JERZY DZIK

ORIGIN OF THE CEPHALOPODA

Cephalopods are postulated to have evolved from planktic monoplacophorans possibly related to the circothecid hyoliths. It is suggested that secretion of a liquid characterized by a density lower than sea water preceded development of a gas containing phragmocone. Phragmocone formation was due to a prolongation of the functioning of the larval hydrostatic apparatus in the adult stages. Attachment of the larval pedal retractor to the apex of the larval shell was a reason why the soft tissue (siphon) remained in the apical parts of the shell and was subsequently surrounded by diaphragms (septa). A possible mode of producing of the light liquid is removal of salt by an ionic pump. The origin of the rhythmic alteration in the septa and liquid secretion was the next step. An osmotic pressure caused by removal of salt from the liquid resulted in slow removal of cameral liquid from older chambers and diffusion of gas from the liquid under conditions of lowered pressure. A model for the evolutionary transformation of the monoplacophoran operculum into the cephalopod lower jaw is presented. Externally calcifying aptychi of the Palaeozoic orthoceratids and the Mesozoic ammonites were produced in the same way as opercula of Recent gastropods Natica and Turbo. The early evolution of the class is reviewed.

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INTRODUCTION

The Lower Cambrian fossils *Volborthella* and *Salterella* attributed by some authors (Balaschov 1966; Balaschov, Zhuravleva and Shimansky 1962; Zhuravleva 1972 b) to the Nautiloidea have recently been considered as tubes of some sessile organisms (Glaessner 1975). The Middle Cambrian *Vologdinella* and *Olenecoceras* (see Balaschov 1966) may not belong to the Nautiloidea. The oldest known cephalopods are thus the Upper Cambrian ellesmeroceratids. They include *Plectronoceras cambria* (Walcott, 1905) presumably a near-bottom living form with short, incurved shell, from the Upper Cambrian of Asia, and the pelagic (?) *Palaeoceras mutabile* Flower, 1954 and *Ectenolites primus* Flower, 1964, both with long, straight shell,

from the uppermost Cambrian of North America. Several other taxa have been designated by authors working on the Cambrian cephalopods but their Cambrian age is doubtful or, if it can be inferred from published illustrations, their species distinction seems to me not well founded.

Attempts to elucidate the evolutionary relationship between the cephalopods and their ancestral gastropod-like molluscs begin usually with *Plectronoceras* (reconstructed as crawling on the bottom animal) as an ancestral nautiloid form that evolved from some diaphragmate bottom-living *Monoplacophora* (Yochelson *et al.* 1973). It is assumed that the most primitive nautiloid had rather large protoconch (Flower 1964; Yochelson *et al.* 1973; Mutvei and Stumbur 1971) indicative of direct development within an egg capsule. The origin of the siphon and the function of septa, the structures most typical for the class, remain without any satisfactory solution (see Yochelson *et al.* 1973).

The aim of this paper is to discuss once more palaeontological data used as the basis for theories concerning the origin of cephalopods. I propose here a somewhat different approach to the problem of the origin of the Nautiloidea. I believe that the keystone is the mode of larval development of the ancestral forms.

LARVAL DEVELOPMENT OF EARLIEST CEPHALOPODS

Much information on the early ontogenetic development of molluscs is given from the size and morphology of larval shell. So far the only known larval shell of the Ellesmeroceratina (for diagnoses of higher taxa see Dzik in press) is *Bactroceras sandbergeri* (Barrande, 1868) from the Llanvirnian of Bohemia described originally by Barrande (1868: pl. 247: 26—28) under the name *Tretoceras parvulum* which has an inflated, subspherical apex of some 2.3 mm in diameter (fig. 1b). The narrowest preserved parts of the shell of *Cochlioceras* sp.n. from the Llanvirnian of Baltic area are less than 2.0 mm in diameter (Dzik in press). The smallest known fragments of the North American Tremadocian Ellesmeroceratina (Flower 1964: pl. 14, 15) and those of *P. cambria* (Urlich *et al.* 1944) are less than 1.0 mm in diameter. It has been recently demonstrated (Hook and Flower 1976) that the Orthoceratida evolved directly from the baltoceratid Ellesmeroceratina. The only known apical portion of an Early Ordovician orthoceratid shell (Balaschov 1957) resembles very closely in outline the larval shell of *Bactroceras*, measuring 0.9 mm in diameter and not differing significantly from later primitive orthoceratid shells (fig. 1a). The dominant trend in the nautiloid evolution was increase in the size of the embryonic shell (Dzik in press).

The small, subspherical embryonic shell associated with a cylindrical larval shell is found also in primitive Gastropoda and Monoplacophora

(Dzik 1978, 1980). Cylindrical part of the orthoceratid shell close to the protoconch (embryonic shell) is often separated morphologically from the remaining shell and is interpreted as larval conch (Ristedt 1968). This part of the shell wall corresponds probably to the first two septa, more closely spaced than subsequent septa of the phragmocone (see Kisielev 1971; here fig. 1a). One may therefore postulate that the ancestral cephalopod displayed a larval shell consistent in morphology with that recorded in the primitive Orthoceratida and Hyolitha (Monoplacophora, see Dzik 1978, 1980). If so, during ontogeny, early cephalopods passed through a spherical embryon or trochophore-like early veliger stage, as reflected by the subspherical embryonic shell, followed by the stage of planktic late veliger, as indicated by presence of the cylindrical, slightly inflated larval shell. In most primitive cephalopods the trochophore probably developed within an egg capsule, as is suggested by the smooth surface of the embryonic shell and its relatively large diameter. At the veliger
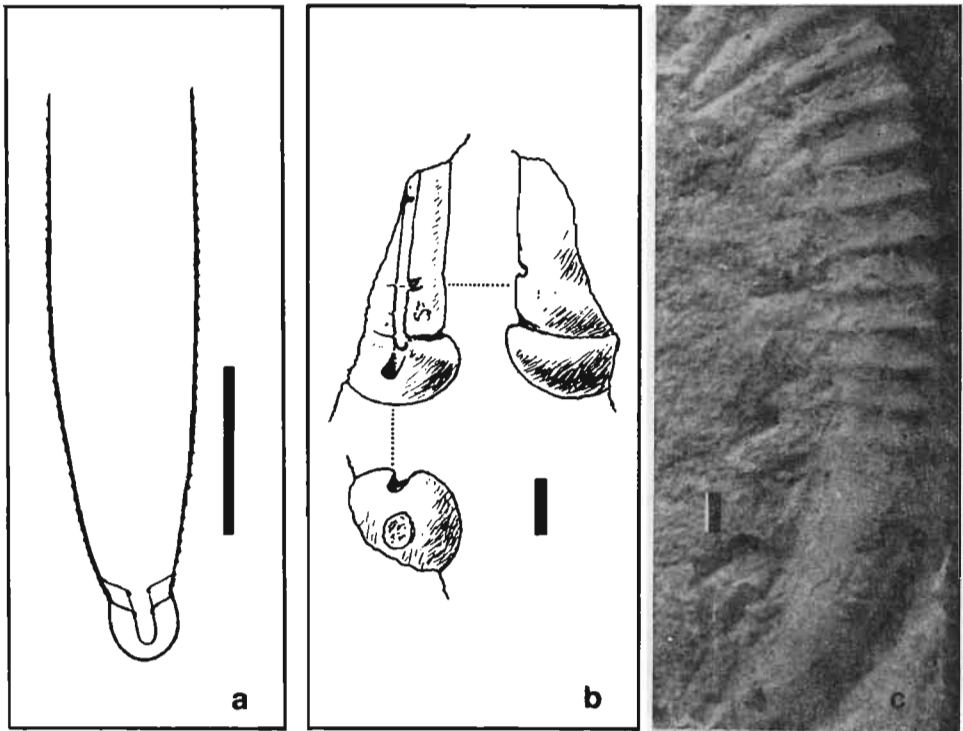

Fig. 1. Larval shells of the early Nautiloidea. *a* *Michelinoceras* sp., Ludlovian, Radotin near Prague, Bohemia; reconstruction of the larval shell in longitudinal section, based on the data of Kisieliev (1971: pl. 1: 3). *b* *Bactroceras sandbergeri* (Barrande, 1868), earliest Llanvirnian (Kundan), Osek near Prague, Bohemia; sketch of the larval shell in ventral, lateral, and apical views (holotype of *Tretoceras parvulum* Barrande, 1868: pl. 247: 26—28, housed in the Narodni Muzeum, Prague). *c* *Cyrtocycloceras* sp., Ludlovian (erratic boulder E-036), Międzyzdroje, Pomerania; apical part of the shell ZPAL N/866. Note the hemispherical embryonic shell, the cylindrical larval shell ornamented only by growth lines, and the annulated teleoconch. Bar scale — 1 mm.

stage, two septa formed to separate the air chambers, as well as a siph-uncle which was attached to the shell wall and penetrated into the embry-onic portion of the shell (fig. 1a, b). This is indicated by the apical morphology of primitive nautiloid shells, as in the few known larval shells (Erben 1965), and the well known mode of growth of the ammonoid larval shell which closely resembles that of the early nautiloids (Erben et al. 1968; Kulicki, 1974, 1979).

