 and 2).

In running seawater under normal conditions calcification of the tube is very rapid. It is retarded in standing seawater within glass dishes, whereas the growth of the worm inside its tube is the same as in normal conditions. This indicates that calcium-carbonate is absorbed by the organic deposits and comes directly from the seawater.

Only after two worm lengths have been reached is the tube of *Protula tubularia* cemented to the substrate. The calcareous layers are now clearly deposited on the outside of the tube and distinct growth lines appear. In further growth the tentacle crown increases in size and complexity and functions as a food collecting device as well as for gas exchange.

Ontogeny of the tube and operculum of *Pileolaria pseudomilitaris*

Pileolaria pseudomilitaris (Spirobinae, Serpulidae) is a sedentary tube worm with spiral left-coiled tube consisting of high-Mg-calcite and attached to some hard substrates like mangrove roots. Only the last portion of the adult tube projects from the coil straight into the water. From a mangrove lake of Ferry's Point in Bermuda animals were transferred and kept in a 20 l aquarium and artificial sea water for several years. Reproduction is continuous and can be observed throughout the year.

Eggs are brooded within special pouches situated under the operculum within the opercular tentacle (Fig. 21). 4 to 20 eggs are to be found here, depending on the size of the mother animal. When eggs have developed into larvae the brood pouch opens and the larvae swim off in a spiral way. Larvae are ready to settle right after hatching and the time of free swimming is restricted to only a few hours (Fig. 17).

In the experiment the young started to settle less than 30 minutes after hatching. The three regions of the adult, head, thorax and abdomen are clearly developed in the larvae. The head is rounded and bears several sensing cilia and two lateral red spots. At its base a ring of dense ciliation forms the prototroch that propels the larva through the water. The first thoracic segment holds conspicuous liquid-filled cavities and forms the thorax with three further segments. Only the two posterior segments have pairs of spear like bristles (setae). The abdominal segments end with long sensing cilia and a tuft of cilia around the anus. The digestive system is ready to function. A mid-dorsal attachment gland is full of liquid shell material and is ready to employ it at settlement (Fig. 17).

The larva swims rapidly but can also crawl propelled by the ciliary beat of the prototroch and attached to the substrate with the thoracic bristles. When it finds a suitable substrate it spins thin threads that anchor it. When shell material is released from the attachment gland a tube is formed within minutes covering thorax and abdomen. Only the head extends from the initial tube. Now the long cilia of the prototroch fall off and are eaten, entering the open mouth through a ciliary groove. Two lobes form on each side of the head which split into two

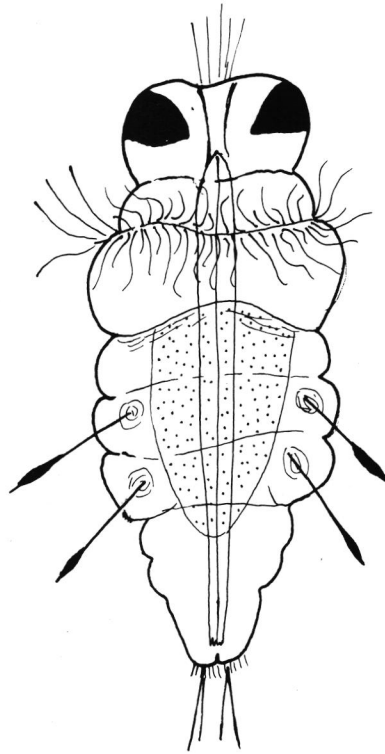


Fig. 17: Sketch of the larva
of *Pileolaria pseudomilitaris*
ready to settle.

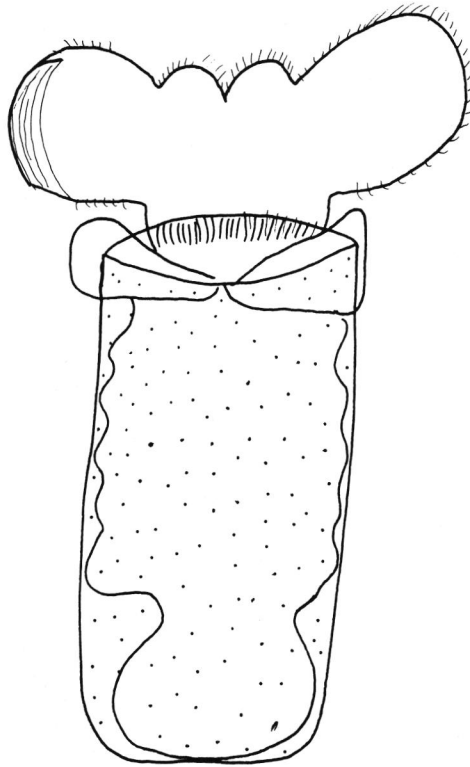


Fig. 18: Sketch of *Pileolaria pseudomilitaris* just after settlement and very rapid secretions of primordial organic tube and transformation into tube worm by growth of tentacles and loss of prototroch-ciliation.

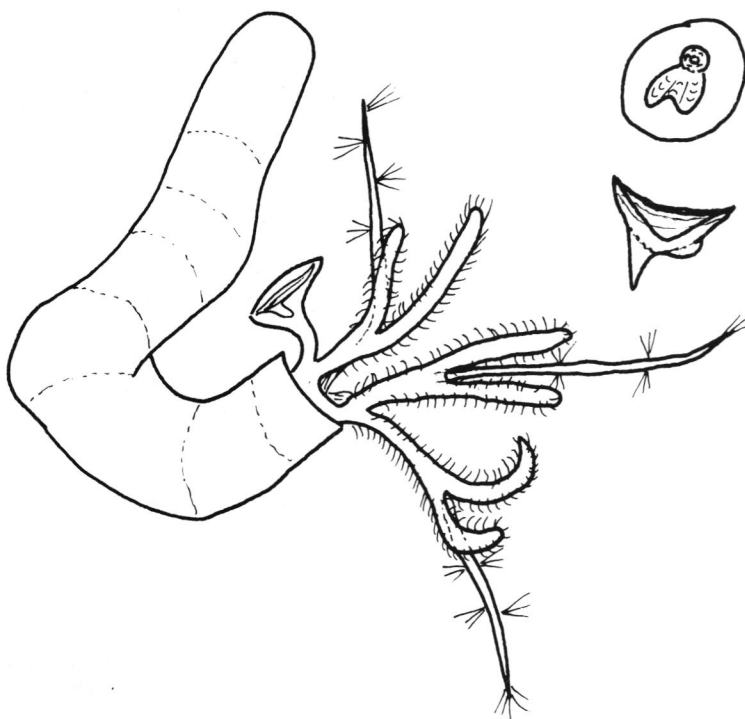


Fig. 19: Sketch of *Pileolaria pseudomilitaris* 3 days after settlement. The tube is attached and calcified, the head has grown a branchial crown as well as an operculum with finger-like inner projection (talon) (drawn in detail at upper right).

branches. At the same time the first thoracic segments form the collar by activating the liquid and pressing it into pre-formed and pre-constructed cavities. Within 30 minutes one of the 4 head lobes begins to secrete an operculum and, shortly afterwards, the tube begins to grow in length with the aid of secretions produced by the collar fold. First calcium carbonate deposition appears and the tube becomes attached to the substrate (Fig. 18; pl. 8, fig. 5).

In a three day old individual the operculum is well mineralized and can seal the tube when the worm retracts into it (Fig. 19). It consists of a slightly concave plate and an eccentric finger-like stalk talon. The operculum grows in size by accretion of shell material to the margins of the lid and to the stalk and is free of tissue on its outside. The operculum develops two ridges to which muscle fibres of the stalk tissue are attached. When the muscles contract the fleshy stalk is shortened and the operculum is pulled down.

By the time the animal reaches maturity the tentacle crown has developed 8 arms, one of which holds the operculum (Fig. 20). The other arms are ciliated and catch food in the form of planktonic organisms from the water. The tentacle now withdraws from the operculum so that it only remains attached to the end of the talon. The opercular tentacle becomes club-like in shape and secretes a helmet-shaped calcified lid under tissue cover and a globular brood chamber above. When the calcareous lid has been completed, spines are added to it from the outside. Their size and number is variable and related to the size of the brood chamber, which depends on the size of the individual (pl. 8, fig. 1-4). Maturity and large size are not correlated in *Pileolaria*. When the chamber and its calcareous spiny lid are finished the old stalked operculum falls off. Fertilized eggs enter the brood chamber through the opercular tentacle and develop in it

margin and is free of tissue on its outside. When the development of the embryos has reached hatching stage, the brood chamber as well as the operculum disintegrate and a new stalked operculum with brood chamber forms below it. Opercula of many spirobids are composed like hyolith opercula as characterized by MAREK (1963). They grow along their plate margins and paired processes project from the dorsal side of the operculum. VINE (1972) described a number of opercula from different species of *Janua* where the talon (operculum stalk) is bifid. MÜLLER (1964) described such opercula in detail and presented a complex nomenclature for the different processes projecting from the plate. According to VINE (1972), different species of *Janua* show quite different ways in their production of brood chambers and opercula that range from operculum loss in each brood to the retention of the operculum for the whole life cycle.

Septa

GÖTZ (1931) was the first to note the presence of septa in the calcareous tubes of fossil serpulids. NESTLER (1963) found septa that had backward turned necks penetrated by a hole. He thought that this hole may have served to anchor the abdominal section of the worm to its tube. MÜLLER (1963) reconstructed the formation of the septa of a fossil "*Ditrupa*" as secreted with the aid of anal glands. Chambers formed by successive septa, in MÜLLER's opinion, could have been involved in brood protection. HEDLEY (1958) had described septum formation in the course of tube construction of the recent *Pomatoceras*. TEN HOVE (1973, pl. 1, C) figured septa from living *Sclerostyla* and mentioned the existence of similar septa in the tubes of recent *Mercierella*.

