Ontogeny of *Bactrotheca* and related hyoliths

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Orthothecid hyoliths *Bactrotheca dens* (Holm) and *B. quadrangularis* (Holm) from the Ordovician of the Baltic province have relatively large, smooth embryonic shells indicating a lecithotrophic type of larval development, probably inside egg capsules. Their embryonic opercula are flat, subcircular in outline. Hatching is marked by the retardation of growth of both operculum and shell, and in the appearance of adult longitudinal sculpture on the shell surface. Juvenile post-embryonic opercula have fully developed structures on their internal side. *Bactrotheca* probably led a sub-sessile mode of life on its postlarval stages, similar to the Recent gastropod *Turritella*. Representatives of other hyolith genera, *Circotheca stylus* (Holm) and *Decoritheca excavata* (Holm) from the Baltic Cambrian, bear small initial shells with mucros, suggesting a planktotrophic mode of life for the larvae. Data presented here document a high diversity of larval development within particular groups of hyoliths (Monoplacophora), similar to that of gastropods. Inclusion of *Semielliptotheca, Quadrotheca, Trapezotheca, Panitheca,* and possibly *Nephrotheca,* into *Bactrotheca* as its subgenera is postulated. □ Bactrotheca, Circotheca, Decoritheca, *Hyolithidae, Orthothecidae, Circothecidae, Hyolithida, Monoplacophora, taxonomy, ontogeny, mode of life, functional morphology, wall structure, Baltic zoogeographical province, erratics, Upper Cambrian, Ordovician, Mójcza Limestone, Święty Krzyż Mountains, Mochty, central Poland, Pomerania, N5050 N5424 E1427 E2042.*

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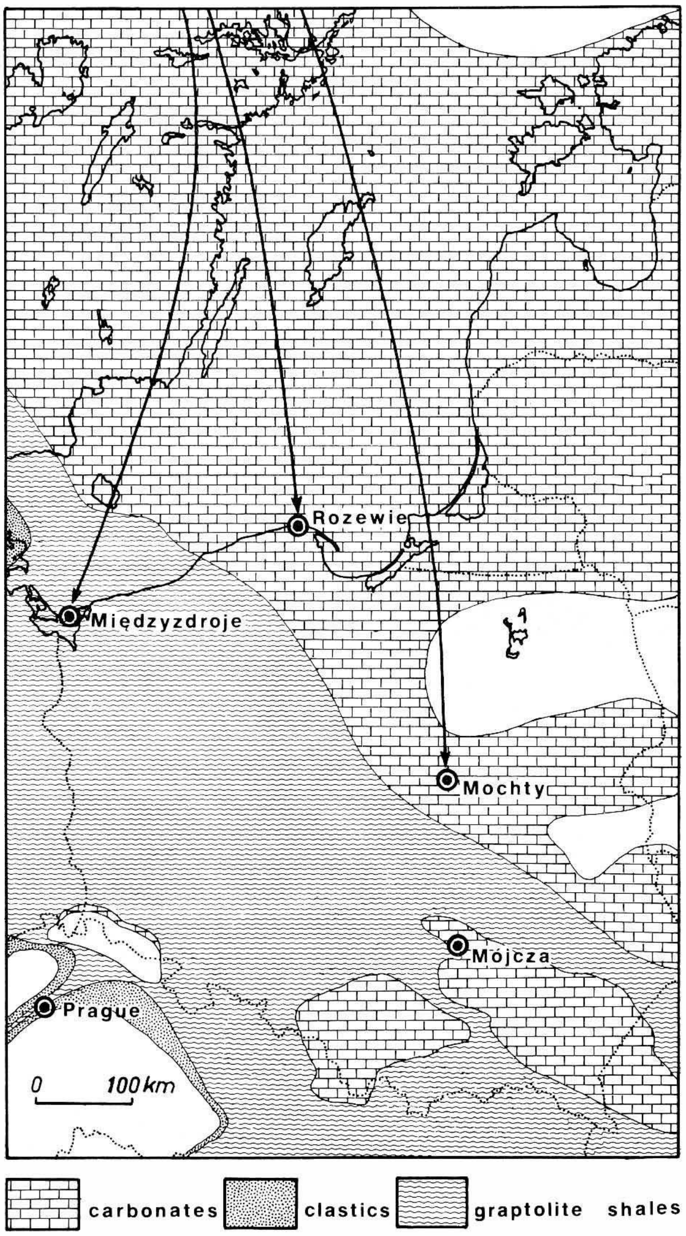
In his classic monograph, Holm (1893, pp. 42–43) presented a '*Försök till naturlig gruppering af de skandinaviska arterna*' of hyoliths which actually was a true scheme of the phylogeny of the Baltic hyoliths. Very few new data have been added since that time. During the past twenty years, since the 'rediscovery' of the importance of hyoliths, their systematics have, however, undergone strong complication at the supraspecific level. Limits of necessity in splitting of taxa have been transgressed in some papers (see, for example, Missarzhevsky 1969; Syssoiev 1972). The reason for irrational evolution of systematic division is the unsatisfactory knowledge of the functional significance of particular structures thought to be important taxonomically. The aim of this paper is to present new data on the larval development of the shells and opercula of a few non-hyolithid hyoliths and to attempt a functional interpretation of particular skeletal structures in connection with their ontogeny.