ANCESTRY OF THE CEPHALOPODA

Following from the above evidence, I believe that the Cephalopoda are closely related in origin to Monoplacophora with elongated and stra-ight larval shells. Most probably all primitive groups of molluscs passed in their ontogeny through a free-living veliger stage (fig. 2). After having
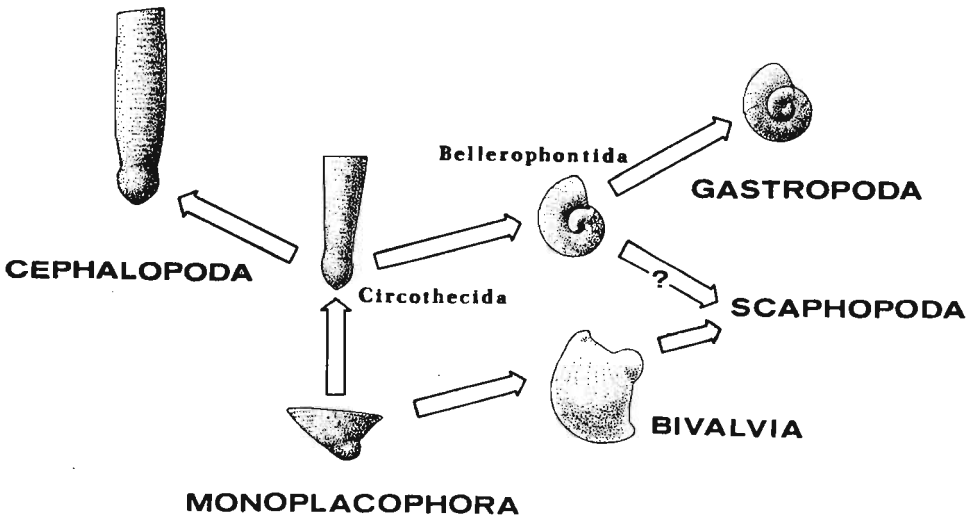

Fig. 2. Proposed evolution of larval shell among the most primitive Mollusca.

achieved a certain shell size, the veliger metamorphosed. In most mollusc groups metamorphosis resulted in a benthic adult stage. However, there are also some molluscs with a planktic adult mode of life (Pteropoda, Heteropoda, Tentaculitoidea). This was probably the case with those cephalopods whose larva developed outside the egg capsule which was typical of the ancestral cephalopods. The origin of the Cephalopoda thus must have been preceded by an evolutionary transition from a benthic to a planktic adult mode of life and hence, an ontogenetic prolongation of the larval planktic habits over the adult stages. Such intermediate forms may actually occur among the poorly known Cambrian circothecid hyol-iths.

ORIGIN OF THE PHRAGMOCONE

The formation of septa in larval development, when the animal has no reason to retreat from the apical part of its shell (the occurrence of diaphragms is a feature of adult specimens in the Hyolitha and Gastropoda) can be explained by the proposition that the apex contained a liquid lighter than sea water and acted as an hydrostatic apparatus prior to the ontogenetic (and maybe phylogenetic) development of the septa (fig. 3). One of the possible ways of making liquid in the apical part of the larval shell of the ancestral cephalopode lighter than sea water is by removing salt by an ionic pump presumably connected with some mechanism neutralizing an osmotic pressure. Such a physiological activity of the tip of the soft tissue could be sufficient to make the animal positively buoyant at the larval stage, when the weight of the weakly calcified shell and the delicate internal organs was not great. The density of tissue of Recent adult cephalopods ranges from 1036 kgm^{-3} to 1080^{-3} (Zuev 1966) with a mean of 1050 kgm^{-3} (Zuev 1966; Denton and Gilpin-Brown 1973; West-
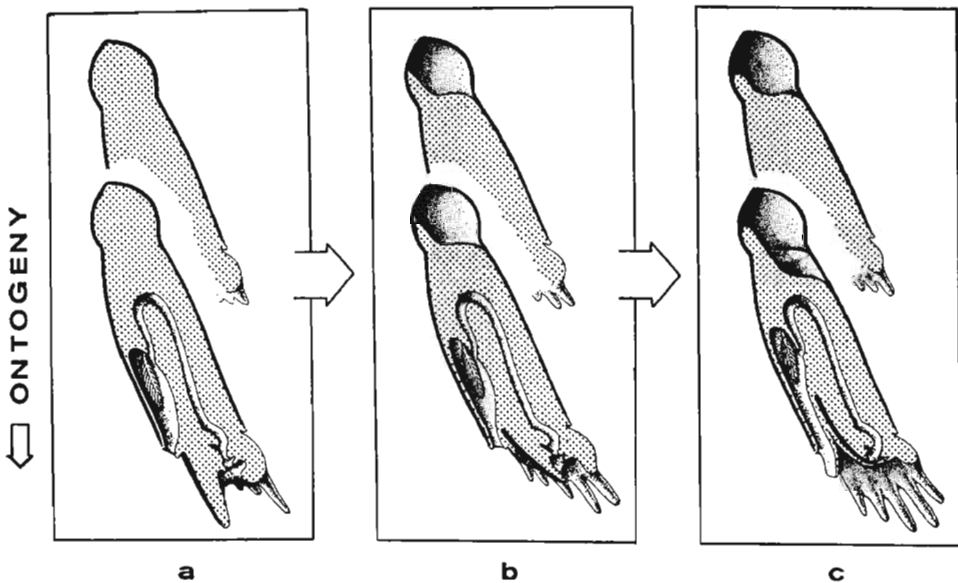

Fig. 3. Evolution of ontogeny leading from planktic Monoplacophora with elongated shell to Cephalopoda; illustrated stages immediately before and after metamorphosis. *a* Monoplacophoran stage — larva without hydrostatic apparatus, the foot begins to undergo a reduction, operculum acts as protection. *b* Intermediate stage — larva produces a bubble of light liquid supporting it in water, foot reduced which puts the operculum close to the mouth, operculum contributes to crushing of food particles. *c* Cephalopod stage — hydrostatic apparatus persists after metamorphosis, posterior part of the body produces calcareous septa, tissue around the larval retractor attached to the wall of embryonic shell is the only soft tissue contacting the cameral liquid which produces gas, operculum acts as a lower jaw, scleritized fold of tissue above the mouth acts as an upper jaw.

ermann 1977). Because the density of sea water is approximately 1030 km^{-3}, they are negatively buoyant with mean buoyancy coefficient -20. The soft body of the larvae of ancestral nautiloids was probably much less dense so slight lowering of density of the "cameral" liquid could be sufficient. Liquid giving similar effect (density 1010—1012 kgm^{-3}) is produced by Recent cranchiid squids but because of the lack of any shell giving isolation from the surrounding sea water some additional mechanisms neutralizing osmotic gradient (high content of ammonium chloride) have evolved. After reaching a certain size and the formation of rigid septa osmotic gradient effected by the ionic transport must have involved removal of the liquid from the apical chambers, and diffusion of gas from the cameral liquid occurred, i.e. normal functional activity of the phragmocone began (Denton and Gilpin-Brown 1966, 1973; Ward and Martin 1978; Ward 1979). Because of the very low permeability of the conchiolin membrane separating the soft tissue from the chambers, removal of liquid is very slow (Chamberlain 1978) in relation to the supposed rate of the formation of larval septa.