Tube worms with calcareous shell quite often show septa that close apical portions of tubes no longer used by the worm. Septa found here can be quite thick and are formed by a solid wall, they can also represent a series of thin porous partitions, as those illustrated by TEN HOVE. Experiments were carried out with living representatives of *Pomatoceras* collected from rocks in the shallow sublittoral and *Serpularia* dredged from deeper bottoms of the Mediterranean Sea near Banyuls-sur-Mer, France. The calcareous tubes were broken in such a way that the tube was still a little longer than the worm. Worms were then placed, oriented in their natural position, in an aquarium with running sea water. Both species of worms within a day or two produced septa near the apical tube-opening. Septa are at first porous, with a larger pore in the most apical end of the septum and paired holes near the sides (pl. 9, figs. 3 and 4). Septa are attached to the inside of the tube in inclined position reflecting the normal orientation of the worm in its tube with branchial crown up, and opercular radiolus (tentacle) towards the substrate and body untwisted. In older septa holes slowly close and only the apical one remains open for quite some time until it is also closed (pl. 8, fig. 6). Holes reflect the end of the worm's body and the position of the parapodia next to the septum wall and serve no specific function.

The analysis of the structure of septa aided by the SEM reveals the formational history. When the worm begins to produce a septum it spins organic threads with its most abdominal segments, until a porous web with irregular fabric is formed. Mucus is deposited onto this web with the worm's abdomen. From it, organic sheets and calcareous crystallites form (pl. 9, fig. 6). Foreign bodies, such as skeletal remains of planktonic organisms, may often get stuck to the mucus and cemented into its products. In thicker septa, crystallites may grow into spherulitic bodies that fuse and form solid mineral layers (pl. 9, fig. 5). Worms with a less fixed position within their tubes would probably form less inclined, more regular septa with a central to subcentral hole.

Tube agglutination in *Lanice*

SEILACHER (1951) and SCHÄFER (1962) described in detail the tube and its production of *Lanice conchilega* (Terebellidae) and also reviewed older literature. Own observations were carried out on the coast of the North Sea of Belgium, where *Lanice* is a very common worm of the intertidal flats.

Lanice is segmented with three different body portions. From the head long mobile tentacles and branching tree-like gills project, which are in continuous movement. The central body portion consists of up to 20 parapodia-bearing segments, each of which carries a pair of bristle bundles. The apical portion of the body (abdomen) is thinner, has parapodia covered with 10–15 tiny bristles besides the most posterior segment with large claw-like bristles and is almost as long as the two anterior portions of the body together.

The largest portion of the tube constructed by *Lanice* lies within the sandy bottom and extends into 10 to 40 cm depth. A small portion of the tube extends up to 4 cm above sediment surface. The construction of the subsurface portions of the tube differs from that built above the sediment. At the bottom, tubes are composed of attached sandgrains that are within the sediment. The tube will collapse once it has been washed out. Above the substrate, tubes show a masonry of particles coarser than the average grain-size and often consisting of shell fragments which are cemented to each other like bricks in a wall. The inner side of the tube is covered all over by an organic pellicle that provides strength and flexibility to the burrow within and above the sediment.

The worm constructs its tube with the aid of the mouth and the first segments of the thorax. A worm taken from its tube swims with undulating movements of its whole body. It then sinks to the bottom where it coils up and secretes mucus from its whole body surface. Peristaltic movement concentrate some of this mucus and the sand glued to it in a ring around the head and thus provide a first base for the construction of a new tube. The 40 long mobile and contractile tentacles of the adult worm can be extended to a length of 2 cm (body length when active 7 cm) and have gutter-like shape with a food groove in the concavity and dense ciliation covering the surface. Tentacles can grasp sand grains which migrate on them towards the mouth where a spoon-like upper lip takes hold of them and collects them in a groove. About 15 grains are assembled and coated by mucus produced in the mouth before the upper lip pushes the mucus-sand-ball up and places it against the edge of the tube. The shorter, straight lower lip now transforms the ball into a sheet in which sand grains no longer change positions. Now the anterior 4 segments of the thorax are pressed against the new sand agglutination which in this way is coated from below by an organic pellicle. Within 3–4 seconds this pellicle is hardened. It is produced by paired glands found on the ventral side of the anterior segments (SCHÄFER, 1962).

Tube production in the sediment is more rapid than outside the sediment, but the activity of the worm is basically the same in the production of both. Within the sediment, secretion of a tube segment and collection of sand particles is more rapid, so that 3 cm of tube could be constructed within 30 minutes time. The end of the tube which extends into free water usually consists of a brush of sand grains agglutinated by organic material to form rows which provide shelter for the tentacle crown and the gill trees.

The worm moves rapidly in its tube. When actively feeding or constructing a tube it stretches the posterior half of its body. This end is anchored to the inner tube wall with the claw-like abdominal bristles. When the worm is disturbed, anterior setae detach from the tube walls and the body contracts with the

posterior claws still attached. When the worm is active the anterior portion of the body climbs up and down in the tube and continuous undulations push water through the tube. When the disturbance is more serious, such as at low tide, the worm climbs into deeper parts of its burrow. Tentacles collect food from the water as well as from the sediment surface and below. *Lanice*, therefore, is a filter feeder as well as suspension collector and deposit feeder. Faeces are expelled by twisting the abdominal part of the body so that it extends beyond the opening of the tube. The worm inside its tube can reverse its position and often does so when it has been washed out of the sediment by tidal currents. To construct the subsurface portion of a new tube, the body undulations create currents to blow a cavity into the sand which is then used for tube construction. As soon as the tube is safely anchored in the sediment the worm changes direction within its tube and constructs the upturned vertical portion of the new tube.

A vagile worm with agglutinated tube

Pectinaria coreni from the coast of the North Sea of Belgium is a free-living annelid that produces a tube which resembles the shell of a scaphopod in shape and in being open on either end. As far as tube construction is concerned, *Pectinaria*, the sand-mason worm, cannot be mistaken for *Dentalium*. In fossil conchs or tubes however, the shell may be strongly recrystallized and altered in such a way that this difference is obscured as in the case of the assumed oldest scaphopods (RUNNEGAR & POJETA, 1979).

Many details of the history and mode of life *Pectinaria* were assembled by SCHÄFER (1962). According to SCHERF (1957), the larvae of *Pectinaria* settle at the bottom and rapidly produce an organic tube of 1 mm length. This tube is enlarged by agglutinated sand grains which are glued to each other by a light grey mortar that consists of organic and carbonate compounds. Since grains used in the construction are carefully matched in size the tube is almost smooth on its outside and the walls are as thick as one layer of sand-grains. Shell particles are glued to each other in such a way that smooth surfaces are oriented to the outside and inside of the tube. The worm selects certain sand-grain sizes and types from the bottom on which it lives, but has to rely on what is at its disposal. Purely calcareous sand would result in a calcareous tube. Young animals use smaller grains than older ones: and on coarse bottoms, tubes are of coarser fabric than those formed on fine grained substrate. The outgrown worm carries a 70 mm long tube which measures 1 mm at the apex and 5 mm at the aperture. The apical portion of the tube in living position commonly projects above sediment surface and may become damaged. When it is repaired, sand is not arranged in a brick-wall pattern, but glued together irregularly by mucus. When the worm is active it does not fill the whole tube, so that the apical portion is empty. Mucus-sediment layers commonly cover the inner side of the apical tube end constricting the apical opening.

The worm is well segmented and consists of three parts. The head shows a ventral mouth, dorsal gills and carries a plate of hard tissue with two rows of spines that are composed of bristles. These two combs of stiff golden bristles close the aperture when the worm withdraws into its tube. Spines are also used to brush sand from the ventral side of the aperture to the dorsal side and thus produce a cavity in the sandy bottom in front of the tube. Afterwards bristle bundles and also about 32 mobile tentacles act as a filter preventing sand entering the tube when peristaltic movements of the body pump water through the tube. Suction is produced by contractions of the segmented mid-body

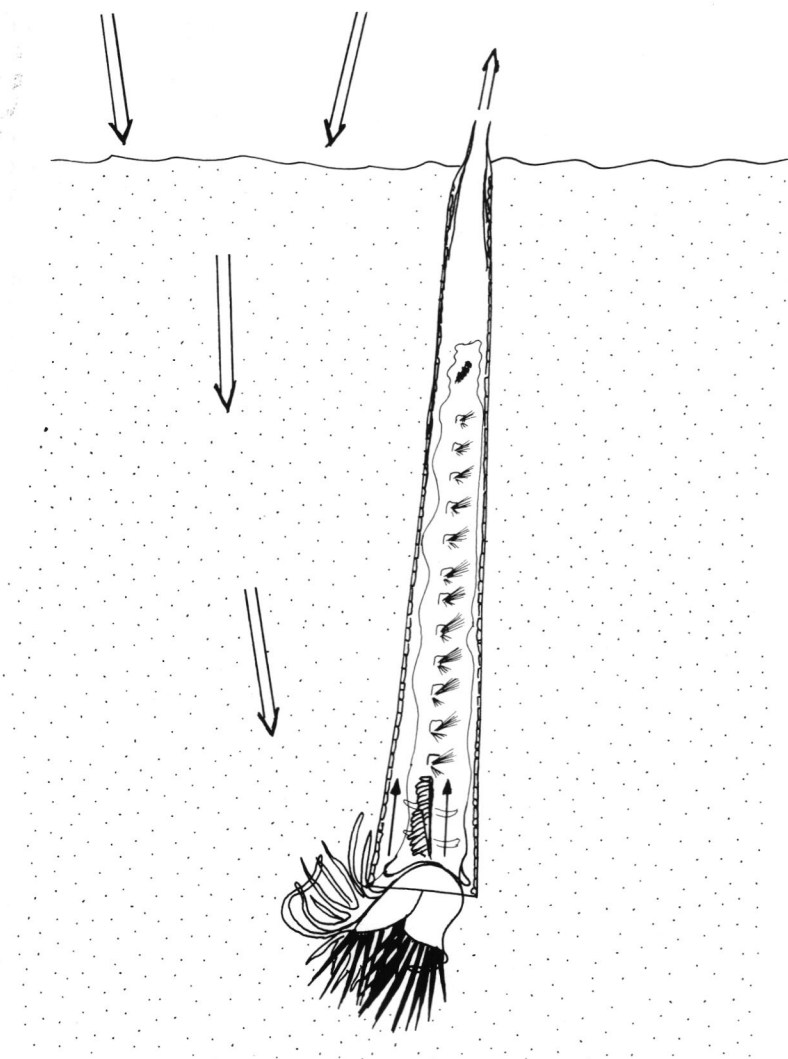


Fig. 23: Sketch of *Pectinaria* in living position in sandy sediment. Water is pumped out of the tube and sucked through the sediment surrounding the worm. In this way, suspended particles become enriched in the sand and can be harvested by the tentacles surrounding the worm's mouth.