Ontogeny of *Bactrotheca*

In the Ordovician of the Baltic palaeozoogeographical province (Fig. 1), orthothecids with shells ornamented by longitudinal, basally undulate cristae (Fig. 2B–C) occur commonly. Because of similarity of ornamentation and morphology of initial parts of their shells, all have been put here into a single genus. The generic name *Bactrotheca*, previously attributed only to a single Bohemian species, is used (see below for taxonomical comments). From Llanvirnian, Llandeilian, and Caradocian erratic boulders of Baltic origin, juvenile conchs of two species of this genus have been collected: *B. quadrangularis* (Holm) and *B. dens* (Holm). Both species display identical ornamentation and elongation of shells. The only difference lies in the cross section of conchs: trapezoidal in the former species and reniform in the latter. Apical parts of the shells are indistinguishable. Therefore description of larval development of *Bactrotheca* is based on these two species together.

Though chamosite(?) and glauconite moulds and casts of *Bactrotheca* shells are common in Baltic erratic boulders, no remnant of the operculum has yet been found in residues. In the Mójcza Limestone (Holy Cross Mountains, Poland) opercula of *Bactrotheca* preserved as chamosite natural casts, associated with fragmented external moulds of shells, are fre-


Rozewie
Międzyzdroje
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0
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quent. These differences in the mode of preservation indicate some difference in the mineralogical composition of the shells and opercula of hyoliths. Specific determination of opercula from Mójcza is difficult because the cross section of associated shells cannot be estimated. Only the single Caradocian sample A-4 (see Dzik 1978*a*) contains natural casts of shells possibly belonging to *B. rediviva* (Marek) but this sample does not contain any remnants of opercula.

Shell. – No signs of growth lines on the surface of the apical parts of *Bactrotheca* shells are seen. This can be interpreted as an evidence for early development inside an egg capsule (Dzik 1978*b*). Therefore, if the stage of free swimming larva were developed here, it was of the lecithotrophic type. Development of the shell, as can be inferred from its shape, began when the embryo (or trochophore-like larva) was of spherical shape. During the growth of the shell the shape of the body became cylindrical – this is indicated by the appearance of the distal part of the embryonic shell (Fig 2A). The boundary of the embryonic stage is abrupt. It is expressed in the thickening of the aperture of the embryonic shell indicating retardation of growth. After this apertural thickening distinct longitudinal ornamentation and growth lines appear. These changes in external ornamentation of the shell can be interpreted as evidence for hatching and conversion of the embryo (covered by the egg capsule) into a free-living marine animal. The majority of shells found in residues are of 0.6–1.2 mm in length (Fig. 3B). The peak of mortality is not so sharp as in the representatives of hyolithid genera (Dzik 1978*b*), and need not to be treated as evidence of metamorphosis. It may be only the effect of increased juvenile mortality. Most probably development of *Bactrotheca* was direct; from an egg capsule a fully developed juvenile animal hatched.

Operculum. – The operculum of *Bactrotheca* was established at an early embryonic stage of development as a very small (diameter approximately 0.085 mm: stage 1 on Fig. 3A) hemispherical cup. Although growth lines on its surface have not been observed, during growth of the embryonic shell the operculum was probably enlarged by marginal increment, up to a size identical with the diameter of the aperture of the shell (approximately 0.35 mm: stage 2 on Fig. 3A). Such an embryonic operculum is flat, almost circular in outline. Its internal structures are not known but probably some muscular processes are developed. It may have been weakly calcified at that stage of development.

Hatching is marked by a strong threshold on the external surface of the operculum, indicating retardation of growth (Fig. 3A). The next distinct growth lines appeared when the diameter of the operculum attained approximately 0.6 mm (stage 3 on Fig. 3A); i.e. at the time when the shell was about 4 mm long. It does not seem that this is evidence for metamorphosis, though such an interpretation cannot be excluded. The subsequent growth lines do not show any regularity in their appearance (stage 4 on Fig. 3A) – there is supposedly natural, stochastically appearing retardation of growth caused by external factors. The sharp peak of mortality at the diameter of 0.6–0.8 mm is difficult to interpret. Slight differences in shell (and opercular) diameter correspond with large differences in the length of the shell. A sharp peak in size frequency distribution of the opercula may be an equivalent of long-term juvenile mortality. This may be connected with recruitment and invasion of biotope.