Septa do not differ from gastropod diaphragms in origin and are the result of secretion of the pearly layer by the surface of the soft body (see Kulicki 1979). A peculiar feature of the phragmocone formation is the rhythmic alternation in the secretion of liquid and septa by the soft parts. Lack of good experimental data on the rate of this proces (see Chamberlain 1978) has resulted in the presentation of several hypotheses concerning the relations between septal formation and external factors, i.a. Kahn and Pompea (1978) stated that septa are produced in a lunar cycle and that the number of growth lines between subsequent septa corresponds strictly to the number of days in the synodic month. The nautiloid shell grows by marginal increments. The rate of this increment depends on the rate of growth of the soft body and on the production of cameral liquid which moves the soft parts towards the shell aperture. This is the reason why the number of growth lines in the distance between two septa never corresponds to the number of growth lines produced during the formation of these septa and why the assumption of Kahn and Pompea (1978) is incorrect. The real relation between formation of the septa and the marginal increment of the shell (the volume of added shell should be equal to the volume of produced chamber plus growth of the soft body in volume at the same time) is very difficult to estimate using fossil material. Among several rhythms in the ornamentation of shells of early cephalopods (fig. 4) annulation seems to correspond to the formation of septa, although it is difficult to demonstrate because of the reasons outlined. Therefore counting the number of growth lines between annuli supplies better data on the rate of septal formation (see Hewitt and Watkins 1980) but still any relation between the formation of particular septa and the synodic month is doubtful (Saunders and Ward 1979).
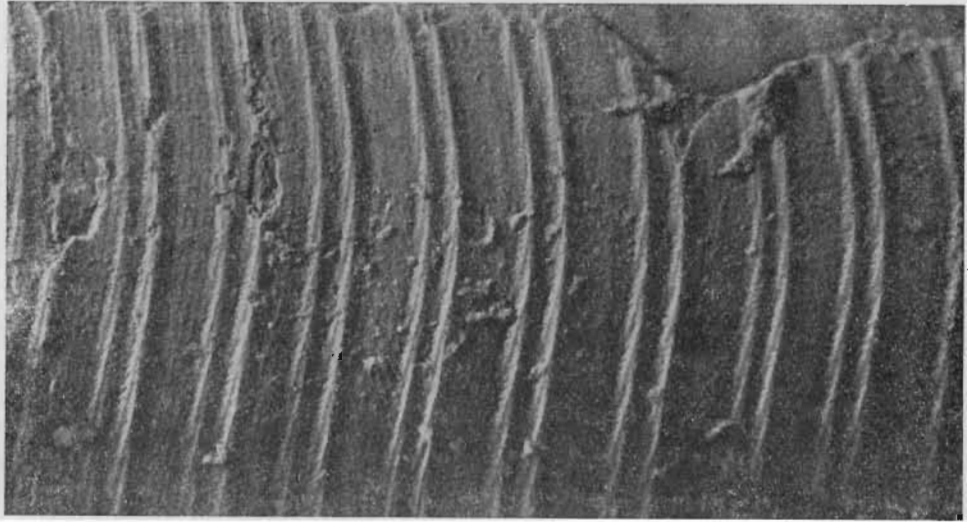
Fig. 4. Rhythms in the development of the shell ornamentation visible on the shell surface of Arionoceras valens (Barrande, 1868), Ludlovian (erratic boulder E-036), Międzyzdroje, Pomerania, juvenile living chamber ZPAL N/867; note delicate daily(?) increments produced in the periostracal groove of the mantle and low annulations produced at the edge of the mantle (not parallel to growth lines), rhythm in the distribution of annulations seems to be correlated with formation of the septa. ×10.

The persistence of soft tissue (siphon) in the apical part of the shell already filled with liquid was necessary because of the attachment of the larval body to the shell in that area (fig. 3). There is an analogy with the attachment of retractor muscles in extant primitive gastropod larvae (Crofs 1955). Among Recent adult molluscs no attachment organ which could be homologized with the siphon (or prosiphon) is known. In the shell apex of the primitive Ordovician monoplacophoran Pilina, however, occurs an enigmatic pit which could be interpreted as an attachment scar of a soft body organ homologous with the cephalopod siphuncle. This small pit has been described as a remnant of the protoconch (Peel 1977; Yochelson 1977) but the preservation of the protoconch on the shell interior is incompatible with the mode of formation of the mollusc shell.

HOMOLOGY OF ADULT RETRACTOR MUSCLES

The above reconstruction of the origin and earliest evolution of the Cephalopoda can be tested partly by a comparison of the supposed course of the larval shell evolution with the evolution of adult nautiloid structures, and a recognition of morphological continuity or discontinuity along the postulated phyletic lineages. Besides the skeletal morphology, the best documented nautiloid anatomical structure is the pattern of the attachment scars of the retractor muscles. In an earlier paper (Dzik 1978) I

pointed to a possible homology in this pattern among the bellerophontid Monoplacophora, Hyolithida, and primitive Cephalopoda (fig. 5).

Contrary to Mutvei's (1957) opinion, variation in retractor muscle scars in the Cephalopoda does not seem to be of high (supraordinal) diagnostic
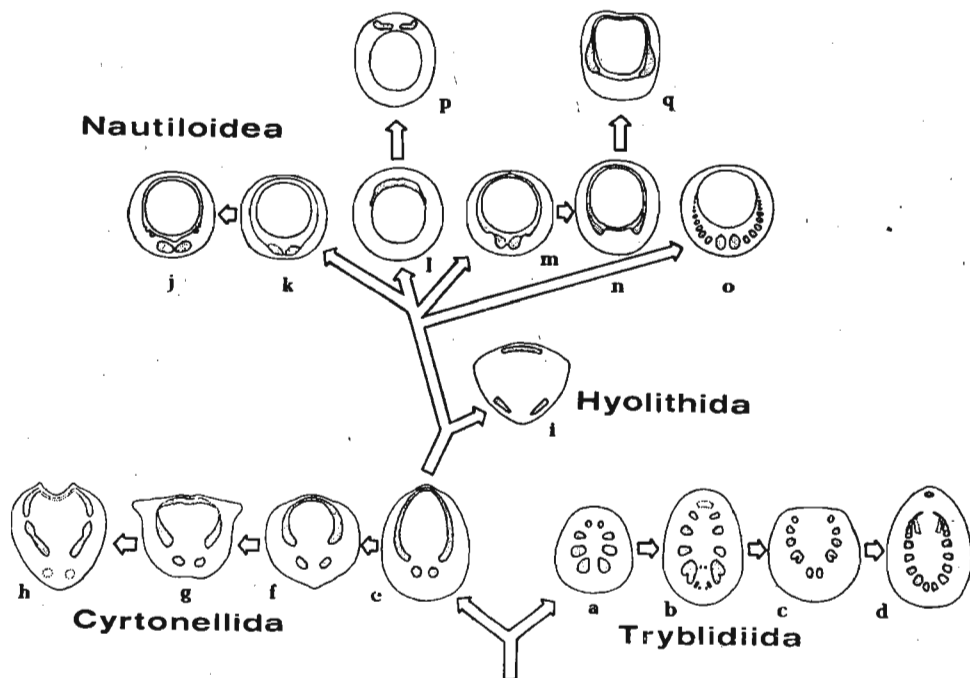

Fig. 5. Hypothetical relationships among paterns of pedal muscle attachment scars of primitive molluscs. *a Aktugaia triangula* Missarzhevsky, Early Cambrian. *b Romaniella aebitensiś* Dogudzhaeva and *Kirengella ayaktchica* Rozov, Early Ordovician. *c Moyerocania miagkovae* Rozov, Early Ordovician. *d Pilina cheyennica* Peel, Late Ordovician. *c Archinacella patelliformis* (Hall), Late Ordovician. *f Cyrtonella mitella* (Hall), Middle Devonian. *g Sinuitopsis acutilira* (Hall), Middle Devonian, and *Cyrtolites ornatus* (Conrad), Middle Ordovician. *h Sinuitopsis neglecta* (Perner), Middle Ordovician. *i Maxilites robustus* (Barrande), Middle Cambrian. *j. Discoceras angulatum* (Saemann), Upper Ordovician. *k Estonioceras perforatum* Schröder, Early Ordovician. *l Cochlioceras burchardi* (Dewitz) and *Orthoceras scabridum* Angelin, Early Ordovician. *m Uranoceras longitudinale* (Angelin), Late Ordovician. *n Kosovoceras nodosum* (Barrande), Late Silurian. *c Doleroceras resimum* Zhuravleva, Middle Devonian. *p Bactrites ausavensis* (Steininger), Middle Devonian. *g Nautilus pompilius* Linné. Compiled from various authors.

value. The large number of homeomorphs as well as the considerable variability observed within some rather low-rank nautiloid taxa (e.g. within Trocholitidae) indicate a close relation of the retractor scar pattern to shell outline and hence, to mode of life (Dzik in press). There is little doubt that a secondary metamerism of muscles was achieved independently in the Ellesmeroceratina (Mutvei and Stumbur 1971), Oncoceratida (Sweet 1959; Zhuravleva 1972a), and Tarphyceratida (Mutvei 1957).