within the tube and water is pumped from the head along the abdomen to be expelled above sediment surface through the narrow apical opening of the tube. Thus a continuous current is pumped by muscular contractions along the dorsal surface of the body. Water is sucked through the sediment in front of *Pectinaria* which is oriented in the sediment with almost vertical tube orientation. Suspended particles from the water are filtered out by the sand which becomes enriched with food collected by long thin mobile, extensible tentacles of gutter-like shape that surround the ciliated food collecting groove of the worm. The same tentacles can also select sediment particles which are to be used for tube construction in a similar way to *Lanice*. *Pectinaria* can thus live an almost sedentary life, but it can also move away or dig into the sediment, should conditions deteriorate. Once the worm has been extracted from its tube

it will soon die, even though body and tube are not attached and the position of the worm in its tube is arbitrary. Within its tube it is moved by 10–12 pairs of setae found on the thoracic segments and it is anchored to the apical portion by three claw-like bristles of the first segment of the abdomen. When the whole body is contracted the abdominal claws will pull the worm into its tube. When the animal defecates, the end of the abdomen is extended into the narrow tube end and current wash wastes out. In order to move within the sediment the animal's head bristles and tentacles dig away the sand in front. An animal washed out of its usual almost vertical position in the sand can burrow into the sand again by anchoring its head bristles in the sand, extending the body from its tube for quite some way and twisting it. A rapid release of this twist, along with contraction of the body, pulls and screws the shell into the sediment. Several such movements bring the worm into feeding position as long as the sand is wet. Once it has dried out, the worm can no longer bury itself in it.

Internal deposits in *Sabellaria*

The production of tubes in *Sabellaria spinulosa* (Sabellidae) from the Atlantic and the North Sea have been studied by several authors and data have been assembled and reviewed by SCHÄFER (1962). The planktotrophic larvae of *Sabellaria* swim from 2 to 8 months before they settle with a size of 0.4 to 0.7 mm (WILSON, 1968a). A purely organic tube is secreted within one or two hours and is enlarged in such a way that more and more particles of sand are included in its construction. Usually many larvae settle on the same spot and several tubes are, therefore constructed at the same time in close contact with each other. Worms grow up to form a single mass of tubes that will grow into the typical sand coral, i. e. a wave resistant mass of tubes composed of sand and organic mortar and an inner organic pellicle (WILSON, 1968b).

Each worm lives in a tube composed of sand grains and shell particles which are glued on top of each other like tiles or bricks. The interior of this tube, which is much longer than the actual worm, is coated by a thick and solid inner organic layer. When the tube becomes longer than is needed by the worm so it can withdraw safely into its shelter it is filled with sediment that is much finer than that used for the construction of its walls. This material is glued to the inner wall in conical sheets which leave a central tube that is as thick as the abdominal portion of the body. This central tube finally also becomes plugged.

Sabellaria shows three characteristic body divisions. The head consists of a pair of half-moon-shaped discs which are closely set with setae (bristles) arranged in three rows. These opercular setae can be pulled together to form a lid that can close the tube. When the animal is feeding the bristles form a comb on both sides of the head while the ventral mouth is supported by 3 pairs of tentacles (oral filaments) which catch food from the water passing by and through the bristle mesh. The central portion of the body (thorax) consists of 22 segments with pairs of parapodia of paddle-shape which are used for gas exchange along with large branchial appendages. A constant current moves down on the dorsal body and up again on the venter. Only the anterior three segments have bristles which are used to climb in the tube. The posterior part of the body consists of the thin abdomen that can be twisted forwards beyond the tube aperture when faeces are expelled. It is usually stretched backwards into the tube which is 5 times longer than the worm and produces the cone-shaped apical fills at the end of the tube.

Mode of life of *Ditrupa arietina*

Ditrupa arietina is a free living tube worm that is common in many soft bottoms of the Mediterranean Sea at depths greater than 40 m. The animals studied were dredged off-shore from Banyuls-Sur-Mer, France. In its normal living position *Ditrupa* lies shallowly buried in soft substrate with the apertural tube end at the surface, the apical tube end just below the surface and the curved portion of the conch pointing downwards.

The worm is composed of three portions, the head with a typical branchial crown of 10–12 filaments, the thorax with six segments and the abdomen with a large number of segments. One of the tentacles has been adapted to enable it to hold an operculum. This arm is thickened below the operculum, which consists of a concave organic shield usually covered by epibenthic organisms on the outside. The operculum is enlarged by a marginal shell growth and its whole lower surface is attached. When the tentacle crown is opened for feeding the operculum on its long stalk falls to the side and out of the way of the food catching filaments. Food particles move on the filaments towards the mouth and enter without the help of lips. *Ditrupa* exploits the suspension as well as deposits on the sediment near the tentacle crown. Peristaltic movements of the body create currents which wash through the tube. Faeces are expelled through the apical aperture of the tube and consist of mucus-covered narrow sinuating rods.

Ditrupa can alter its position on the sediment, it can leave its location and escape burial. In the experiment 3 cm of fine silty sand deposited on the worm were overcome. The way in which *Ditrupa* moves is quite different from that of other tube-living organisms such as *Dentalium-Pectinaria*, *Caecum* or caddis fly larvae. While moving, *Ditrupa* employs the operculum-tentacle as a piston, the tentacle crown is used as an anchor and the twisted body serves as a drill. When the worm has become covered by sediment it climbs up in its tube by setae movement of the thorax and at the same time pushes sediment away from the tube aperture with the help of its operculum-tentacle which acts as a piston with the other tentacles wrapped around it as enforcement. The whole crown pushes a cavity open and widens it by rotating movements until sufficient room has been made and the collar of the anterior thorax can thus extend over the apertural edge of the tube. Now the tentacle crown unfolds and filaments are pushed into the sediment and anchored in it. The worm inside of its tube twists its body by 90–180°. This twist is released at once and the body retracts slightly. The jerk pushes the tube to one side and up. Many such jerks will finally transport the tube to the sediment surface and into its preferred position there, it can also transport the tube on the sediment to a preferred location.

The fossil record of *Ditrupa* tubes can easily be confused with scaphopods like *Cadulus* and with the tubes of attached living worms as was probably done by MÜLLER (1969) in the case of *Ditrupa mosae* from the Upper Cretaceous of Belgium. However, the genus *Ditrupa* seems to be quite old, and can at least be found in characteristic shape and structure as early as in Lower Jurassic times, in quite similar surroundings to those in which recent forms on a muddy bottom in 40 to 1500 m depth have been found (own observation).

Structure and formation of the tube of *Ditrupa arietina*

The tube of *Ditrupa* consists of high Mg-calcite and organic material. Its outer surface is smooth with fine lines of growth. Most tubes show regular to irregularly undulating surface and more or less clear varix-like thickenings. On adult individuals such varices were found about 1 cm from the aperture and 3 varices can be observed on many individual tubes. A varix may represent an

interruption of normal shell growth during winter, and if so, animals are at least three years old when fully grown. But winter temperatures do not make much difference below 50 m depth in the Mediterranean Sea so that varix formation cannot be safely related to the ontogenetic cycle of *Ditrupa*.

The tube is regularly bent with a somewhat stronger curvature in its early portion. Tube diameter increases slowly so that apical angle only amounts to about 3°. Complete specimens reach a tube length of 35 mm and a width of 2 mm. The worm inside this tube measures 20 mm when the body is contracted, when active and stretched it fills the whole tube except the very narrow end, which is broken off in many specimens. The initial tube is about 0.2 mm wide and open on both ends. It forms in a similar manner to that of *Protula* and *Pileolaria*, but remains unattached in further growth like that of *Pectineria*.

The tube grows on its apertural end by adding shell material to the apertural rim (inner layer) and to an inclined zone outside of it (outer layer). The outer layer is transparent and its extension on the outer side of the tube depends on the width of the collar of the first segments of the thorax. The inner layer is white to reddish in colour and shows a fine annulation of its inner surface which serves as a holdfast for the bristles of the worm that climbs up and down in its tube. In this sections and when the tube is slowly decalcified with diluted acetic acid growth lines of both layers become well visible. The outer layer shows slightly sigmoidal zones of more or less strongly calcified layers that follow the contour of the aperture. Organic material is more concentrated in periods of insignificant tube growth. The inner layer shows evenly bent lines of apposition at the end of the tube only. A sharp boundary divides both layers (pl. 10, figs. 3 and 5).

When the tube is fractured and both layers are viewed with the SEM, additional structures are revealed. The outer layer consists of rods of highly organized high-Mg-calcite that starts its growth on the dividing line of both layers with a somewhat spherulitic structure. The rods are oriented in a vertical position to the surface of growth and show a composition of regular beam-like crystallites. In a superficial way this structure resembles a crossed lamellar structure. Three vital differences can however be noted: 1.) No basal units (elements) compose the needle or beam-like crystallites of the rods; 2.) each of the rods forms an independent intitety of no uniform pattern (3. order lamellae are absent); 3.) and material consist of a different modification of the calcium carbonate, not aragonite but high-Mg-calcite (pl. 10, fig. 1 and 2).

The inner layer is composed of an irregular meshwork of needle-like crystallites reflecting their rapid formation within an organic slime added to the tube margin. In polarized light thin sections of the tube reflect this difference of structure by showing zones of similar extinction vertical to growth surface in the outer layer and a dark inner zone at the inner layer.