Both external and internal characteristics of the juvenile opercula of *Bactrotheca* are slightly variable. Each operculum bears two long processes on its internal side. Basally the processes continue onto the marginal rim, which runs around the whole operculum. A medial crest connects this rim with the anterior (lower) base of the processes. Two concave fields in the center of the operculum are separated by this crest (Figs. 4B–C, 5A). Some specimens with an exfoliated central part to the external layers illustrate the mode of growth of the operculum (Fig. 4B). It is seen that marginal parts of the operculum grow concentrically, retaining the oblique orientation of extra-rim surfaces. Probably the central fields of the operculum were secreted separately from the marginal parts. This is suggested by the appearance of the rim which separates margins from the center of the operculum and the obscure suture on the prolongation of its negative (see Fig. 4B). These features can be interpreted by analogy with opercula of Recent neritid gastropods as a separation of two fields of increment by marginal muscle attachment (Fig. 6A). Migration of the

Fig. 1. Locality map, also showing facies distribution during early Middle Ordovician (not palinspastic; after several authors, see Dzik 1978*a*) and directions of transport of glacial erratics (after Overweel 1977).

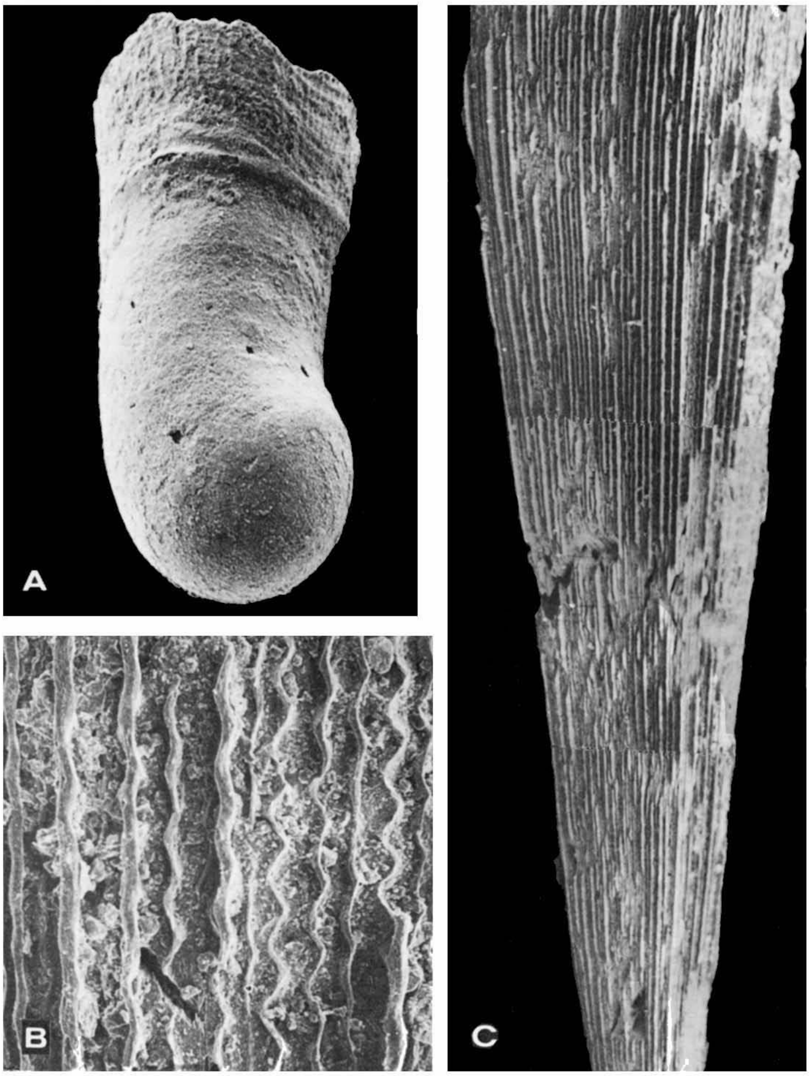

Fig. 2. Bactrotheca dens (Holm, 1893). ☐A. Juvenile shell (early postlarval stage of development); erratic boulder E-113, Uhakuan (Llanvirnian), *Eoplacognathus robustus* Zone, Rozewie, Pomerania; ZPAL Ga I/1–005, ×200. ☐B. Ornamentation of juvenile shell; erratic boulder E-149, Lasnamägian (Llanvirnian), *E. reclinatus* Zone, Międzyzdroje, Pomerania, ZPAL Ga I/21, ×200. ☐C. Ventral (anterior) side of juvenile shell; erratic boulder E-294, Uhakuan, *E. robustus* Zone, ZPAL Ga I/22, Mochty, central Poland (Masovia), ×50.