ORIGIN OF CEPHALOPOD JAWS

New data on the morphology and internal structure of the cephalopod jaws presented by Closs (1967), Lehmann (1970, 1971, 1972, 1975, 1978), Kaiser and Lehmann (1971), Gąsiorowski (1973), Turek (1976, 1978), Ferinacci *et al.* (1976), and Saunders *et al.* (1978) put new light on the problem of their origin. Cephalopod jaws are unique in the Mollusca. The marine Gastropoda and Monoplacophora crush their food using only the radula (Hickman 1980). When in the course of their evolution the "need" for a jaw-like structure arose, this function was also performed by the radula (e.g. the *Stenoglossa*). Jaws must therefore have developed after the separation of the Cephalopoda from the stem common with Gastropoda. There was no preadaptive structure close to the mouth in the common ancestor of the gastropods and cephalopods permitting an independent appearance of jaws in non-cephalopod molluscs. All extant cephalopods have their jaws adapted exclusively to biting or gnawing, hidden within the soft tissues around the mouth. The ammonoid lower jaw (aptychus) functioned as both a jaw and an operculum (see Schindewolf 1958; Lehmann 1975, 1976). Turek (1978) demonstrated recently that the Silurian Orthoceratida had bivalve calcareous aptychi which closely resembled the aptychi of Mesozoic ammonites. Their mode of growth, outline, and position close to the shell aperture indicate that they acted as an operculum. According to Turek (1978), they are analogous with the hood of the extant *Nautilus* rather than its jaws. Palaeozoic nautiloid opercula, reported commonly from the Silurian, are usually preserved as two aptychus-like valves interconnected by a marginal suture. The wedge shaped interspace sometimes contains another plate. The operculum thus presents a solid structure covering the shell aperture (Turek 1978; Holland *et al.* 1978). Among some dozens of nautiloid aptychi from the Ludlovian of Prągowiec, Holy Cross Mountains, Poland (fig. 6a, b) I have found no specimen with this third plate in place. This suggests a more stable contact of the two aptychus-like plates with each other than with the medial plate.

Contrary to Turek's (1978) opinion, I believe that the medial plate may have acted not only as a part of the operculum but also as the upper jaw (fig. 7). In involute shells the venter of the preceding whorl lies between the upper parts of the aptychi. There is a need for additional cover in the nautiloid shell with subcircular section; it seems very plausible to suppose that this function was performed by the upper jaw. On the other hand, some functional analogies may be recalled to support the supposed homology between the orthoceratid aptychi and the primitive mollusc operculum. Some Recent gastropods use their operculum as a tool to injure a prey or to open a bivalve shell. It appears feasible that the cephalopod ancestors used their opercula in the same way. This could be
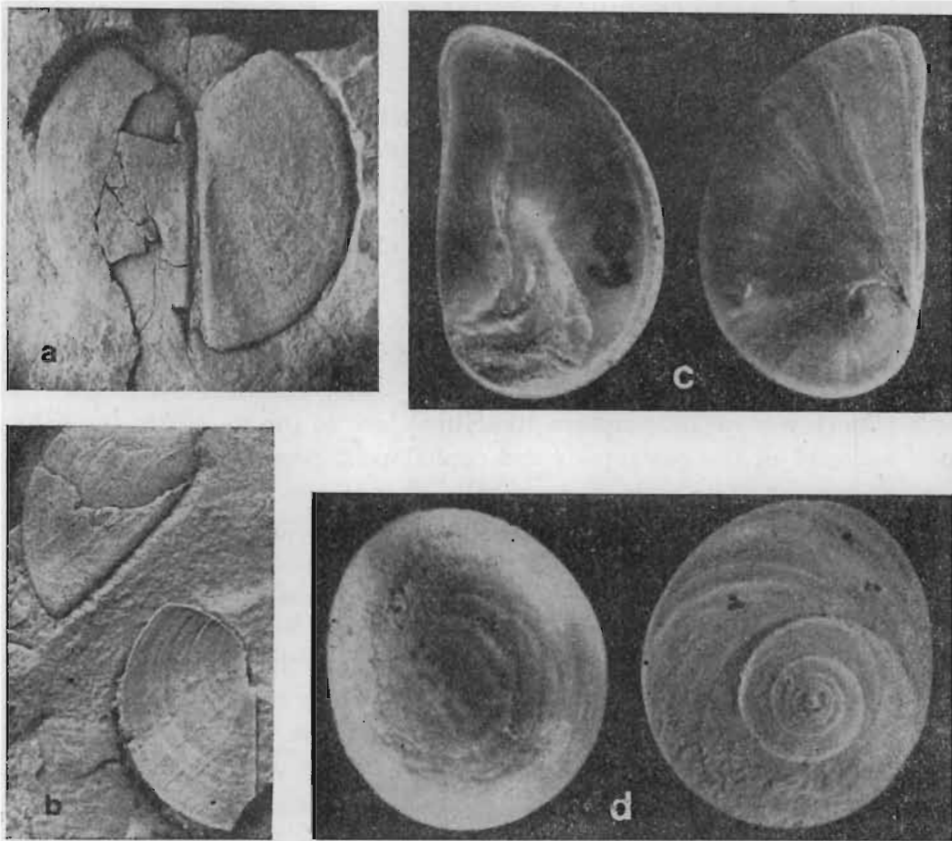
Fig. 6. Calcareous opercula of Silurian nautiloids (*a, b*) and Tertiary gastropods (*c, d*); note smooth external surface and ornamented with growth lines internal one (horny layer not preserved). *a, b Arionoceras* (?) sp., Ludlovian, Prągowiec, Holy Cross Mountains, ×2. *c Natica millepunctata* Lamark, Miocene, Korytnica near Jędrzejów, ×5. *d Astraea mamillaris* (Eichwald), Miocene, Łychów Szlachecki near Kraśnik, ×5.

facilitated considerably by the reduction of the foot (fig. 3), placing the operculum close to the mouth — a precondition to its function as a jaw.

Since little is known about the diet and feeding habits of ancient cephalopods, one can only speculate on the usage of the initial, unmodified operculum in food gathering. If this hypothesis holds true, folds of soft-tissue over the mouth could also contribute to food crushing. Their hornification and subsequent calcification could then have resulted in formation of the upper jaw, i.e. the third, medial plate completing eventually the secondary, composite operculum-jaw. Completion of the jaw through filling the space between the two lower plates was unnecessary in the ammonites. The original function as an operculum was abandoned and the jaw hidden among soft tissue folds independently in various cephalopod lineages (figs 8, 9). This was probably related to a shift upwards in the trophic pyramid and an improvement in the biting ability of the jaws.
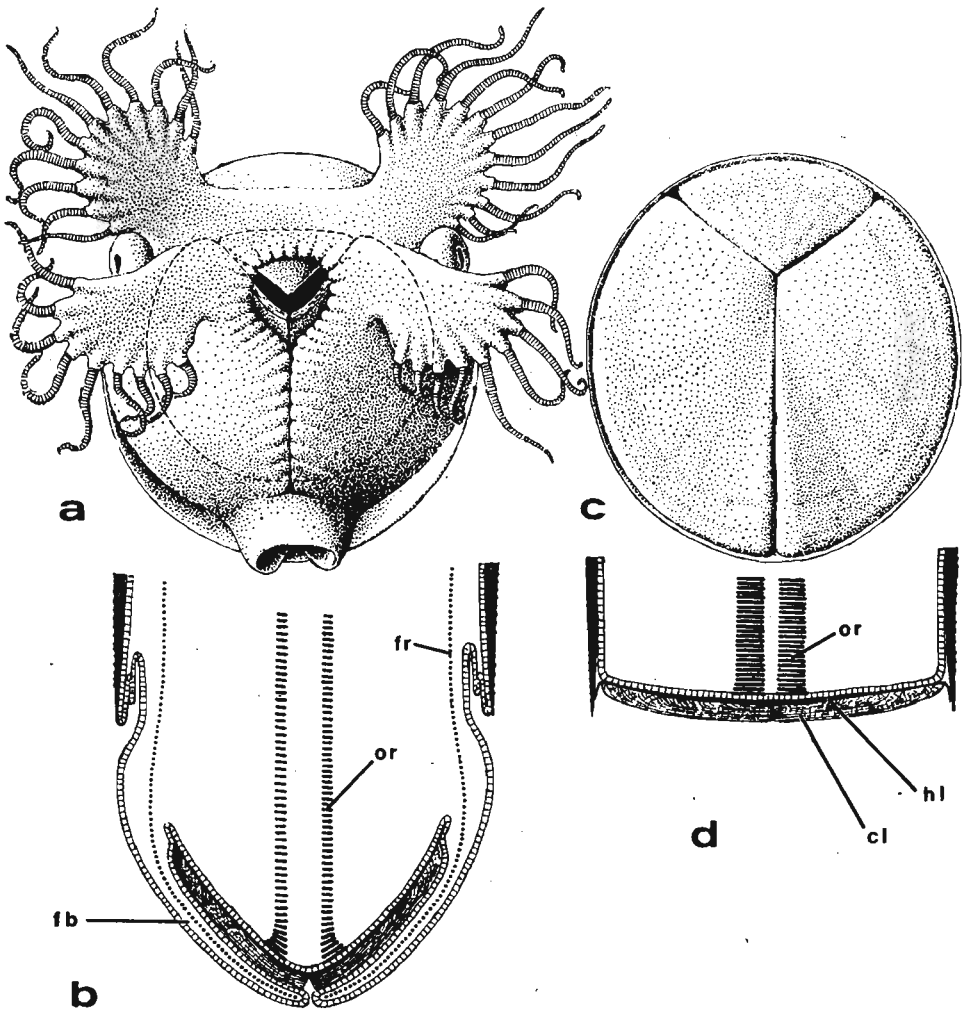
Fig. 7. Proposed interpretation of mode of development and function of the nautiloid aptychi; apertural views (a, c) and longitudinal sections, (b, d) of protruded (a, b) and intruded (c, d) animal. Soft parts quite hypothetical. cl calcareous layer of the operculum, hl horny layer, fb fold of the soft body (foot) covering operculum and secreting calcareous layer, fr retractor of the fold, or — opercular retractor.