5. Reconstruction of "*Hyolithes kingi*" as Annelid Worm

General features among tube-living annelids

Members of the polychaete families Sabellariidae and Serpulidae construct tubes in which they live but to which they are not attached. Although similar in this respects, ORRHAGE (1980) considers both families as not closely related to each other. Both Annelida Sedentaria construct tubes using a variety of different substances; many Serpulidae secrete calcareous material; Sabellariidae, in contrast, prefer to agglutinate particles with mucus. The Sabellariidae feed by

use of clusters of extensible tentacles originating around the mouth. The branchial crown of serpulids also acts as respiratory apparatus and is composed of a circular fan in which each of the filaments has fringes of side pinnules which bear cilia of two sorts. Long lateral cilia drive water current upwards between the pinnules towards the centre of the crown. Food particles from this current are intercepted by frontal cilia, carrying them along to the base of the pinnules, after which they pass in mucus strings down the filaments to the mouth. In many serpulids, one of the pinnae (radioles) is modified into a stalked conical plug, forming an operculum to close the mouth of the tube.

In sabellariids, rows or semicircles of bristles on the strongly modified head serve as operculum. Tentacles surround the mouth and have only transport cilia that carry intercepted or sorted particles to the tentacle base. Here gas exchange is not connected with the feeding apparatus. Leaf-like or strongly branching paired gills as outgrowths of the thoracic limbs produce respiratory flow.

Both groups of modern Annelida Sedentaria consist of a large number of sessile benthic species and a much smaller number of benthic vagile species, such as *Ditrupa* and *Pectinaria*. Both genera can be traced back into Early Mesozoic time. The branchial crown and the operculum of free-living *Ditrupa* resemble that of the attached *Pomatoceras*. The head with its semicircles of bristles and the tentacles in the vagile *Pectinaria* is similar to the of the sessile *Sabellaria*.

Tubes of worms have a great range of structures from purely aragonitic on one side to agglutinated sand and shells and calcareous walls on the other side. A number of species of serpulids construct tubes of a rather characteristic morphology while others have few features that can be used for the differentiation of species.

The inner cavity of tubes may remain open, or may be closed by inner walls or by attached particles of sediment. *Sabellaria*, for example, fills the posterior portion of the tube with well sorted, fine sediment; *Pectinaria* restricts the diameter of the posterior tube by conical collars of organic material and fine sediment; *Pomatoceras* closes off posterior portions of the tube by septa. Many worms can thus reshape the apical interior of their inhabited tube.

Considering calcareous tubes, a variety of structural and constructural types are observed. The ontogenetically earliest tube is always organic, and the inner lining of each tube is also organic. LOWENSTAM (1954) observed that cold-water species have calcitic tubes, while tropical species construct mainly aragonitic tubes. BORNHOLM & MILLIMAN (1973) found that more than temperature control, as in LOWENSTAM's suggestion, generical differences control the carbonate mineralogy of serpulids. Deposition of minerals like aragonite and calcite are species-specific and only to a very limited extent under environmental control. While some species use exclusively aragonite, others only use calcite and some use both modifications of the calcium carbonate in their tubes. NEFF (1971) observed that some serpulids are able to produce aragonite and high Mg-calcite in different gland zones at the same time. To conclude: Serpulid worms construct their tubes of organic material, high Mg-calcite, aragonite and low Mg-calcite or a mixture of these. There seems to be no apparent systematic correlations visible as yet.

Regarding the structure of the tube deposits, studies concerned with thin-sectioned tubes and light optical methods of observations (REGENHARDT 1961; LOMMERZHEIM 1979) commonly reach results different from studies in which the Scanning Electron Microscope (SCAN) was used. The problem can be understood when figs. 1 and 2 and figs. 3 and 5 (pl. 10) of the tube of *Ditrupa* are

compared. In the SCAN-photo (pl. 10, figs. 1, 2), the fabric of the crystal structure, the false "crossed lamellar structure", shows well while in the optical view through a thin section (pl. 10, figs. 3, 5) the pattern of growth additions predominate over the other features. TEN HOVE & ZIBBROWIUS (1986) noted large differences in structural types ranging from simple irregularly prismatic in *Laminatubus* to complex, regular feather-like prismatic in *Placostegus*. Even though, up to date, not much is known about the structure of the tubes of most species of serpulids, it can be stated that, in contrast to the molluscan shell for example, tubes of related polychaete worms may be constructed in a different way and may be composed of different material. The onset of tube construction in polychaete worms seems to be very similar throughout, and no differences in size, morphology and shape are noted when the settling larva had been living in the plankton for a long time, or when it had only been swimming for minutes or a few hours before final settlement to the substrate.

Reconstruction of a possible life of "*Hyolithes kingi*" as a worm

Modern polychaete worms belonging to Serpulidae and Sabellariidae have hard parts that are similar to those of hyoliths like *Hyolithes kingi*. But when all morphological features of the tube and the operculum of *Hyolithes kingi* are assembled, the outcome is neither a member of the Serpulidae nor one of the Sabellariidae; but it is an intermediate form with characteristic features of its own. Cambrian hyoliths, salterellids and volborthellids belong into one, probably monophyletic group of animals with a conical tube constructed of calcareous, organic and agglutinated materials. Similar materials are used by Annelida Sedentaria of our time when serpulids and sabellariids are seen as a unit. The conical tube of the fossil hyoliths was not attached and the animals lived free on

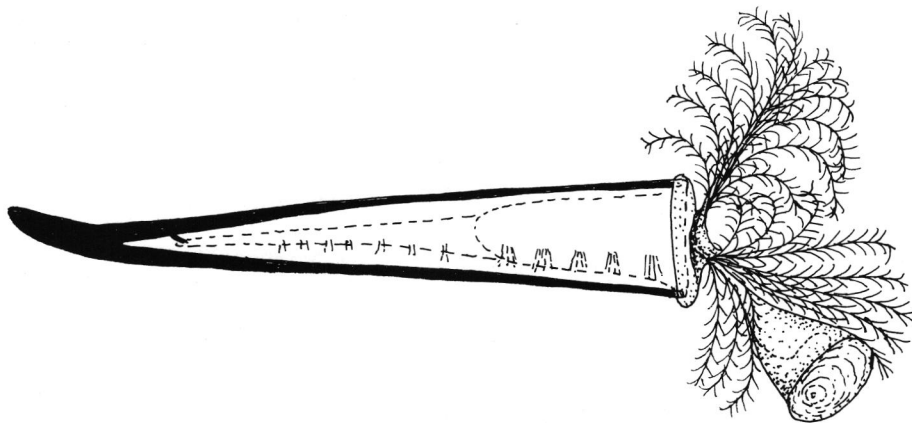


Fig. 24: A possible reconstruction of *Hyolithes kingi* as tube-living worm similar to modern *Ditrupa*. (From BANDEL 1983, Fig. 9).

soft bottoms; similar to modern polychaetes like *Ditrupa* and *Pectinaria*, but in contrast to them with only one aperture to the tube. As in a number of modern serpulids, *Hyolithes kingi* carried an operculum that is quite similar in shape to some spirorbid opercula. Assuming this hyolith operculum was secreted and held by one of the radioles of the branchial crown, as in serpulids, the head of hyoliths, salterellids and volborthellids can be reconstructed as a circular fan composed of two main stems branching into numerous ciliated pinnules. This crown with feather-like radioles was used for respiration as well as feeding. Some hyoliths produced two long, slender horn-like processes, the helens,

which also issued from the head. These find no obvious counterpart in any organ of modern Annelida Sedentaria.

Shell structure of some hyolith tubes reflect a composition of high Mg-calcite of false crossed lamellar habit as is seen in modern *Ditrupa*. Tube fillings of hyoliths such as *Hyolithes kingi* in general shape are similar to those found in modern *Sabellaria*. As this worms, *Hyolithes kingi* had an abdominal portion of its body that was much thinner than the thoracal portion. Here it had claw-shaped bristles that anchored the worm in its tube. When faeces had been expelled, the abdominal end was twisted forwards and projected beyond the aperture, as is the case in modern *Sabellaria*.

Septa in the tube of *Hyolithes kingi* and many of its relatives were produced in a similar way as in recent *Pomatoceras* and for similar reasons. They sealed off portions of the tube that were no longer inhabited by a worm that had grown in size.

The larvae of *Hyolithes kingi* can have settled like modern larvae of tube worms. The earliest tube section does not reveal whether the larva had lived in the plankton for some time, or had settled right after hatching from the egg, since polychaete larvae do not carry a tube. *Hyolithes kingi* may have lived several years, such as modern *Ditrupa*.

As result, *Hyolithes kingi* (together with its hyolith relation, salterellids and volborthellids) is an extinct representative of a monophyletic group of the Annelida Sedentaria that in earliest Cambrian or Late Precambrian time had a common ancestor with the Annelida Sedentaria that are represented by Sabellariidae and Serpulidae in the recent fauna. *Hyolithes kingi* can be reconstructed by comparison with modern polychaete tube worms. Tubes of probably serpulid and sabellariid origin can be found in the Early Paleozoic rocks indicating that all three types of tube producing polychaetes are in existence since the beginning of the Cambrian time. While sabellariids and serpulids survived into our time, hyoliths became extinct with the end of Paleozoic time.

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Plate 1

- Fig. 1: Outcrop of Cambrian rocks of about 1.6 m thickness near the mouth of the Zarga Ma'in river at the NE-shores of the Dead Sea. The arrows point at the hyolith-bearing layer.
- Fig. 2: Thin section of tube of *Hyolithes kingi* with the operculum still present within. $\times 50$.
- Fig. 3: Thin section of other biogenes and small *Hyolithes kingi*. $\times 60$.
- Fig. 4: Cellular echinoderm fragment found within the hyolith-bearing limestone. $\times 60$.

