Larval development of hyolithids

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The larval development of hyolithids is inferred to have been closely similar to that of primitive gastropods. A trochophore-like larva produced a swollen initial conch and a convex operculum. The initial conch was either subsphaerical and smooth or fusiform with a pointed apex and growth lines. This is taken to indicate an initial development within egg covers or free-living, respectively. A pelagic veliger phase followed, preceded by hatching in the first case. Veliger shells are similar to adult ones. Metamorphosis (transformation of veliger into benthic adult animal) in both hyolithids and gastropods was accompanied by an increase in mortality.

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Very small hyolith shells are common in open-sea limestones of the Baltic Ordovician, usually occurring together with gastropod larval shells of similar size (Jaanusson 1960), and are also known from Cambrian sediments (Matthews & Missarzhevsky 1975; Marek 1976). They have been interpreted as representatives of minute species or as fossils of juvenile animals. During extraction of Ordovician conodonts from erratic boulders of Baltic origin and from the Mójcza limestone in the Holy Cross Mts, Poland (Dzik 1976, 1978), I collected a large number of such minute shells of gastropods and hyoliths preserved as chamosite moulds or casts. The majority of them have preserved an aperture. Large hyolithid shells are commonly associated with minute ones in the erratic boulders, but because of the slight difference in shell morphology of different species of adult hyoliths and the generalized morphology of the larval shells it is usually difficult to determine to which species the larva belongs. Hyolith opercula are relatively rare in fossil material. The reason is that they can be found in residues only as natural chamosite casts, which are not as common as the moulds.

It is possible to match some opercula with conchs on the basis of the shape of the aperture. Minute opercula do not significantly differ from large ones of the same species.

Morphology of minute hyolithid conchs and opercula

Minute hyolithid shells representing seven species occur in erratic boulders of Llanvirn and Llandeilo age (Kunda to Uhaku Baltic stages). All seven species have bulbous apical parts belonging to one of two types: (1) subsphaerical, smooth, separated from the remaining part by a callosity (Fig. 1A) or (2) fusiform with a pointed apex, marked growth lines and not quite as distinct a boundary with the remaining part as in the previous case (Fig. 1C). Typical ornamentation of adult hyolithid shells originated distally to the boundary constriction (Fig. 1; Marek 1976). Samples of minute hyolithid conchs show a characteristic size–frequency distribution (Fig. 2). There is a clear frequency peak and the histograms are somewhat right-skewed. The forms having the fusiform apical part with growth lines are characterized by a sharper peak of length frequency distribution than the forms with the subsphaerical smooth apex.

The central part of the hyolithid operculum is hemisphaerical (Fig. 3). Its diameter is similar to the aperture of the bulbous, apical part of the shell (Marek 1976). This is also true for some orthothecid opercula (see Matthews & Missarzhevsky 1975). There is a distinct boundary between this central, smooth part and the ornamented surface of the operculum. Opercula of the size comparable with the aperture of minute hyolithid shells have fully developed internal structures. They do not differ from opercula of similar large hyolithids (Fig. 7; Marek 1976).