The mode of ontogenetic growth of the aptychi is an important problem for phylogenetic and functional aspects. There are no data on the micro-structure of Silurian nautiloid aptychi, but there is little doubt that they were secreted from the convex instead of the concave side (Turek 1978). The same mode of growth has been recorded in the Mesozoic aptychi (Schindewolf 1958; Farinacci et al. 1976) indicating their functional simil-arity, if the considerable morphological similarity is also taken into ac-count. The occurrence of growth lines on the concave side (fig. 6a, b) is incompatible with the mode of growth found in the jaws of extant ce-

phalopods. This apparent inconsistency cannot be accounted for by Schindewolf's (1958) hypothesis that the aptychi developed by calcification of the tissue of modified tentacles contributing to the hood; this hypothesis has been refuted by Lehmann (1971, 1975). Farinacci et al. (1976) demonstrated that the aptychi grew by marginal secretion of a calcite tissue with a peculiar microstructure. Later, the wall was thickened by secretion of a laminar outer layer on the convex side. During the Jurassic, the marginally produced tissue was transformed into a thick layer with a tubular structure, while the laminar outer layer increased in thickness. Well preserved primitive Early Jurassic aptychi sometimes show the inner organic layer (Farinacci et al. 1976). I have found a relatively thick organic layer covering the concave side in a well preserved specimen from the Upper Cretaceous of Mielnik on the Bug, Poland. Organic matter has also been described from the concave side of some Silurian aptychi (Turek 1978: 132).

One may therefore claim that the aptychi present only the calcified outer part of cephalopod jaws. The chitinous layer, homologous to the jaw of extant cephalopods, was secreted basally. The marginal secretory organ, adding a calcite layer to the inner organic layer of the jaw, would then have been related to the function as an operculum. The outer, laminar calcite layer could be secreted only when the aptychus acted as a jaw within the folds around the mouth (figs 7, 9). The lines visible on the concave side of calcareous aptychi are imprints of those on the organic layer homologous to the jaw of other cephalopods. One can hardly suppose that the calcitic(?) Silurian aptychi were directly ancestral to the Mesozoic aptychi. More probably, the outer layer of the organic operculum-jaw was undergoing calcification whenever there was in cephalopod evolution a need for strengthening the operculum. The structural analogy is then due mostly to the recurrence of anatomical "preadaptations".

The above interpretation of the mode of growth of aptychi is supported by the mode of secretion of the calcareous operculum in some extant gastropods (Wrigley 1949; Abatino et al. 1972). In contrast to the conchiolin operculum secreted from the basal side (as in the case of the chitinous cephalopod jaw and the organic layer of aptychi), the calcareous operculum of Natica and Turbo (fig. 6c, d) is secreted marginally and outwards by a fold of the foot (as in the case with the calcareous layers of aptychi). The calcareous aptychi and opercula are thus secreted each in two distinct directions: the basal conchiolin layer is secreted from inside, while the calcareous layer is secreted obliquely from outside. The calcareous layer of the hyolith operculum is not homologous to the calcareous layer of either the aptychi or the opercula of the gastropods Natica or Turbo. In the Hyolithida, the operculum grew as in the modern gastropods of the Neritidae (Dzik 1980). The conchiolin layer of their original operculum was supplemented by calcareous layers on the basal side (as in

the case of rhyncholites — Saunders *et al.* 1978), whereas basal processes of the operculum intruded into sof tissue of the foot. Thus, one may conclude that the ancestors of the Nautiloidea should be looked for among the most primitive hyoliths with a non-calcified operculum. The mechanism of operculum calcification developed independently in the Hyolitha and Nautiloidea, just as it did in various gastropod groups.

SOFT PART ANATOMY OF EARLY CEPHALOPODS

Direct evidence concerning the soft part anatomy of fossil nautiloids is almost lacking. Ehrenberg (1942) reported the occurrence of an ink sac in an Upper Silurian orthoceratid from Bohemia. The living chamber of a nautiloid described by Ehrenberg contains an oval iron nodule interpreted by him as a fossilized ink sac. In the same living chamber several fragments of other nautiloids are seen. This indicates that the living chamber was filled with sediment in conditions of high energy of environment after the soft body was fully destroyed. Therefore interpretation of the iron as the remains of an ink sac seems improbable. X-ray photographs of Devonian orthoceratids presented by Zeiss (1969) are too unclear to be interpreted with sufficient certainty. Interpretation of a peculiar trace fossil as the imprint of *Orthonybyoceras* tentacles by Flower (1955) is weakly substantiated.

Thus, the only remaining method is the inference of soft part anatomy from hard tissue remnants. The significance of externally calcified opercula, and the interpretation of muscle scars, was discussed above. There is also another biologically important record of the soft part anatomy preserved in the modes of aperture constriction. Constricted apertures occur in almost all orders and suborders (for systematics see Dzik in press) of fossil Nautiloidea (fig. 8). The oldest records are the constricted apertures of the ellesmeroceratids *Burenoceras* and *Buehlersoceras* from the Tremadocian of North America (Ulrich *et al.* 1944; Flower 1964). The mode of aperture constriction in these genera is almost identical with the better known Silurian discosorid *Phragmoceras*. In extreme cases the aperture is fully closed medially with two openings retained (Hedström 1917): the larger one corresponding to head organs and the smaller "ventral" opening to the funnel. These cephalopods thus present a very peculiar mode of locomotion with an infundibulus oriented opposite to the head in the same line. Other discosorids (i.a. *Gomphoceras*) have the head opening of the aperture divided by lateral lappets into a few (3—4) pairs of lobes. One can expect that these lobes correspond to particular head organs; it is, however, not clear what these are. Large samples of discosorids and oncoceratids (similar in this respect) from the Silurian of Bohemia and Gotland examined by me in the Narodní Muzeum, Prague and Naturhistoriska Riksmuseet, Stockholm show an extremely large intrapopulation

variability of apertural morphology. A sample from a single bedding-plane often contains specimens with a single pair of lobes or with several lobes and there is a continuous morphological transition between them (only fully mature specimens were considered). It is difficult to imagine such a wide intrapopulation variability of a biologically important organ. Possibly apertural lappets separated groups of tentacles (cf. fig. 7). Independent origin, in diverse groups of early Nautiloidea, of very similar apertural constrictions strongly supports the view that ancient cephalopods had a very different organization of soft body parts from both Recent *Nautilus* and Coleoidea.

It should be noted that lappets similar to those of nautiloids occur in ammonites (i.a. *Ebrayiceras*) but they indicate a very different distribution of soft organs, with supposed eyes close to the infundibulus and a very small opening for the mouth organs (fig. 9). It can be interpreted as the next step in the evolutionary disappearance of the foot, and the mouth moving closer to infundibulus.