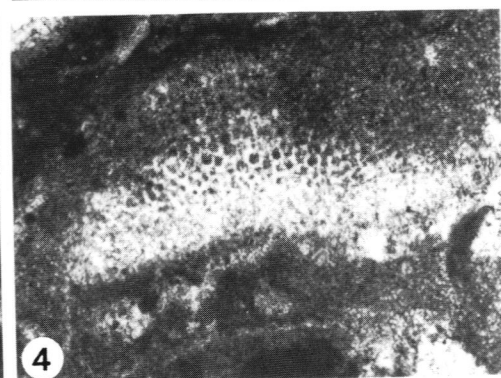
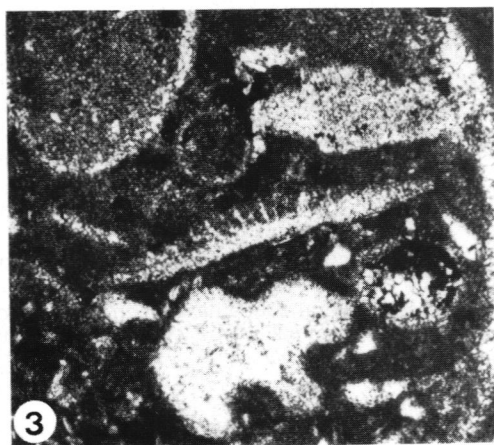
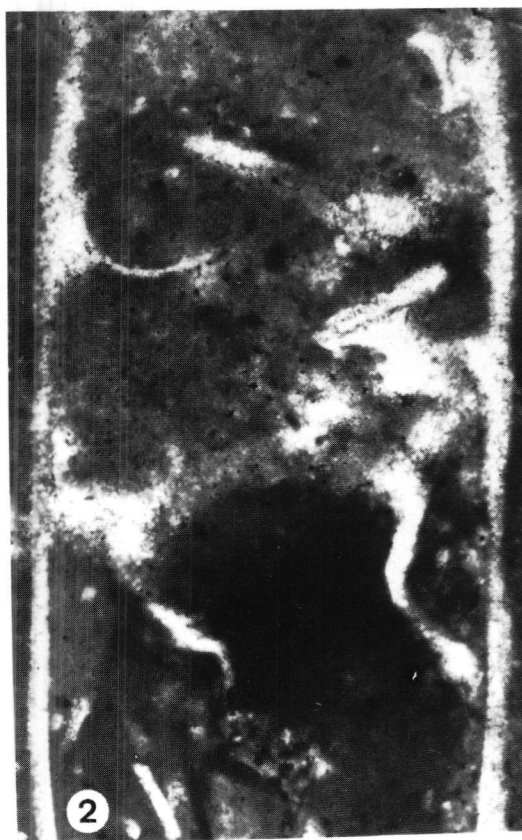
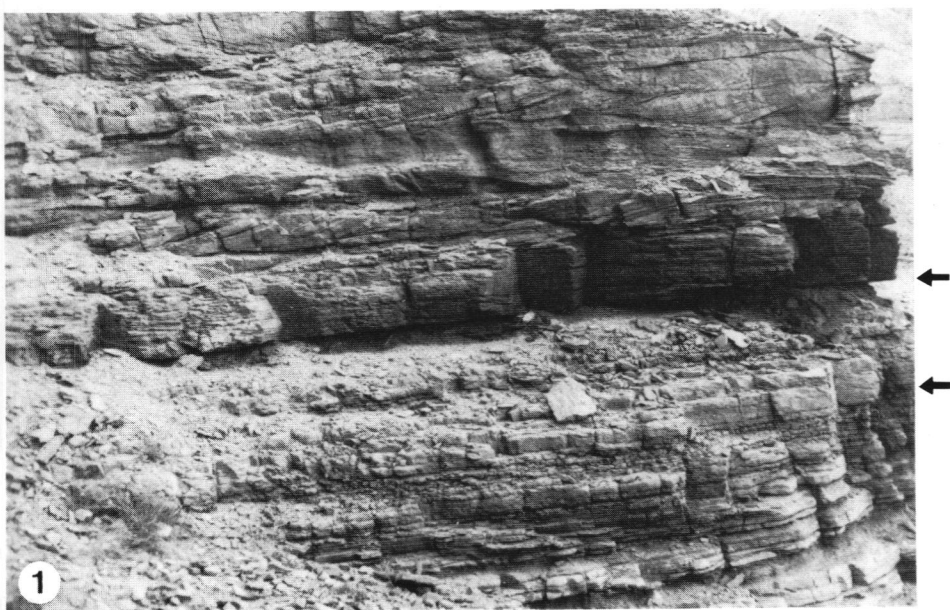


Plate 2

Thin sections of *Hyolithes kingi*

- Fig. 1: First septum in an individual tube still curved and with little internal, apical additions. $\times 50$.
- Fig. 2: Apical plug of a tube that has broken away from a larger individual. The apical part of the tube was fractured, and the central canal became filled with sediment. $\times 30$.
- Fig. 3: The last formed apical plug is very large. It covers a septum that closed off an apical space with a small plug and a fine sediment filling. $\times 10$.
- Fig. 4: Apical end of hyolith with angular corners where the apex broke off and with small internal shell additions to the sides and the septum. $\times 35$.
- Fig. 5: Apical end of hyolith with septum and apical fracture corners without internal tube additions. $\times 35$.
- Fig. 6: Apical end of hyolith with apical angular corners and internal shell additions only to the apical sides. $\times 20$.
- Fig. 7: Several tubes pushed into each other have been cut vertical to their long axes. $\times 10$.
- Fig. 8: Several tubes have been pushed into each other before final burial. The ventral side of each tube is less rounded than the dorsal side. $\times 10$.

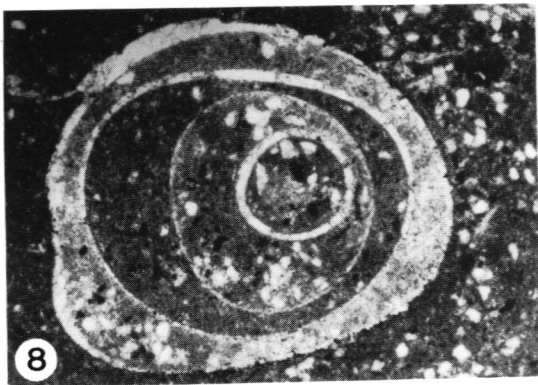
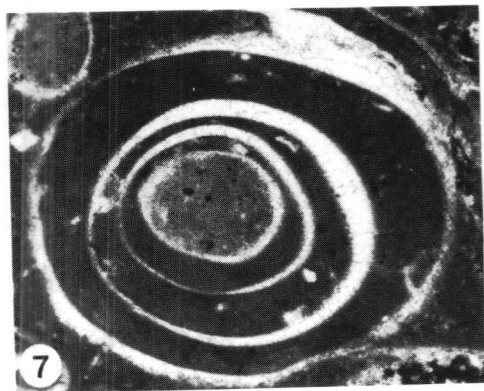
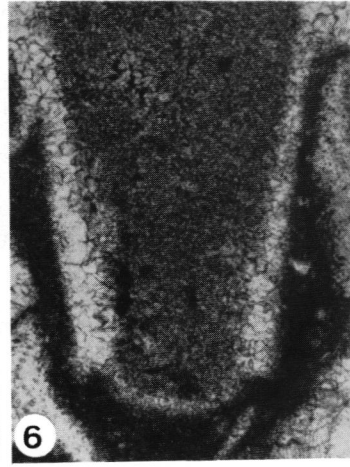
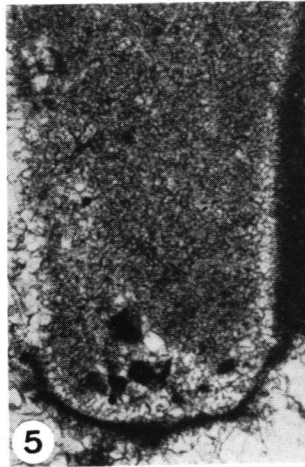
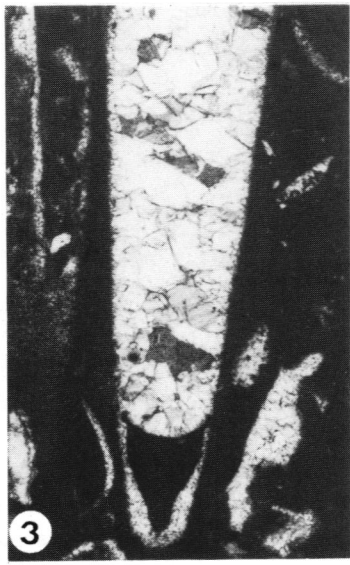
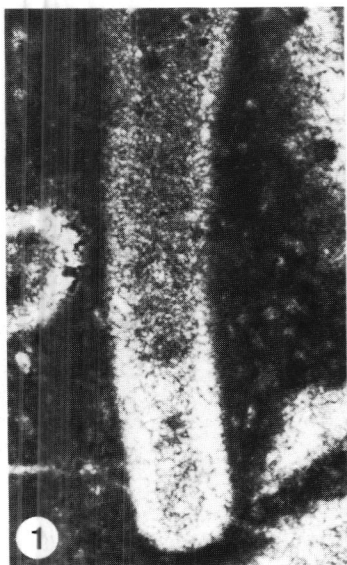


Plate 3

All thin sections of *Hyolithes kingi*

- Fig. 1: Hyolith tubes pushed into each other to form a pile of 4 visible individuals, each with a different apical fill structure. $\times 4$.
- Fig. 2: The large tube shows a short apical fill and contains two more tubes, the smallest representing the most apical and ontogenetically earliest portion of an individual tube. $\times 4$.
- Fig. 3: Hyoliths cut in all directions. The central lower one shows straight and curved external shape and apical fill plugs of different size. The fossil between tubes is a part of a trilobite. $\times 4$.
- Fig. 4: Apical tube fill (recrystallized spar) with central tube filled with fine-grained sediment and sealed off by a septum (lower centre). $\times 15$.
- Fig. 5: Apical spar plug cut along the central tube. $\times 30$.
- Fig. 6: Apical fill structure with conical shape. $\times 20$.