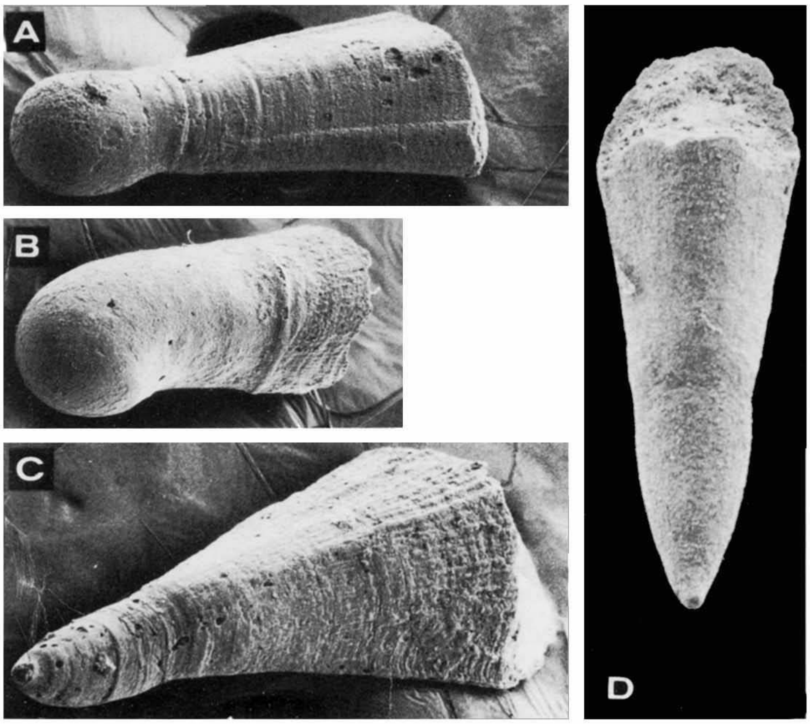

Fig. 1. Larval shells of hyoliths, chamosite natural casts, × 115. □ A. *Carinolites* cf. *tantulus* Marek, erratic boulder E-113, Upper Llanvirnian, Uhaku stage, *E. robustus* Zone, ZPAL GaI/1-006. □ B. *Nephrotheca* sp., same erratic boulder, ZPAL GaI/1-005. □ C. *Recilites* sp., same erratic boulder, ZPAL GaI/1-009. □ D. *Eomorpholites?* sp., erratic boulder E-145, Upper Llanvirnian, Lasnamägi stage, *E. reclinatus* Zone, ZPAL GaI/1-008.

Larval conchs of Early Paleozoic gastropods

Well preserved chamosite or limonite natural casts of Ordovician and Devonian gastropod larval conchs show a sharp boundary between the embryonal trochophore shell (prodissoconch I) and the larval veliger shell (prodissoconch II). Usually a callosity is developed at the distal end of the embryonal conch (Fig. 4A, C, D). The ornamentation of the shell begins in front of the callosity. The number of coils and the size of the larval shell unquestionably depends upon the egg size. The boundary between the larval and adult shells is usually indistinct with the exception of forms inferred to have been directly developed within the egg covers (lecithotrophic type of development). In such cases the entire larval shell is smooth and morphologically separated from the adult shell (Fig. 4B).

The larval conchs of Paleozoic gastropods do not significantly differ from those of Recent ones (Robertson 1971; Shuto 1974; Bouchet 1976). The callosity separating trochophore and veliger shells is formed at hatching or at transformation from trochophore to veliger. The trochophore shells developing within the egg covers are smooth and show a more distinct terminal boundary than shells of free-living trochophores. In the majority of Recent gastropods, a planktic

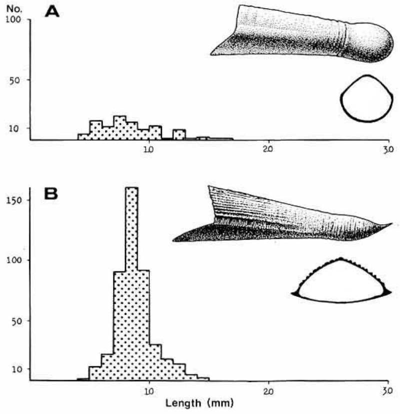

Fig. 2. Size–frequency distribution of samples of hyolithid larvae, erratic boulder E-145, Upper Llanvirnian, Lasnamägi stage, *E. reclinatus* Zone. □ A. *Carinolites* cf. *tantulus* Marek. □ B. *Recilites* sp.

veliger stage is followed by metamorphosis and a benthic stage. Most often this metamorphosis is not expressed in the external ornamentation of the shell.

Samples of fossil minute gastropod shells comparable in size and number of coils to Recent gastropod larval shells show a size–frequency distribution with a sharp peak in the size class corresponding to that of Recent gastropod veliger shells at the time of metamorphosis (Fig. 5). This may be interpreted as an effect of the increase of mortality during metamorphosis.