EARLY DIVERSIFICATION OF THE CEPHALOPODA

Relationships of particular groups of the early Cephalopoda have been discussed by Donovan (1964), Teichert (1967), Zhuravleva (1972), and Flower (1976). My own studied lead to conclusions somewhat different from those of the authors mentioned (fig. 10). A monograph containing description of new data and extensive discussion will be published soon (Dzik in press), below only a short review of the early phylogeny of the class is presented.

Ellesmeroceratina

In most ellesmeroceratids, the siphon retreated during ontogeny from the apical part of the phragmocone and the abandoned part of the siphuncle was separated by diaphragms (see Mutvei and Stumbur 1971). Cameral liquid exchange was therefore confined to those phragmocone chambers lying close to the living chamber. Consequently, there are no calcareous deposits in the siphuncle and air chambers of the ellesmeroceratid phragmocone. In some Ellesmeroceratina, namely the Baltoceratidae, the siphon did not retreat from the shell apex; in turn, it was gradually constricted with secondary deposits growing inside the siphuncle. The occurrence of calcareous deposits is characteristic of most nautiloid groups derived from the Ellesmeroceratina. At least at the beginning of nautiloid evolution, the calcareous deposits were functionless and reflected merely an imperfection in management of the calcium carbonate. The primitive Ellesmeroceratina show relatively thin connecting rings,
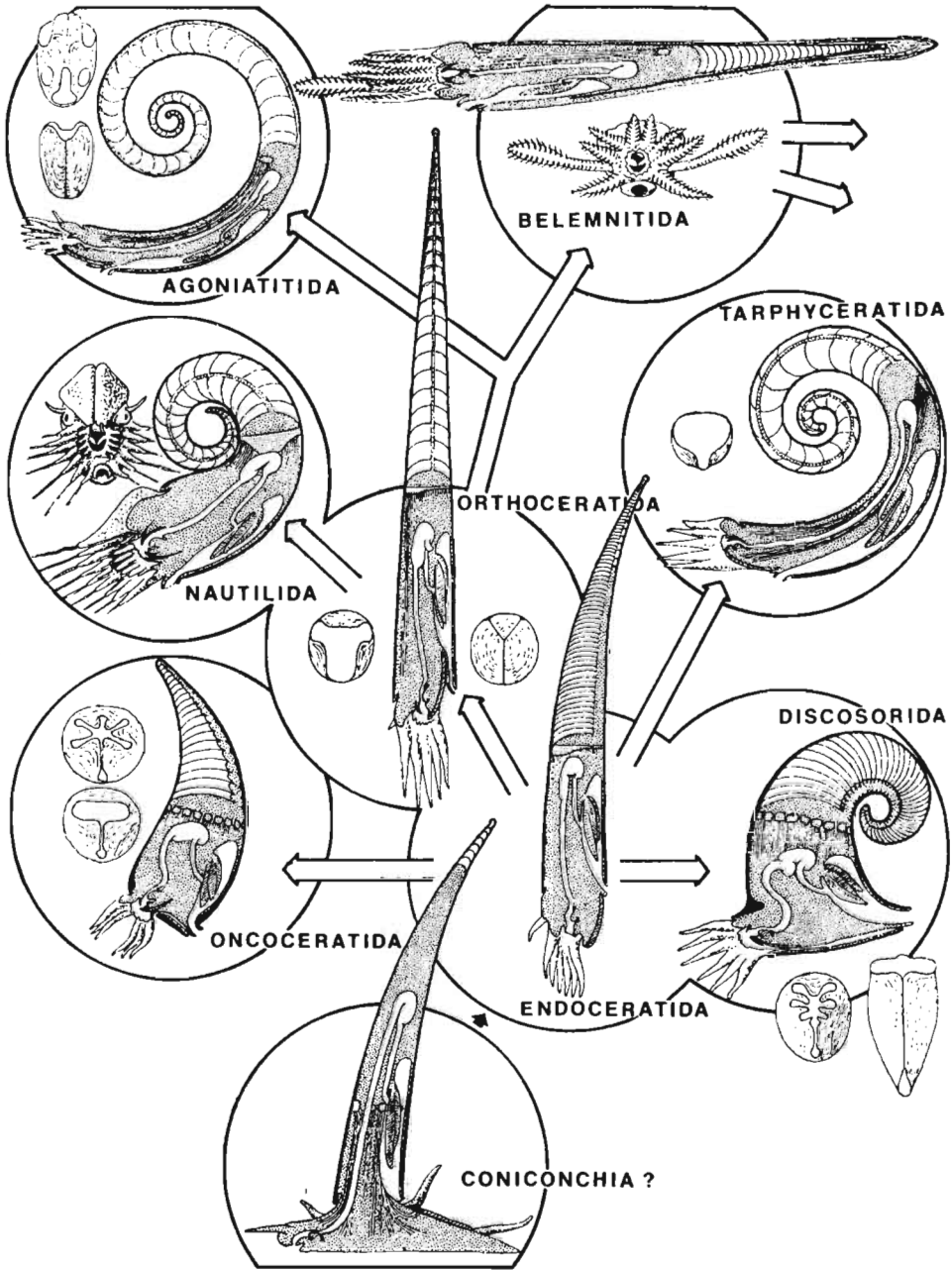
Fig. 8. Evolutionary relationships between main groups of early Cephalopoda. Medial section of the body, apertural view of the body and/or constricted aperture of a typical representative of each group are illustrated. Ranges of orders according to Dzik (in press), i.e. Endoceratida incl. Ellesmeroceratida, Orthoceratida incl. Ascoceratida, Actinoceratoidea, and Bactritoidea (*partim*).

whereas thick connecting rings homogenous in microstructure are typical of more advanced representatives of the suborder. The connecting rings expanded in width and intruded the siphuncle independently in the longiconic *Bathmoceras* (Holm 1899) and the breviconic *Conocerina*. An increase in thickness is not a gerontic process. Strongly developed connecting rings occur in phragmocone chambers adjacent to the living chamber and intrude the posterior wall of the viscera.

Endoceratina

The endoceratids resemble very closely the Baltoceratidae in shell outline and ornamentation, muscle scar pattern, phragmocone structure, and morphology of the siphuncular deposits. The elongation of septal necks appears as the best diagnostic characteristic of the Endoceratina, marking their derivation from the baltoceratids (fig. 10). The endoceratid septal necks expanded in length and reached finally the preceding septa, which made cameral liquid exchange impossible in the phragmocone. Consequently, there are no cameral deposits, while siphuncular deposits are strongly developed. There is great intrapopulation variability in the morphology of these deposits (Mutvei 1964). The primitive as well as the typical Endoceratina have long and straight shells (e.g. *Suecoceras*). However, a short and strongly endogastrically curved shell resembling the Discosorida in outline developed independently in two endoceratid lineages, namely the Tremadocian piloceratids (their affinities to other Endoceratina are not certain) and the Llanvirnian lineage of *Cyrtendoceras*. The dominant trend in the evolution of the Endoceratina is towards an increase in size of the embryonic shell (cf. Holm 1897). Even the earliest representatives of the suborder are believed to have differed from the baltoceratids in the absence of small planktic larva. Arenigian endoceratids had embryonic shell less than 5.0 mm in diameter. In more advanced Llanvirnian forms (*Proterovaginoceras*), the embryonic shell attained 25.0 mm in diameter and the air chambers developed only after the hatching.

Discosorida

The discosorids probably evolved from some breviconic, endogastric Ellesmeroceratina. The main difference between the two groups is in the considerably inflated connecting rings in the Discosorida. Very poorly known forms, possibly intermediate between these groups, occur in the Arenigian of North America (Flower 1964), but the oldest typical discosorids (*Protophragmoceras* = *Strandoceras*) are recorded from the Llandeilian of the Baltic region (Sweet 1958). The discosorid affinities of the

family Ruedemannoceratidae, believed by Flower and Teichert (1957) to be ancestral to the order, are disputable. The ruedemannoceratids appear to be related to an orthoceratid family, the Sactoceratidae. The endogastrically curved, compressed shell is typical of the Discosorida up to the end of the stratigraphic range of the order. Laminar deposits fill up the wide siphuncle of various robust discosorids. Connecting rings are thought to be very thick but I believe that most representatives of the Discosorida have thin connecting rings supplemented by irregularly developed cameral deposits at their outer side (cf. Marek 1976; Crick and Teichert 1979).