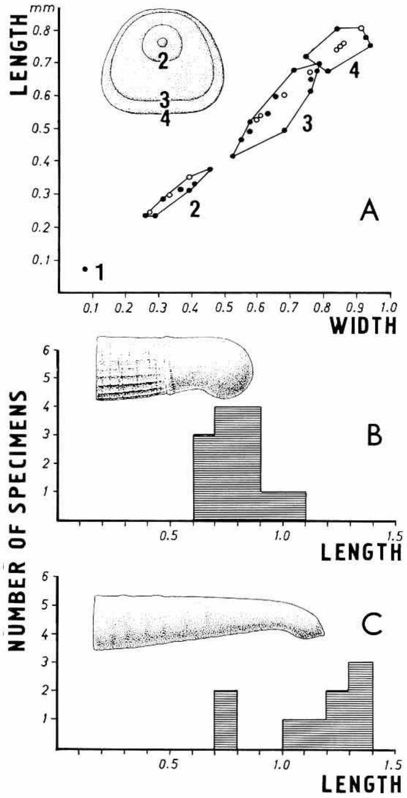

Fig. 3. A–B. *Bactrotheca* sp. □A. Length of operculum plotted against width; material of chamositized(?) opercula from several samples of Mójcza Limestone, Holy Cross Mountains; Llanvirnian to Llandeilian. Circles indicate that only one dimension has been accurately measured, the other estimated roughly. □B. Size–frequency distribution of juvenile shells from erratic boulder E-113, Uhakuan (Llanvirnian), *E. robustus* Zone, Rozewie, Pomerania. □C. *Circotheca* sp., same erratic boulder.

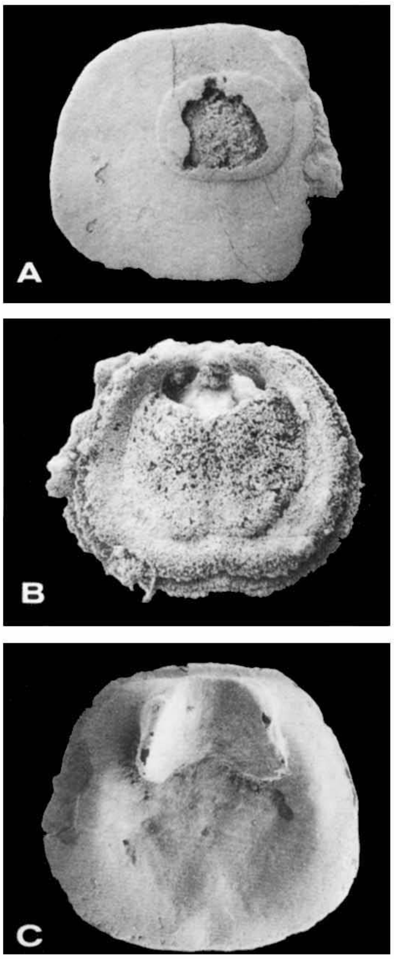

Fig. 4. Opercula of *Bactrotheca* sp. from the Mójcza Limestone, Holy Cross Mountains. □A. External side; sample A-29, Lasnamägian (Llanvirnian), *E. reclinatus* Zone, ZPAL Ga I/23. □B. Partially exfoliated external side; sample A-18, Llandeilian, *Pygodus anserinus* Zone, ZPAL Ga I/24. □C. Internal side; sample A-30, Lasnamägian? (Llanvirnian), ZPAL Ga I/25. All ×66.

muscle scar during growth may produce a distinct boundary between calcareous layers secreted on both sides of muscle attachment. Similarly migration of muscle scars in bivalve molluscs causes separation of two pearly layers by a layer of myostracum. However, study of mineralogically unchanged opercula is needed for verification of this hypothesis. Probably the band of muscle scars also enters on processes (Fig. 5A) similarly to in neritid opercula (see Fig. 6).

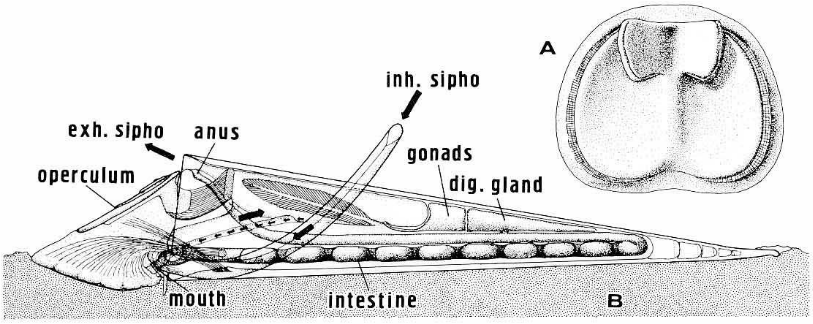

Fig. 5. Reconstruction of living *Bactrotheca*. □A. Internal side of operculum with supposed distribution of muscle attachments. □B. Schematic drawing of soft part anatomy, life position. Uncalcified inhalant siphos reconstructed by analogy with hyolithid helens.