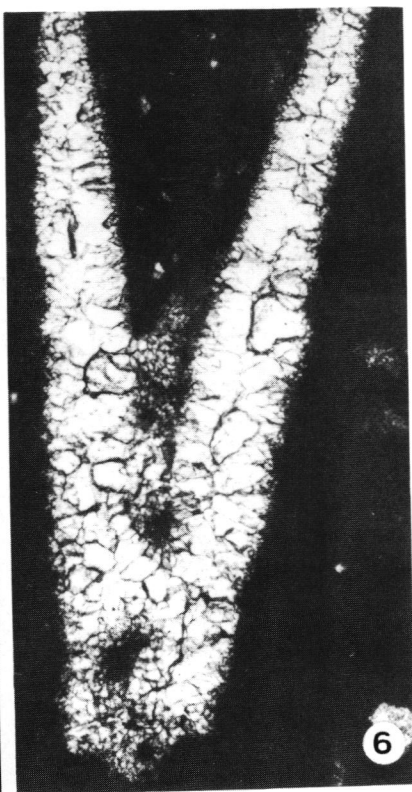
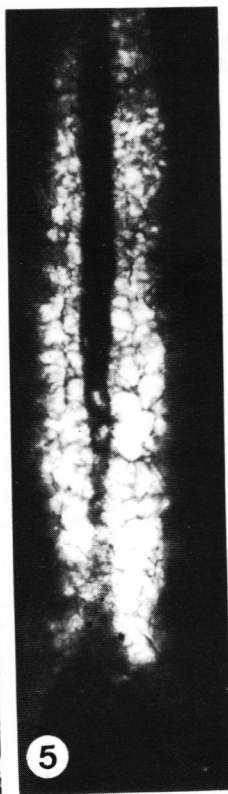
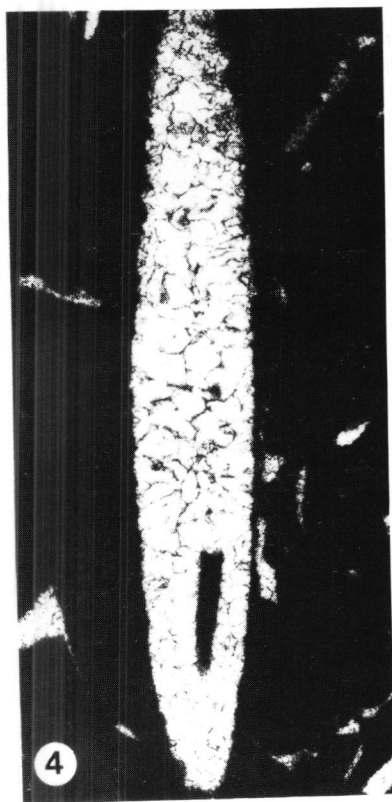
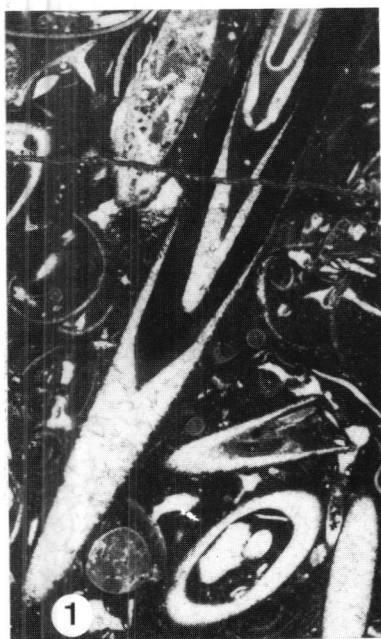


Plate 4

All thin sections of *Hyolithes kingi*

Fig. 1: The operculum of *Hyolithes kingi* cut vertically, with inner projections cut symmetrically. $\times 50$.

Fig. 2: The operculum of *Hyolithes kingi* cut vertically cut inclined to symmetry. $\times 50$.

Fig. 3: Operculum of young individual cut vertically. $\times 60$.

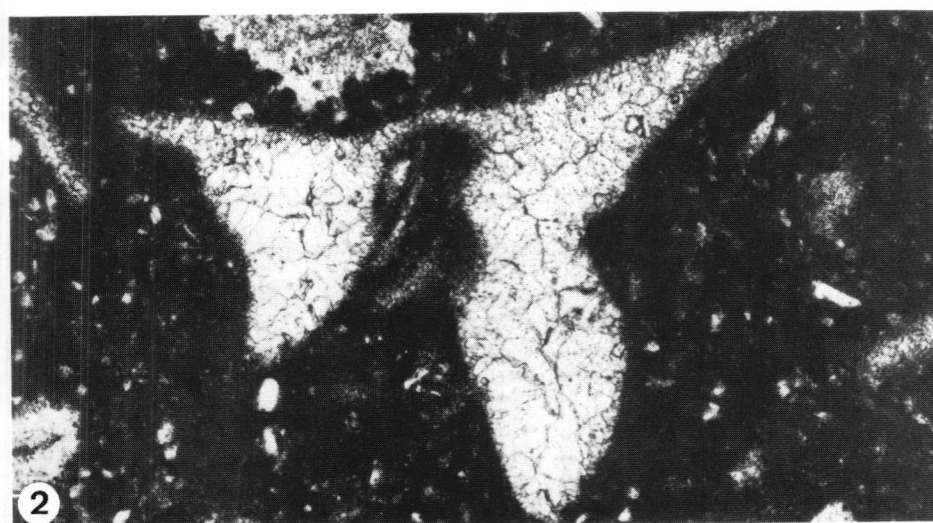
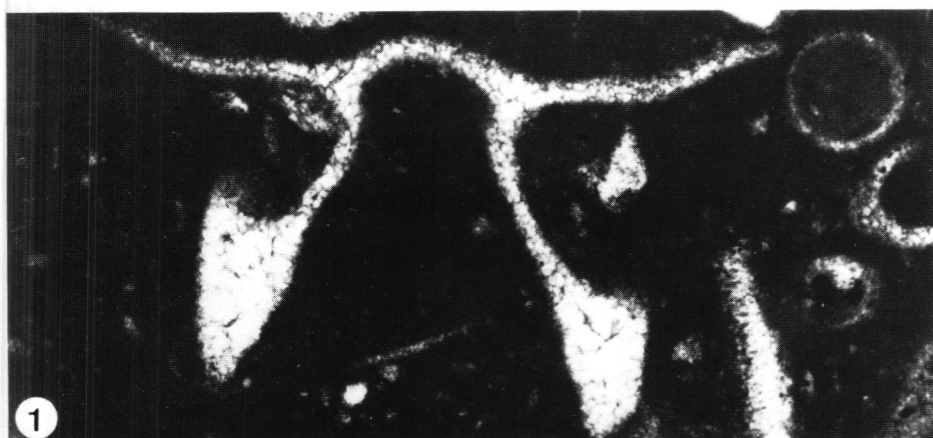


Plate 5

Photographs of thin sections

- Fig. 1: *Salterella* cut along the central canal. $\times 20$.
- Fig. 2: *Volborthella* cut along the central canal. A wide chamber (tube section) lies in front of the fill structure. $\times 20$.
- Fig. 3: Sections vertical to the long axis of *Salterella* show the central canal within the conical fill structures. $\times 20$.
- Fig. 4: *Volborthella* with a long and sediment-filled tube anterior of the "chambered" posterior portion. The tube wall was organic. $\times 20$.
- Fig. 5: *Volborthella* with well preserved central canal that was closed with independent septa closing off different portions of sediment fill. $\times 20$

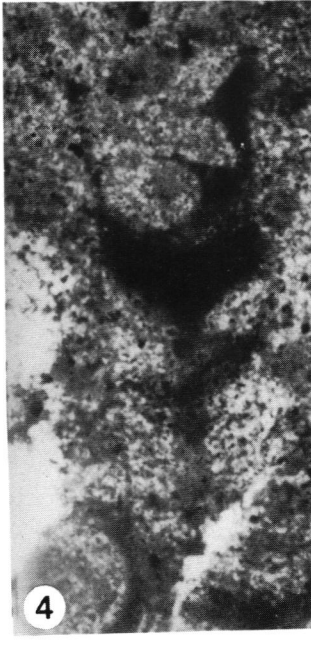
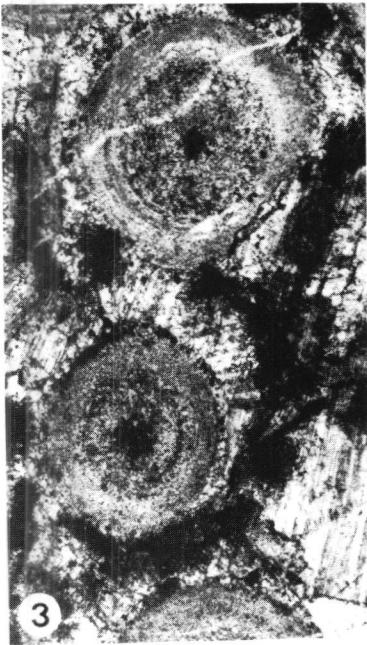


Plate 6

- Fig. 1: The sectioned hyolith from the upper Lower Cambrian of Australia with septum and inner shell additions. The closed part of the tube is filled by cement crusts and the open tube by coarse sediment. $\times 40$.
- Fig. 2: Thin section of hyolith from the Lower Cambrian of Sweden showing a much less bent ventral than dorsal side. $\times 40$.
- Fig. 3: Section through hyolith (like Fig. 2) demonstrating the chambered apical portion of the shell as well as different wall and septum thickness. $\times 60$.
- Fig. 4: Wall of hyolith (like Fig. 2) preserving the inclined additions of calcareous layers to the tube from inside. Polarized light. $\times 150$.
- Fig. 5: Section of anterior tube of hyolith (like Fig. 2) that is still closed by the operculum in its original position. $\times 50$.