Interpretation of minute hyolithid shells

Comparison of minute hyolithid shells with larval gastropod shells shows a close similarity. No other phyla that have been compared with Hyolitha (Annelida, Brachiopoda, Sipunculoidea) show this type of development. The type of ontogeny typical of gastropods is the most primitive one within the phylum Mollusca. Similarly, cephalopod shells pass in ontogeny through the stage of subsphaerical embryonal shell, separated from the larval shell by a callosity or constriction (Erben *et al.* 1968). Primitive orthoceroids have larval shells somewhat expanded and slightly set off from the adult ones (Ristedt 1968). The conchs of *Janospira* from the Ordovician of Spitsbergen (Fortey & Whittaker 1976) show initial parts almost identical with those of bellerophontid gastropods (see Fig. 4D). The uncoiled apertural part of this conch is extended adaperturally by tubular excrescence of supposed selenizone (anal tube), which could be a larval structure as may be the case in *Yochelcionella* (Runnegar & Jell 1976). This fossil may be ancestral to the Scaphopoda (Runnegar 1977). Therefore, in respect to the morphology of the larval conch, hyoliths are similar to early representatives of several conchiferan mollusc classes, and their molluscan character is evident.

Fig. 3. Larval operculum of *Carinolites* sp., outer surface, initial hemisphaerical part visible, erratic boulder E-085, Upper Llanvirnian, Uhaku stage, *E. lindstroemi* Zone, ZPAL Gal/1-010, × 150.

By analogy to Recent gastropods it may be assumed that hyolithid shells were formed initially by a 'shell gland' of the trochophore. Supposedly, development of the trochophore in forms having smooth subsphaerical initial conchs proceeded within the egg covers (Fig. 6). The thick callosity characteristic of such forms may be connected with hatching. Fusiform initial conchs, ornamented by growth lines, were produced by free-living trochophores. The boundary between trochophore and veliger conchs is not very distinct here (Fig. 6). Growth lines might express changes of external conditions (see Fretter & Pilkington 1971). A convex non-ornamented operculum was produced by a germ of the foot (Fig. 6).

The larva led an active planktic life during the veliger stage. It produced an ornamented shell

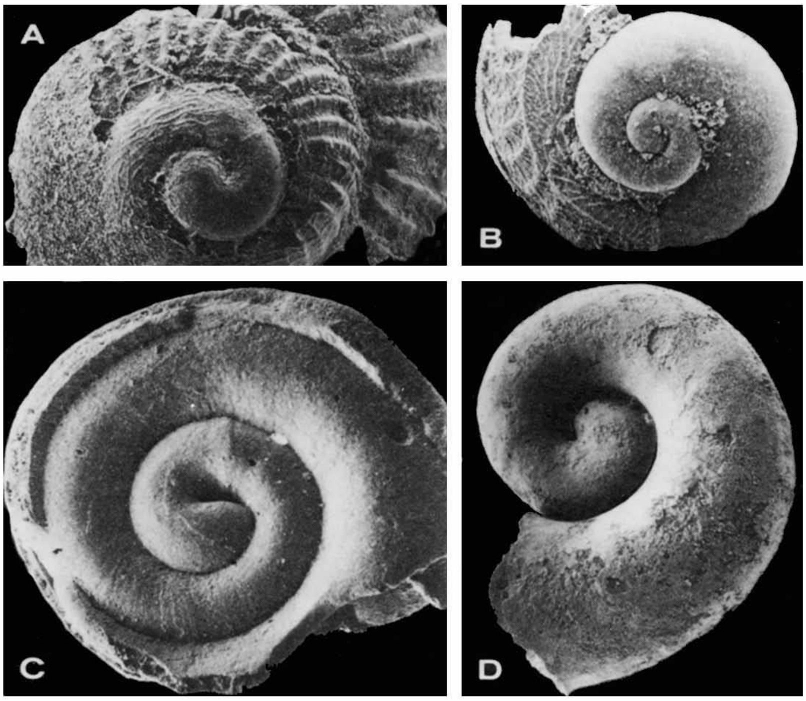

Fig. 4. Initial parts of shells of Paleozoic gastropods, ×100. □ A. *Naticopsis* sp., note small separated embryonal trochophore shell indicating planktotrophic type of development, Łagów-Dule, Famennian, natural limonite cast, ZPAL Gal/1-003. □ B. *Mourlonia* sp., large, smooth larval shell indicating lecithotrophic type of development, same locality, horizon and preservation, ZPAL Gal/1-004. □ C. *Leseurilla* sp., Mójcza Limestone, sample A-4, Upper Caradocian, natural chamosite cast, ZPAL Gal/1-002. □ D. *Modestospira?* sp., Mójcza Limestone, sample A-5, Lower Caradocian, chamosite mould of complete larval conch, ZPAL Gal/1-001.

more and more similar to the adult one, developing gradually a specific form of aperture (Fig. 6). Opercula of veligers have internal structures identical with those of adults (Fig. 7). The metamorphosis probably did not involve any fundamental anatomical reorganization.