Mode of life of *Bactrotheca*

It has been shown above that *Bactrotheca* had a larva of lecithotrophic type which developed inside an egg capsule. Hatching, possibly connected with metamorphosis, involved changes in shell ornamentation. Subsequently, on a span of a few millimeters the shape of the cross-section of the shell changed to become typical of this species. There is no significant evidence for the existence of any postembryonic stage of planktic larva, though the presence of metamorphosis when the diameter of the aperture was approximately 0.6 mm cannot be excluded. Most probably, immediately after hatching *Bactrotheca* began to lead a benthic mode of life. There is still little known about the biology of adult *Bactrotheca* or of hyoliths at all. Some limited premises can be derived by analogy with adaptively similar groups of Recent animals.

It has previously been suggested (Dzik 1978*b*) that hyoliths were monoplacophoran molluscs, and that their shells and opercula can be homologized with the corresponding parts of other molluscs. Therefore it should be expected that the functional significance of particular morphological features is similar within hyoliths, other monoplacophorans, and primitive gastropods. The close similarity in morphology of the operculum between hyoliths and neritid gastropods is remarkable. In operculate gastropods muscles attached to opercular processes connect the operculum with the columella of the shell (see Schileyko 1977). In non-torted, bilaterally symmetrical molluscs like hyoliths, separation of attachments of opercular (pedal) and cephalic retractors should be expected. All known muscle scars on hyolithid shells have a similar arrangement: simple, wide attachment on the flat side of the shell, and a pair of attachments on the convex side (Marek 1962, 1972). Sometimes additional small scars are developed on lateral sides of the shell (L. Marek, Prague, personal communication 1977). All the abovementioned scars compose a band around the shell near its aperture, similarly to in bellerophontid (Dzik 1978*b*) and tryblidiid Monoplacophora. Paired muscle scars are situated opposite to the processes of the operculum and they may belong to muscles attached to opercular processes at their other end (Marek 1962; Marek & Yochelson 1976). The unpaired scar on the flat side of the shell may be from the attachment of the head and/or foot retractor; small lateral attachments may belong to retractors of epipodial tentacles or helens (Fig. 5B).

If the homology of muscle scars presented above is correct, then the flat side of the hyolith shell is anterior (abanal) and convex side is posterior (adanal; Dzik 1978*b*). Such an orientation is in accordance with that of Marek & Yochelson (1976) although interpretation of the unpaired muscle scar by those authors is different. They believe that this muscle scar is connected with scars in the centre of operculum – a feature unusual for molluscs.

It is evident that representatives of the families Hyolithidae and Orthothecidae differ in anatomical features (Marek & Yochelson 1976). Orthothecids did not have any calcareous appendages (Marek 1967). There are several finds of orthothecid gut filled with sediment. They are known from the Ordovician of Montagne Noire (Thoral 1935) and Bohemia (Marek 1967), and from the Cambrian of Antarctica (Runnegar et al. 1975). No such structures are known among hyolithids. Data on the biology of these groups should therefore be treated rather separately and evidence concerning one should be applied with some reserve to the other. The mentioned finds of intestines filled with sediment indicate that orthothecids were benthic detritus-feeders or filter-feeders. According to the accepted orientation the folded band of intestine close to the flat side of the shell represents the anterior part of the digestive system (Marek & Yochelson 1976). There is good evidence that hyolithids lay on their flat side on the bottom. This is indicated by growth of symbiotic corals only on the convex side of the shell (Marek & Galle 1976) and common occurrence of elevated ornamentation only on this side (cf. Holm 1893). It seems that this life orientation can also be applied to orthothecids (Marek 1962).

The horizontal life position of the conch, its general proportion with lack of distinct allometry in growth, and well developed operculum suggest that hyoliths led a similar mode of life to turritellid gastropods. Hyoliths were probably Palaeozoic ecological analogues of Recent Turritellidae. These gastropods are filter-feeders partially embedded in the sediment during life but able to move by use of their small foot (Andrews 1974; Hofman 1978). They fed employing the gill chamber as a filtering apparatus. Captured food particles are supplied to the mouth through the ciliated food groove. In contrast with Turritellidae, hyoliths were bilaterally symmetrical. Probably they lay on the sediment surface on their 'backs', with the exhalant sipho opening near the upper convex side margin, and with inhalant siphos, which were most probably disposed in the lateral corners of the aperture, above the sediment surface. Helens of hyolithids – tubular calcareous appendages of unknown function (Yochelson 1974; cf. Marek 1967) – occupied such a position. There are very few data on the morphology and mode of growth of helens (Marek 1962; Yochelson 1974), therefore any speculation on their function can only be weakly substantiated but their interpretation as a skeleton of inhalant siphos seems to be coherent with other assumptions on hyolith biology. Orthothecids did not have any calcareous appendages (Marek 1967) but the presence of uncalcified tubular siphos in the place of helens seems probable (Fig. 5B).