Various Discosorida have constricted living chamber apertures, which gives an insight into their anatomy. The phragmoceratid aperture is almost entirely covered, except for small, oppositely situated funnel and head openings (fig. 8). The shell is drop-like in section which contributes to its streamlining. The arched shape of the head channel is indicative of a near-bottom mode of life, with feeding organs pointing obliquely downwards. The evolutionary lineage that started with the genus *Phragmoceras* displayed a trend towards development of radial-lamellar siphuncular structure. Radial lamellae occur only in proximity of the septal necks in the Silurian representatives of the lineage, whereas they run along the entire siphuncle in their Devonian relatives (*Bolloceras*). The Gomphoceratidae also show considerably developed radial lamellae in the siphuncle but they have a multipartite head aperture. The Devonian Archiacoceratidae display a simple aperture and relatively weakly curved shell. They may be oncoceratid homeomorphs of the Discosorida.

Tarphyceratida

The tarphyceratids evolved from an exogastric and longiconic group of the Ellesmeroceratina, the Basslerocertidae (Flower 1976). The considerable length of their living chamber and the correlated shell elongation probably are inherited from the ancestral Ellesmeroceratina. The order may have begun with the origin of exogastric shell (then, the Bassleroceratidae with long living chamber are to be assigned to the Tarphyceratida; Flower 1976), or with shell coiling (then, *Aphetoceras* with loosely coiled shell is to be recognized as the earliest representative of the order). The shell coiling increased during evolution, especially in the juvenile stages; the mature living chamber remains uncoiled in the majority of advanced forms. The primitive Tarphyceratida have a ventral siphuncle indistinguishable in structure from that of the Ellesmeroceratina and a more or less undifferentiated attachment scar of the retractor muscle (Mutvei 1957). There are two distinct ventral (*Discoceras*) or umbonal (*Trocholites*) scars in more advanced forms (Mutvei 1957; Dzik in press). The aperture morphology is constant in the Tarphyceratida, i.e. very obli-

que, with wide ventral sinus. The only exception is in the *Weberoceras* from the Upper Ordovician of Kazakhstan, which shows a transverse aperture without any sinus (Barskov 1972).

Oncoceratida

The oncoceratids also evolved from exogastric representatives of the Ellesmeroceratina, but from forms with a short living chamber. The first typical members of the order are known from the Arenigian-Llanvirnian boundary (Kundan) of the Baltic area (Dzik in press). In addition to the considerably exogastrically curved shell, they also display inflated connecting rings typical of the Oncoceratida. Connecting rings are greatly variable in thickness in the Oncoceratida. Some forms (e.g. *Oonoceras*) show connecting rings approximating in thickness and structure to those of typical Ellesmeroceratina, and are much thicker than those in the Discosorida (contrary to the definition of the Discosorida given by Flower and Teichert 1957; Zhuravleva 1972).

Among the longiconic descendants of *Oonoceras*, especially interesting is a lineage of forms ornamented with undulated lamellae. This lineage started with the Llandeilian genus *Zitteloceras* and displayed during the Silurian (*Hercocyrtoceras* = *Corbuloceras*) a trend towards fusion of the undulated lamellae into longitudinal ribs which produced, along with interconnecting lamellae, a reticulate pattern of shell ornamentation. The Silurian forms with curved shell probably gave origin to the Lower to Middle Devonian Rutoceratidae with loosely coiled, reticulated shell. The rutoceratids were recognized as ancestral to the Nautilida. However, there are no morphological intermediates between Rutoceratidae *s.s.*, characterized by a ventral siphuncle, peculiar shell ornamentation consisting of thick longitudinal ribs, and metameric muscle scars, and the typical Nautilida with subcentral siphuncle, finely longitudinally striated shell, and lateral scars of the retractor (Mutvei 1957). The muscle scar pattern of *Hercocyrtoceras* (*Corbuloceras*) *corbulatum* from the Pridolian of Bohemia gives unequivocal evidence for its assignment to the *Oncoceratida* (Horný 1965). Early Devonian *Ptenoceras* was considered to be close to the Oncoceratida and ascribed to the Rutoceratidae, but my re-examination of the Barrande's material (Dzik in press) did not confirm the occurrence of siphuncular radial lamellae, a feature previously used to support that hypothesis. The Eifelian genus *Doleroceras*, supposedly close to *Ptenoceras*, shows a metameric muscle scar pattern (Zhuravleva 1972a) which seems to refute its assignment to the lineage ancestral to the Nautilida, even though this character is not diagnostic of its true systematic position. Therefore, I consider the hypothesis that the Nautilida evolved from the Oncoceratida as implausible, the more so since the Nautilida can be der-

ived easily from *Lechritrochoceras* (*Kosovoceras*) of the family Urano-ceratidae *s.l.*

More typical representatives of the Oncoceratida, known also since the Arenigian-Llanvirnian boundary, are those with short and bulging shell. They include some groups varying mostly in shell cross section and siphuncular structure. The Westonoceratidae are ecological equivalents of the Discosorida, but with exogastric shell. Their siphuncles when found in isolation cannot be distinguished from those of Discosorida and this is why the Westonoceratidae were ascribed (Flower and Teichert 1957) to the latter order. The Westonoceratidae may have evolved from *Hemibeloito-ceras* (= *Metephippiorthoceras*) from the Llandeilian (Chazy) of Siberia. One of the Silurian branches (*Rizosceras*), possibly related to the westono-ceratids, displays an unusually wide intrapopulation variability in extent and direction of apical shell curvature. This group may have give rise to the Devonian endogastric genera *Sthenoceras* and *Alpenoceras* assigned previously to the Discosorida.

Most Upper Devonian representatives of the Oncoceratida are devono-cheilids with narrow siphuncle and depressed, bulging shell. One of the devonocheilid branches displays a great variation in extent and direction of shell curvature (*Devonocheilus*, *Ukhtoceras*), which results in homeo-morphy with some discosorids (*Flowerites*). The abundant materials from the Holy Cross Mountains, Poland and Timan show great intrapopulation variability of the devonocheilid mature shell size and shape. The frequent finding of populations with variably constricted mature aperture may in-dicate a dependence of the extent of apertural constriction on the envir-onmental conditions.

There are two main evolutionary branches of the Oncoceratidae, both of them ranging from the Llandeilian through to the Lower Carboniferous, and differing in the extent of radial lamellae in the siphuncle. The lamel-lae are confined to the septal necks in the family Poterioceratidae *s.l.* (in-cluding Diestoceratidae). This family flourished in the Silurian of Bohemia and Gotland (*Mandaloceras s.l.*). Most of species show a T-shaped adult aperture. There is a great intrapopulation variability, especially in shell ornamentation. The Bohemian poterioceratids present a complete morpho-logic spectrum of species with ventral to subdorsal siphuncles. A similar spectrum occurs in the Upper Devonian genus *Mecynoceras rex* from Central Russia, but subdorsal in the almost coeval *M. polonicum* from Poland (Dzik in press).

The radial lamellae continue from one connecting ring to another in the family Jovellaniidae *s.l.* There is a complete fossil record of the main evolutionary lineage of this family from the Llandeilian through to the Siegenian. This lineage may have given rise to coiled forms (*Nothoceras*), as well as to those with straight and elongate shell (*Tripleuroceras*). In the latter lineage, the siphuncle shifted from ventral to dorsal position. There

are also some tightly coiled forms with subcentral (*Nothocerina*; see Barskov 1972) as well as dorsal(?) siphuncles (*Kotelnyoceras*; see Balaschov 1975).

Orthoceratina

The orthoceratids evolved from an ellesmeroceratid family, the Baltoceratids (Hook and Flower 1976). The only difference between *Cochlioceras*, a baltoceratid, and *Tajaroceras*, an orthoceratid, is in the slightly more centrad siphuncle of the latter, whereas their siphuncular and cameral deposits, phragmocone structure, and shell outline are indistinguishable (cf. Dzik in press). The occurrence of calcareous deposits in the apical part of the shell is characteristic of all the Orthoceratidae, including the genus *Orthoceras*. The primitive Orthoceratina resemble their ancestors, Ellesmeroceratina, in possessing a planktic larval stage. The morphology of the embryonic and larval shells gives the diagnostic characters of orthoceratid species (Ristedt 1968; Kolebaba 1973; Serpagli and Gnoli 1977).