Relations of hyoliths

The mode of larval development is very variable in the Mollusca. Therefore more detailed comparisons between Cambrian and Ordovician hyoliths and Recent gastropods might lead to misconceptions; for example, the most specialized Recent Pteropoda (Almogi-Labin & Reiss 1977) show a morphology of the initial conch very similar to that of the hyoliths. The different organization of the musculature excludes close relation of hyoliths to Recent gastropods. According to Marek (1963) and Marek & Yochelson (1976) muscle scars on the conch and operculum belong to muscles joining simply the cardinal process of the operculum with the convex side of the conch and the central part of operculum with the flat side of the conch. It is difficult to imagine such an organization of a mollusc body. Opercula of the primitive Ordovician gastropod *Maclurites* (see Troedsson 1928; Knight *et al.* 1964) apart from being asymmetrical, are morphologically very similar. These show processes and distinct retractor muscle scars. *Archinacella, Cyrtonella* and related monoplacophoran forms have transversally elongated pedal muscle scars surrounding the lateral sides of the conch; usually a posterior (adanal) pair of scars is the largest one (Horný 1965; Rollins 1969). I have also found such scars in Caradocian *Pharetrolites elegans* (Koken). Also, muscle scars on the shells of ancient cephalopods show similar arrangement (Mutvei 1957). All have a similar pattern to the muscle scars on hyolithid shells (Marek 1963). This suggests that the scars seen on the hyolithid conch belong to pedal muscles and the scars on the operculum to retractor muscles of the operculum. Occasional metameric arrangement of muscle scars in the conch is caused by step-wise growth (resulting also in the formation of septa). Similar 'metameric' muscle scars are common on nautiloid shells. Runnegar *et al.* (1975) constructed totally nonfunctional model of hyolithid soft parts with metameric pairs of vertical muscles connecting these scars. If muscle scars on the hyolithid shell really belong to

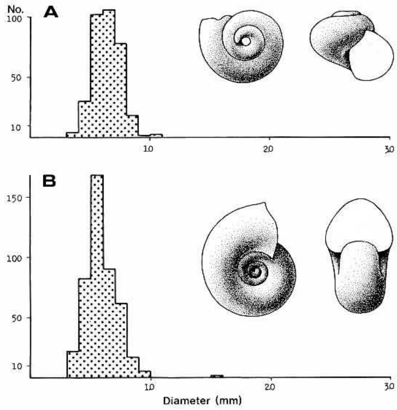

Fig. 5. Size-frequency distribution of samples of Ordovician gastropod larval shells, erratic boulder E-149, Upper Llanvirnian, Lasnamägi stage, *E. reclinatus* Zone. □ A. *Clathrospira elliptica* (Hisinger), whole larval development inside egg covers as in Recent *Pleurotomaria* (Hickman 1976). □ B. *Kokenospira estona* (Koken).