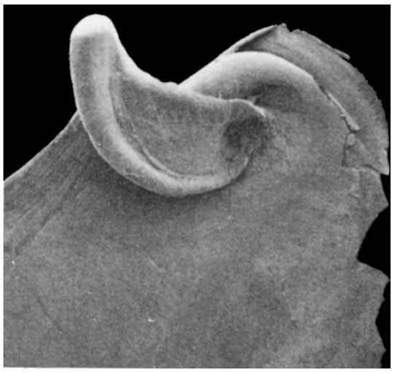

Fig. 6. Operculum of Recent gastropod *Theodoxus fluviatilis* (Linné); anterior part of internal side with myophorous process, ×25.

Ontogeny of other non-hyolithid hyoliths

Representatives of the family Circothecidae which are characterized by a subcircular cross-section of shells appear as the first hyoliths in geological documentation (Missarzhevsky 1969). The operculum of the type species of the genus *Circotheca: C. stylus* (Holm) from the *Paradoxides forchhammeri* Zone (Middle Cambrian) of Skåne, Sweden, bears two large cardinal processes (Holm 1893), very similar to those of *Bactrotheca*. An almost identical operculum has been illustrated from the earliest Cambrian of Siberia as *Turcutheca* (?) sp. by Missarzhevsky (1969; Pl. 11, Fig. 5). It is not known if similarity between *Circotheca* and *Bactrotheca* in opercular morphology expresses close relationship between these genera or if it is an effect of convergence. It seems that the presence of long cardinal processes is an advanced characteristic because other early hyoliths did not bear any pronounced elements on the internal sides of their opercula (see Missarzhevsky 1969; Syssoiev 1972). Well preserved juvenile shells of *Circotheca,* probably conspecific with Middle Cambrian *C. stylus* have been found in acid residues of Upper Cambrian erratic boulder E-278 from Międzyzdroje, Western Pomerania. Age estimation of this boulder is based on the presence of the exclusively Upper Cambrian conodont *Westergaardodina tricuspidata* Müller. No more precise age indicators have been

Fig. 7. Circotheca stylus (Holm, 1893); erratic boulder E-278, Upper Cambrian, Międzyzdroje, Pomerania. □A. Apical view of chamositized(?) juvenile shell. ZPAL Ga I/15, ×85. □B. Apertural part of juvenile shell, ZPAL Ga I/16, ×130.

found, although the boulder contains a rich associated fauna of acrotretid brachiopods, hyolithids, gastropods *Pelagiella*, eocrinoids, ostracods, and rostroconch(?) bivalves. The state of preservation of these shells is not very good, no growth lines can be observed on their apices but the shape of apical parts is seen well (Fig. 7A). The initial part of the conch is very small, many times smaller than in *Bactrotheca* and significantly smaller than the initial conchs known for other hyoliths (see Marek 1976; Dzik 1978*b*). Presence of mucro suggests, by analogy with *Recilites* and *Eumorpholithes* (Dzik 1978; Fig. 1C–D), a planktotrophic mode of life of trochophore-like larva (= early veliger).

Juvenile shells of circothecids, very similar to those described above, have been described from the earliest Cambrian of China by Quian et al. (1979, Pl. 2, Figs. 14–16) under the name *Paragloborilus* cf. *subglobosus* He. Together with the mentioned Siberian operculum they indicate antiquity of the genus *Circotheca*.

Numerous juvenile shells supposedly belonging to the genus *Circotheca* occur in Ordovician (Llanvirnian to earliest Caradocian) erratic boulders of Baltic origin from Poland. Their initial parts are similar in size and shape to the Cambrian representatives of the genus (Fig. 6C). Size–frequency distribution does not present any sharp peak of mortality (Fig. 6C) which is usually distinct in associated hyolithids (Dzik 1978*b*). Abundance of juvenile shells of *Circotheca* may be an effect of juvenile mortality; introduction of metamorphosis is not necessary for its explanation (similarly as in *Bactrotheca*).

Together with *C. stylus* in the Upper Cambrian erratic boulder E-278 shells of *Decoritheca excavata* (Holm) occur. This is a peculiar orthothecid hyolith with a sharply triangular cross section of the juvenile conch and *Bactrotheca*-like adult (Holm 1893). If internal moulds of juvenile conchs occurring in this boulder (Fig. 8A) are correctly identified with slightly larger natural casts which certainly belong to *Decoritheca* (Fig. 8B–C), then *Decoritheca* had an initial conch very similar to hyolithid *Recilites* (Dzik 1978*b*; Fig. 1C). Inadequate preservation does not allow more detailed studies. The operculum of this genus is not known. Undescribed juvenile shells with regular triangular cross sections also occur in the Upper Caradocian of the Mójcza Limestone, Holy Cross Mountains, Poland.