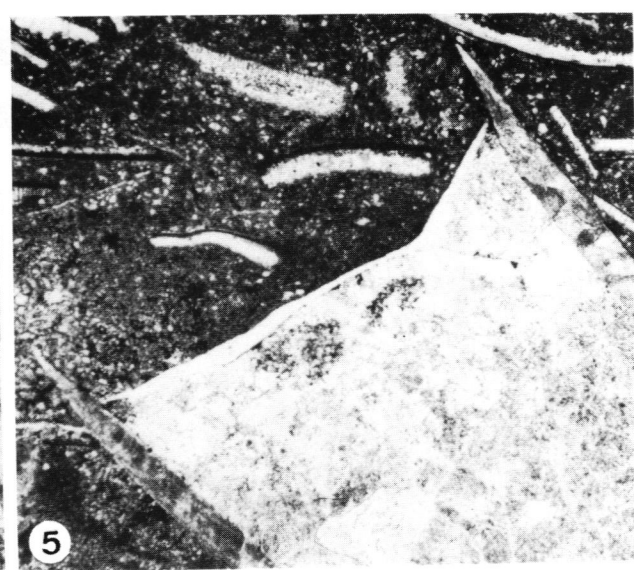
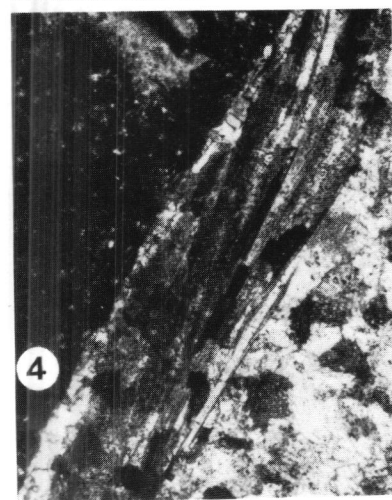
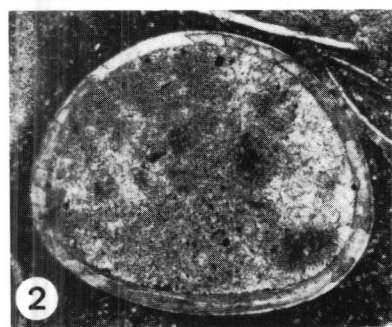
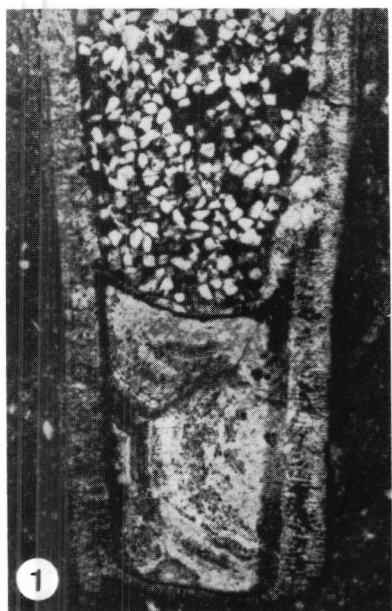


Plate 7

Thin sections of "*Hyolithes kingi*" from slightly deformed and recrystallized carbonates of Lower Cambrian age from the Montagne Noire, Southern France.

Figs. 1 and 2: Opercula with characteristics processes (downward) and lid with inclined rim. $\times 40$.

Fig. 3: Several tubes pushed into each other and cut parallel to tube axis. $\times 15$.

Fig. 4: Apical shell addition in the tube look like those of *Hyolithes kingi* from the Dead Sea. $\times 10$.

Fig. 5: Tubes are parallel to each other due to current orientation and are usually several are pushed into each other. $\times 3$.

Fig. 6: Several tubes pushed into each other show different degree of apical fill. $\times 5$.

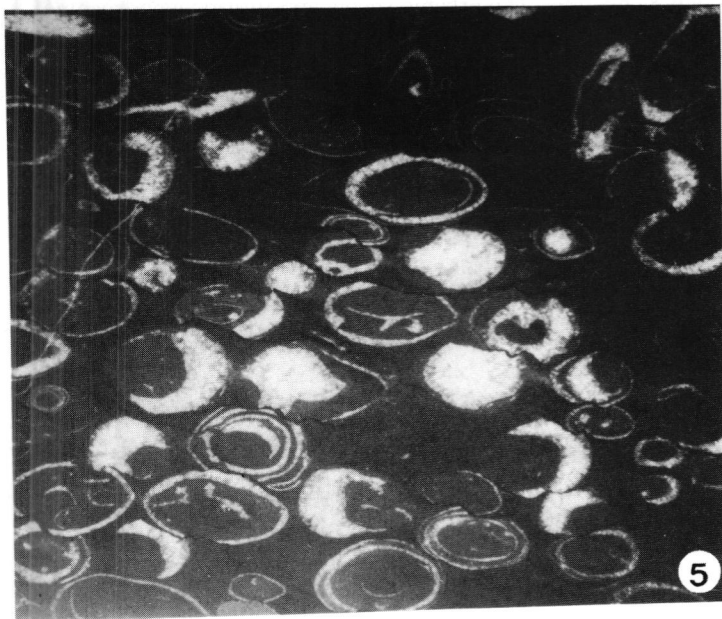
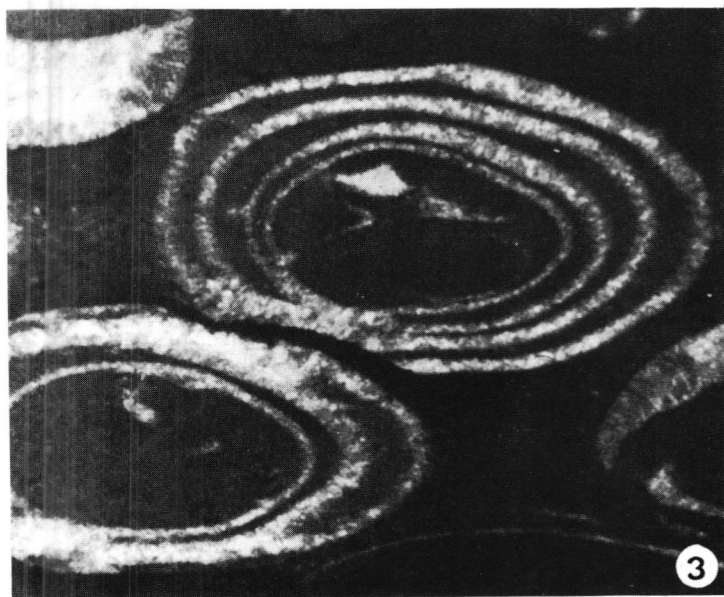
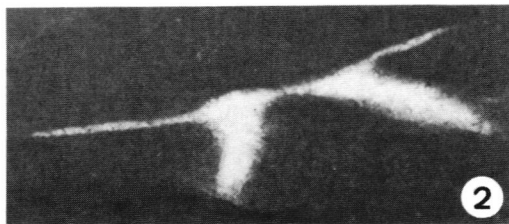
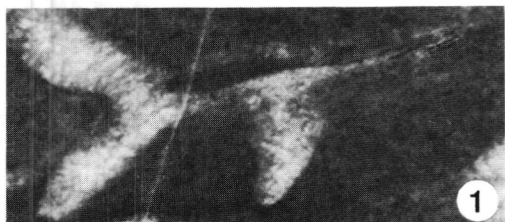


Plate 8

- Fig. 1: *Pileolaria* opercula. The upper is the calcareous protective cover of the brood chamber, followed by an operculum not covering a brood chamber; both still attached to each other by tissue of the arm. $\times 50$.
- Fig. 2: *Pileolaria* opercula. Both represent calcareous covers of brood chamber in an individual where a hatched brood chamber was replaced by a new brood chamber. The spiny ornamentation of the operculum varies. $\times 50$.
- Fig. 3: A *Pileolaria* operculum not connected to a brood chamber, seen from the upper side, shows the concave lid and the projecting talon. $\times 80$.
- Fig. 4: *Pileolaria* operculum (like Fig. 3) seen from below with projections that extend into the tissue of the arm. At the grooves, the tissue of the arm is attached. $\times 80$.
- Fig. 5: The tube of a newly settled *Protula tubularia* is mineralized and attached to the substrate only by organic threads. $\times 60$.
- Fig. 6: Septum in the tube of *Serpularia*. The organic sheets and threads have become mineralized and holes have mostly become closed by mineral layers except the bigger one (lower right) that shows a backturned ("retrochoanic") rim. $\times 60$.