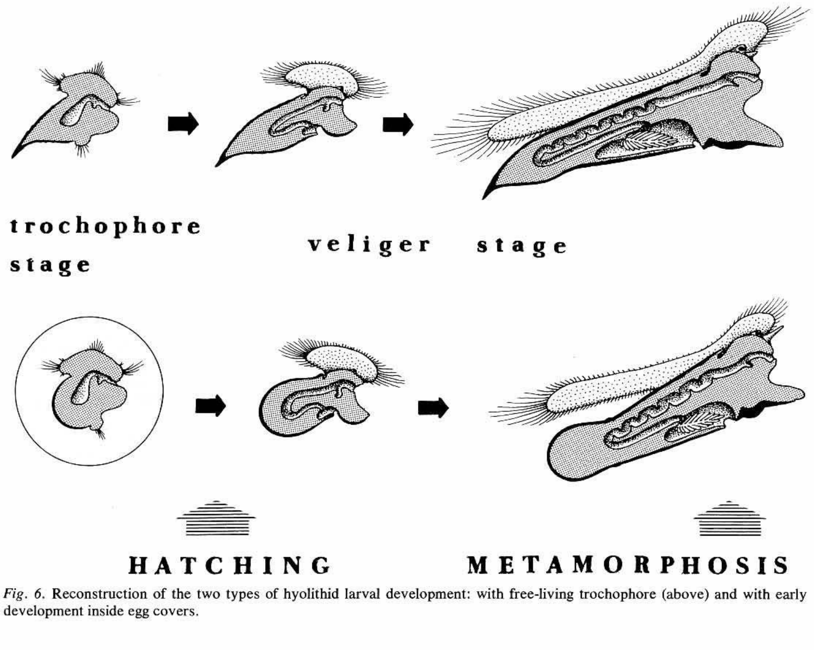

Fig. 6. Reconstruction of the two types of hyolithid larval development: with free-living trochophore (above) and with early development inside egg covers.

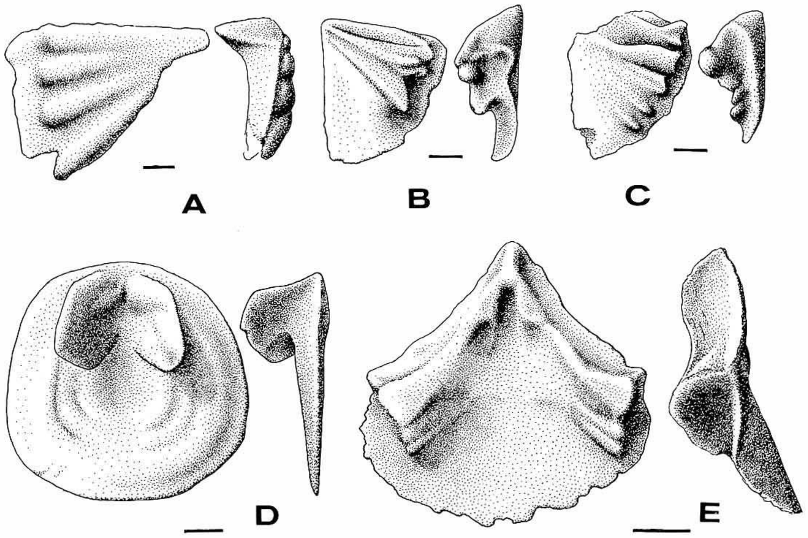

Fig. 7. Internal morphology of larval opercula of hyoliths. □ A. *Leolites* sp., Mójcza limestone, sample A-4, Upper Caradocian, ZPAL Gal/1-011. □ B. *Recilites* sp., Erratic boulder E-124, Lower Llanvirnian, Kunda stage, *A. variabilis* Zone, ZPAL Gal/1-012. □ C. *Chimerolites* sp., same erratic boulder, ZPAL Gal/1-013. □ D. *Circotheca* sp., Mójcza limestone, sample A-8, Llandeilo, ZPAL Gal/1-014. □ E. *Carinolites* sp., Erratic boulder E-085, Upper Llanvirnian, Uhaku stage, *E. lindstroemi* Zone, ZPAL Gal/1-010. Bar scale 0.1 mm.

pedal muscles, then the convex side with a pair of large scars is adanal (posterior) and the flat side with undivided scar is abanal (anterior) (Fig. 6). As the arrangement of scars indicates pretorsional architectonics of internal organs, the hyoliths might be included in the class Monoplacophora. There is little reason to create a separate class Hyolitha.

Among Lower Paleozoic fossils the tentaculites are the most similar to hyoliths in the morphology of the initial conch (Bouček 1964; Alberti 1972), microstructure of the shell (Alberti 1975) and musculature (Lardeux 1964). Perhaps they also had an operculum (Blind 1969; Blind & Stürmer 1977). The relation of tentaculites to hyoliths seems to me more probable than their cephalopod nature (Blind & Stürmer 1977) because of the lack of unquestioned evidence for a siphuncle in the tentaculite conchs.

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The specimens described herein are housed in the Institute of Paleobiology of the Polish Academy of Sciences in Warsaw (Zakład Paleobiologii PAN), abbreviated as ZPAL.

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