Taxonomical conclusions

As has been shown above, hyoliths are characterized by high diversity in their larval development and opercular morphology in each of their families. Therefore the type of larval development and morphology of the operculum are moderately important taxonomically, similarly to in Recent gastropods. These characteristics can be used with certainty in systematics only at the species level. Grouping of species into higher taxonomical units on the basis of only these characteristics may involve mistakes caused by common convergence and homeomorphy.

I do not see any substantiated reasons for elevating hyoliths to the class (Marek 1967; Marek & Yochelson 1976) or phylum (Runnegar et al. 1975) rank. It seems obvious that morphological diversity within the class Monoplacophora should be comparable with that of other classes of Mollusca. Even if one includes into Monoplacophora all bellerophontids (Runnegar & Jell 1976), hyoliths, and tentaculites (Dzik 1978*b*), the morphological range of this group will be much smaller than in other mol-

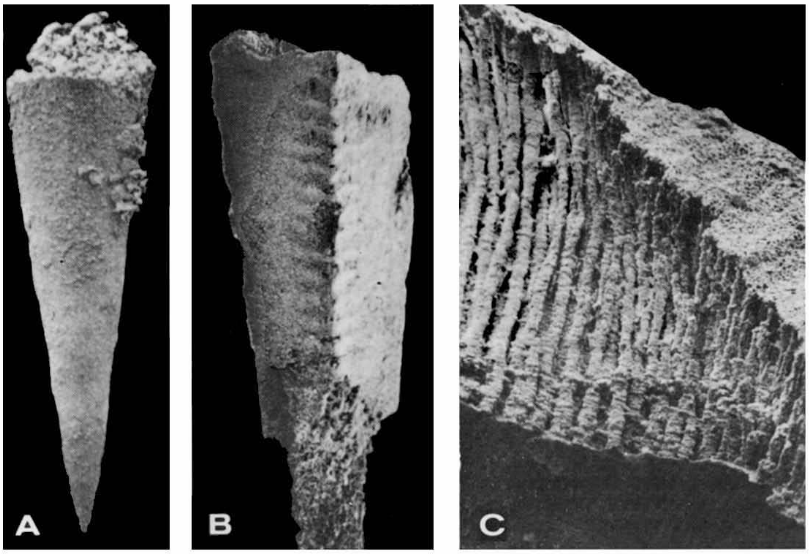

Fig. 8. Decoritheca excavata (Holm, 1893); erratic boulder E-278, Upper Cambrian, Międzyzdroje, Pomerania. □A. Larval(?) shell possibly belonging to this species, internal mould, ZPAL Ga I/17, × 100. □B. Upper (adanal) side of juvenile shell, natural cast, ZPAL Ga I/18, × 70. □ C. Broken wall of natural cast of shell, ZPAL Ga I/19, × 300.

luscan classes. There is no anatomical feature in hyoliths which cannot be found among gastropods or typical Monoplacophora. It has been shown that opercula of hyoliths are closely similar to those of neritid gastropods except that in the former they are symmetrical. Diversity of opercular morphology within the whole group of hyoliths is a small part of the diversity of gastropod opercula. They vary from internally (basally) calcifying opercula of Neritidae, through uncalcified specialized operculum of *Strombus,* up to externally calcifying opercula of *Natica* and *Turbo*. Ecologically hyoliths may be Palaeozoic equivalents of turritellid gastropods. There is no evidence for different ecological adaptation among known hyoliths. If helens are the skeleton of inhalant siphos, as has been suggested above, then only their calcification is a unique feature to support elevation of hyolithids to the subordinal or ordinal level.

A peculiar microstructure of the wall of the hyolith shell (Runnegar et al. 1975; see also Fig. 8C herein) has been used as the most important argument against the monoplacophoran nature of hyoliths (E. Yochelson, Washington, personal communication, 1979). This microstructure is however very similar to the microstructure of the shell of pteropod gastropods. In opposition to other Recent molluscs conchs of Cavoliniidae (Pteropoda) are composed of helically arranged crystallites of aragonite (Bé et al. 1972; Bé & Gilmer 1977). Each layer of the multi-layered wall has the orientation of its crystallites in a direction opposite to that of neighbouring layers. It seems that in the shell of Ordovician *Hyolithes columbanus* Reed (Runnegar et al. 1975: Fig. 6) the structure of the wall is very similar. The shell structure of Permian *Hyolithes lanceolatus* (Morris) (Runnegar et al. 1975; Fig. 5) can be compared with crossed-lamellar microstructure of the shell of Limacinidae (cf. Bé & Gilmer 1977: Pl. 10, Figs 1–2).