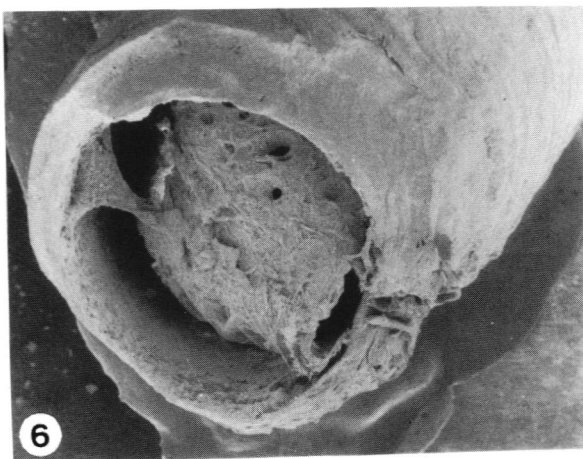
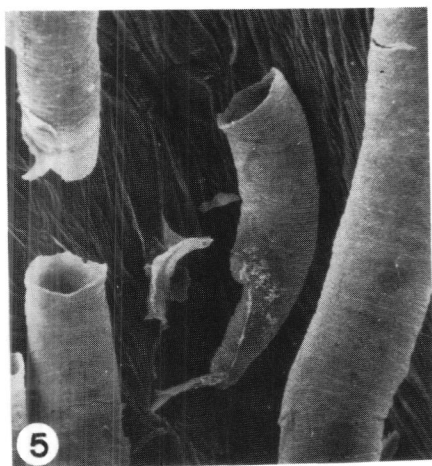
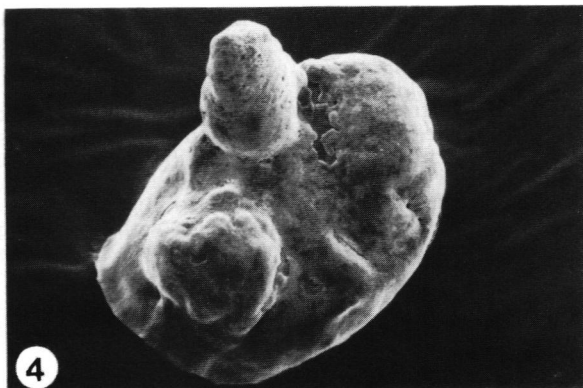
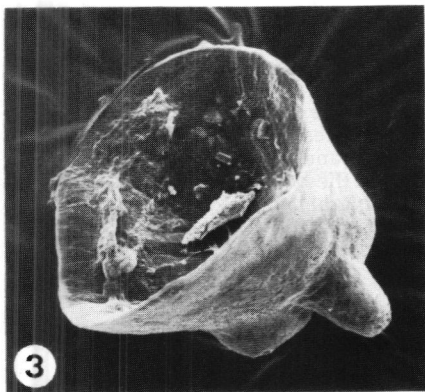
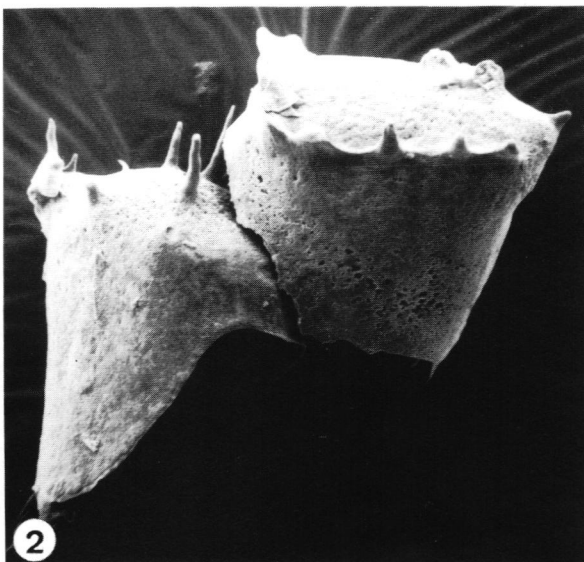
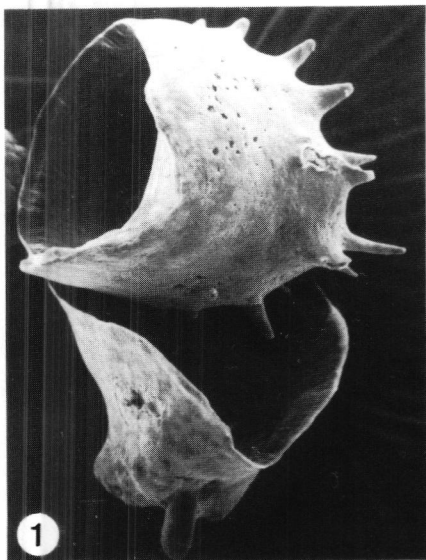


Plate 9

- Fig. 1: Young animals of *Protula tubularia* in their tubes. The tentacle crown is small since the worms have settled only a few hours before. $\times 25$.
- Fig. 2: Settling larvae and one just established metamorphosed young of *Protula tubularia*. $\times 25$.
- Fig. 3: Septum produced by *Pomatoceras* to close its tube at the apical end. A most apical hole (base) is accompanied by a row of holes on the sides. $\times 20$.
- Fig. 4: Septum in *Pomatoceras* tube with most apical hole and several holes still seen, reflecting the position of the bristles (parapodia) on the body of the worm. Later, these holes are closed by additional organic and mineral layers. $\times 30$.
- Fig. 5: Solid calcareous (calclitic) growth encrusting older septa in *Pomatoceras*. $\times 1000$.
- Fig. 6: The beginning calcification of the organic septum is spherulitic. Detail to Fig. 4. $\times 300$.

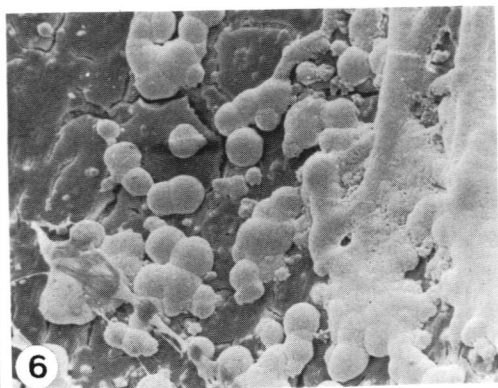
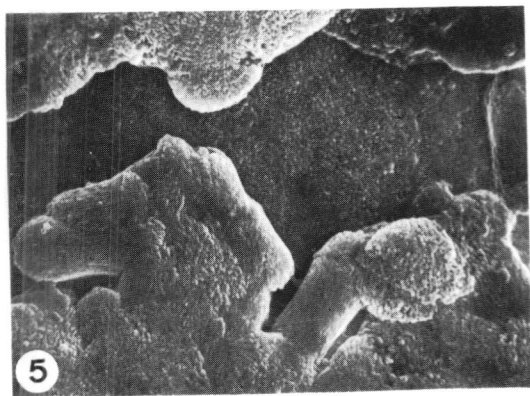
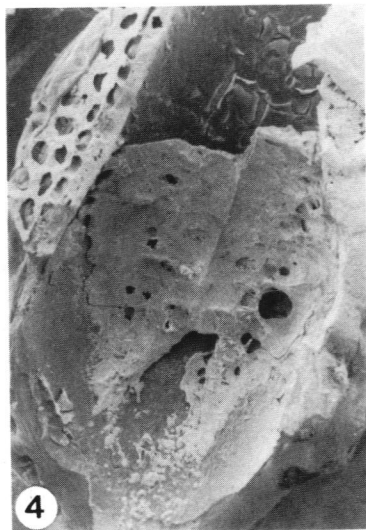
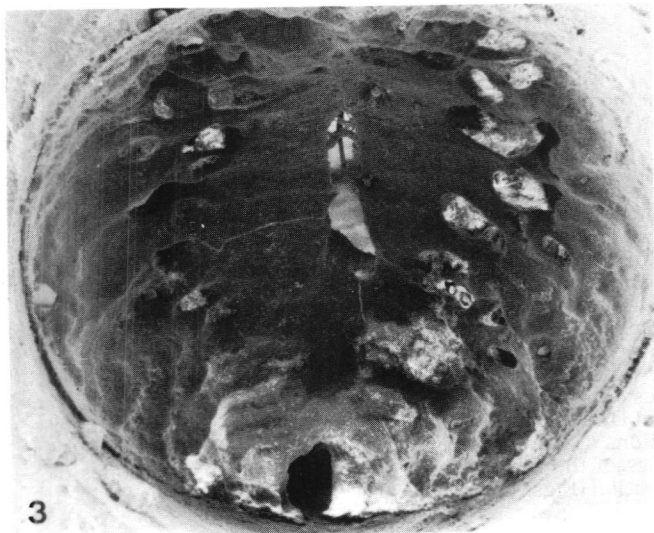
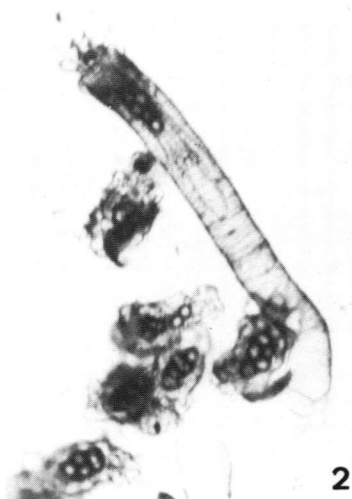
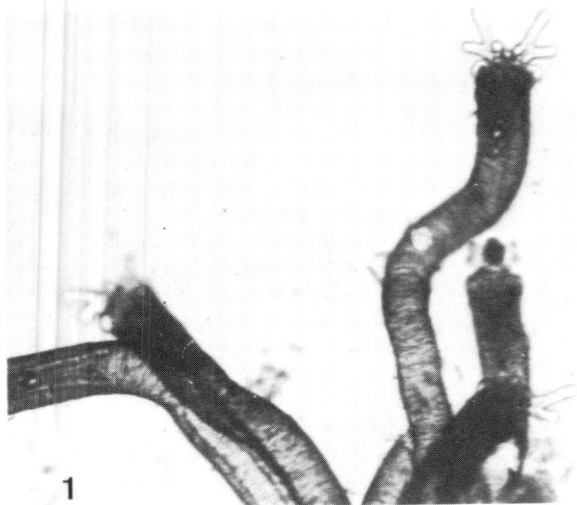


Plate 10

- Fig. 1: High Mg-calcite prisms of the tube of *Ditrupa arietina* are organized in zones with rods of similar orientation bordering other zones with rods pointing to a different direction. $\times 7000$.
- Fig. 2: The pattern seen in detail in Fig. 1 in less enlargement resembles the crossed lamellar structure which is present in many aragonitic shells of molluscs. But its organisation differs in details both regarding composition and fabric. $\times 3500$.
- Fig. 3: Thin section of the tube wall of *Ditrupa arietina*. The outer layer (left) shows well visible layers of tube additions with growth lines inclined towards the outside. The inner layer is opaque and rich in organic material (right). $\times 50$.
- Fig. 4: A fossil tube of an attached worm from the Upper Jurassic of Franken shows a characteristic pattern that could develop from a *Ditrupa*-like structure when organic material is decomposed. Here, the outer layer is as in *Ditrupa* (Fig. 3) while the inner layer has lost its high contents of organic material and shows an inclination of growth lines opposite to the outer layer. $\times 40$.
- Fig. 5: Transversal thin section of *Ditrupa arietina* under polarized light shows the inner layer (dark) with annulations of the organic material and the outer, more mineral layer with prismatic zones of the same optical character, representing zones of prisms of the same orientation (Figs. 1 and 2). $\times 50$.