Larval and embryonic shells of hyoliths are almost identical with those of Pteropoda (cf. Bé & Gilmer 1977; Almogi-Labin & Reiss 1977). The same can be said of tentaculites. Therefore grouping of these two orders (or superorders) into a single subclass Coniconchia Ljashenko, 1955 seems to me the proper way to rationalize systematics of early Mollusca. Similarity between Coniconchia and pteropods in microstructure and morphology of larval shells seems to be an effect of convergence rather than of evolutionary relationships, although little is known still about early evolution of Pteropoda.

The systematics of Cambrian and Ordovician hyoliths currently accepted actually follow Holm's (1893) *naturlig gruppering* although different names are in use. Species here assigned to *Bactrotheca* were by Holm assigned to his *Grupp 4–5, Semielliptici–Quadrangulares* (Bactrotheca *Nov.*).

Genus *Bactrotheca* Novák, 1891

Systematic position. – Class Monoplacophora Wenz, 1952; Subclass Coniconchia Ljashenko, 1955; Order Hyolithida Syssoiev, 1957; Suborder Orthothecina Marek, 1966; Family Orthothecidae Syssoiev, 1957; Genus *Bactrotheca* Novák, 1891 (including *Semielliptotheca* Syssoiev, 1957; *Quadrotheca* Syssoiev, 1957; *Trapezotheca* Syssoiev 1957; *Panitheca* Marek, 1967; ?*Nephrotheca* Marek, 1962).

Type species. – *Hyolithes teres* Barrande, 1867.

Emended diagnosis. – Shell long with flat or slightly concave basal (anterior) side, ornamented by longitudinal thin ribs, commonly basally undulate.

Remarks. – *Bactrotheca* differs from *Orthotheca* Novák, 1886, in its fine ornamentation, as opposed to thick ribs of the latter genus; from other representatives of Orthothecidae it differs in the presence of numerous longitudinal ribs.

Species included. – *B. teres* (Barrande, 1867); *Quadrotheca? rediviva* Marek, 1967; *Panitheca collector* Marek, 1967; *Nephrotheca? dubecensis* Marek, 1967; *Quadrotheca quadrangularis* (Holm, 1893); *Trapezotheca aemulus* (Holm, 1893); *Semielliptotheca rosmarus* (Holm, 1893); *Hyolithus (Orthotheca) ornatellus* Holm, 1893.

Distribution. – Upper Arenigian (Volkhovian) to Ashgillian of the Baltic region, Holy Cross Mountains (Poland), and Bohemia (see Fig. 9).

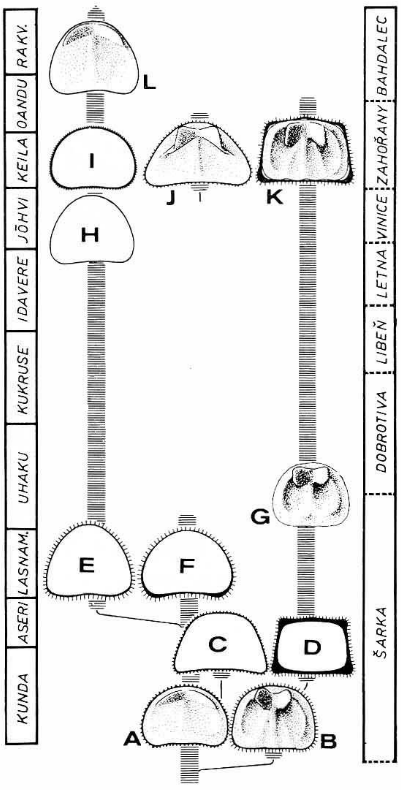

Fig. 9. Stratigraphical distribution of the species of the genus *Bactrotheca* in Baltic region (left scale), Holy Cross Mountains, and Bohemia (right scale, after Havlíček & Vanék 1966). □A = *B.*(?) *(Nephrotheca) sarkaensis* (Novák, 1891), Bohemia. □B = *B. (B.) teres* (Barrande, 1897), Bohemia. □C = *B. (Trapezotheca) aemulus* (Holm, 1893), Baltic. □ D = *B. (Quadrotheca) quadrangularis* (Holm, 1893), Baltic. □ E = *B. (Semielliptotheca) rosmarus* (Holm, 1893), Baltic. □F = *B. dens* (Holm, 1893), Baltic. □G = *B.* sp., Holy Cross Mountains. □H = *B.*(?) *(Nephrotheca) paupera* (Marek, 1967), Bohemia. □I = *B.*(?) *(Nephrotheca) dubecensis* (Marek, 1967), Bohemia. □J = *B. (Panitheca) collector* (Marek, 1967), Bohemia. □K = *B. (Quadrotheca) rediviva* (Marek, 1967), Bohemia and Holy Cross Mountains. □L = *B.*(?) *(Nephrotheca) housina* (Marek, 1967), Bohemia. Illustrated cross-sections of shells and internal sides of opercula (if known).

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