The families Choanoceratidae and Ascoceratidae represent aberrant lineages derived from the Orthoceratidae and differing from the remaining Orthoceratina in their peculiar septa, exogastric shell and the ventral position of the retractor scars. This is a small, though taxonomically oversplit, group very close to the Orthoceratidae, and there is no reason to recognize it as a distinct suborder or order. The hypothesis that they were undergoing shell truncation during ontogeny is untenable (for discussion see Dzik in press).

An important branch of the Orthoceratida started in the earliest Llanvirnian with the genus *Clinoceras*. These orthoceratids with inflated connecting rings are among those nautiloids evolving at the lowest rate; the Carboniferous species of *Clinoceras* (= *Dolorthoceras* and *Pseudorthoceras* *sensu auct.*) are almost indistinguishable from their Ordovician, Silurian, and Devonian congeners (Dzik in press). *Clinoceras* gave rise to several lineages of variously ornamented Orthoceratina.

Actinoceratina

The family Sactoceratidae, with subspherical connecting rings, is among the most important of descendants of *Clinoceras* from the evolutionary standpoint, because it fills the morphological gap between the Orthoceratina and actinoceratids. The Sactoceratidae are known to have occurred since the Llandeilian but, nevertheless, they can be recognized as ancestral to the Actinoceratina. I reject direct origin of the actinoceratids from such ellesmeroceratid groups as Bathmoceratidae (Flower

1976), Baltoceratidae(?) (Collins 1976), or Plectronoceratidae (Chen *et al.* 1979).

The actinoceratids were considered to form a distinct subclass or superorder, because of the radial pattern of their siphuncular deposits interpreted as being of mesodermal origin. Their calcareous siphuncular deposits do not differ in origin and microstructure from those observed in other nautiloids (Mutvei 1964), while siphuncular deposits in the form of radial blocks occur also in *Clinoceras* and some other Orthoceratina. The only difference between the Orthoceratina and Actinoceratina is in the size of the embryonic shell. Erection of a taxonomic unit using this single diagnostic feature may result in a polyphyletic taxon because a trend towards increasing size of egg is widespread in evolution, including various groups of the Nautiloidea. It may be more reasonable to attribute the family Sactoceratidae to the suborder Actinoceratina, as the inflation of connecting rings would then mark the origin of the suborder. However, one cannot guarantee that such a group would be monophyletic. To this end, a more detailed understanding of the actinoceratid shell structure and evolution is needed.

"Lituitina"

Arising from the orthoconic Orthoceratina, this group (for diagnosis see Dzik in press) proved to be successful with elongate septal necks and connecting rings undergoing destruction during the life of the animal. The destruction of the connecting rings in the apical part of phragmocone resulted in fusion of the siphuncular and cameral deposits. Commonly, the connecting rings were only partly destroyed; the preserved structures demonstrate that soft tissues of the siphuncle could not intrude into the chamber. Then, the idea of a cameral mantle (Teichert *in* Fisher and Teichert 1969; Kolebaba 1974) must be refuted. In fact, that hypothesis is incompatible also with the occurrence of cameral deposits in belemnite phragmocones (Jeletzky 1966), the later being doubtlessly homologous to the rudimentary shells of the extant Cephalopoda. In my opinion, the hypothesis that the calcium carbonate was deposited from the cameral liquid can account even for the radial pattern of secondary deposits in *Arthrophyllum*.

The earliest representative of that group with connecting rings undergoing destruction is *Rynchorthoceras* ranging from the Arenigian upwards. *Rhynchorthoceras*, or its relative, may have given rise to the Silurian "leurocycloceratids", with *Sinoceras* representing an intermediate stage. Exogastrically coiled apical part of the shell appears in *Rhynchorthoceras* at the Arenigian-Llanvirnian boundary (early Kundan). A divergence in the morphological evolution of juvenile and adult lituitids indicates different modes of life. The juvenile lituitids, coiled and with

a deep funnel sinus, were vagile, and possibly lived near the bottom. In turn, the adult lituitids, with straight shell, complex mature aperture and shallow funnel sinus, were probably pelagic forms. Typical representatives of the Lituitidae, with spirally coiled juvenile stages, can be derived from orthoconic *Rhynchorthoceras* through a morphologically continuous series of forms. Attribution of the Lituitidae to the Tarphyceratida is disproved by the stratigraphic sequence of development of siphuncular structures and modified shell aperture.

The aberrant genus *Sphooceras*, with an exceptionally large protoconch(?) and a phragmocone consisting of only a few chambers, may be related to orthoconic *"Lituitina"* - like *Sinoceras* or *Murchisoniceras*. Reexamination of the original material housed at Narodní Muzeum, Prague did not confirm the occurrence of shell truncation in *Sphooceras*.

Agoniatitida

The Orthoceratidae gave rise to the Bactritidae, with the genus *Plagiostomoceras* ($=$ *Protobactrites*) as an intermediate stage. The evolutionary transition consisted mainly of the development of a compresed shell and a shift of the siphuncle towards a marginal ventral position, i.e. in the convergence to the Ellesmeroceratina. The hypothetical phylogenetic relationship of the bactritids to orthoceratids is corroborated by their stratigraphic sequence, as well as by the apertural outline, shape of the living chamber, siphuncular structure, and morphology of the embryonic and
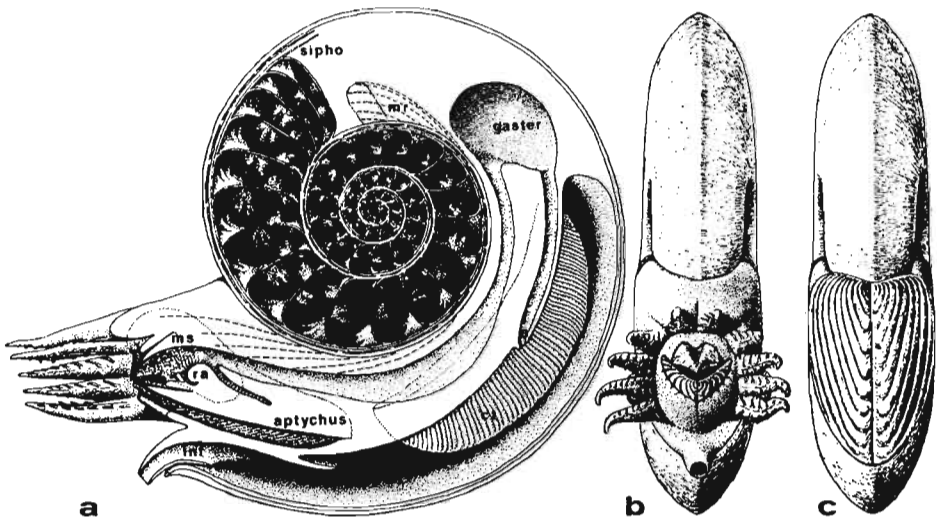

Fig. 9. Tentative reconstruction of soft part anatomy of a Jurassic ammonite (cf. fig. 7), sagittal section (*a*) and oral views with protruded tentacles (*b*) and aperture closed with aptychi (*c*). Data from Lehmann (1967, 1972, 1975) and other sources. *ct* ctenidium, *ms* upper jaw, *mr* retractor muscle, *inf* funnel, *ra* radula.

larval shells. A relationship of the Bactritidae to *Bactroceras* (= *Eobactrites*), a baltoceratid, appears to be much less likely.

A relative of *Plagiostomoceras*, the genus *Lobobactrites*, gave rise to *Cyrtobactrites* and *Kokenia*, with the evolutionary change consisting of exogastric curving of the shell (Erben 1960). The appearance of an exogastric shell in this lineage appears to be the best character for the unequivocal distinction between the subclasses Nautiloidea and Ammonoidea; therefore, *Cyrtobactrites* and *Kokenia* are to be assigned (Dzik in press) to the family Anetoceratidae of the Agoniatitina. *Lobobactrites* is the earliest form with pedal retractor scars; a pair of elongate, oblique scars at the dorsal side of shell, which is typical of the Ammonoidea (cf. Erben 1960). One may also assign the whole family Bactritidae to the Ammonoidea, as well (Erben 1960). *Kokenia* and *Anetoceras* (the latter may be a junior synonym of the former) show an oblique aperture, as in the Tarphyceratida or later Goniatitida, but atypical of the earliest Ammonoidea. A much more ammonoid-like aperture, which is also similar to that of the Lituitidae, occurs in *Cyrtobactrites*. Typical, tightly coiled ammonoids resembling *Cyrtobactrites* in their apertural form (*Mimagoniatites*) appeared almost coevally with the earliest representatives of *Anetoceras* (see Chlupač 1976).

The general structural pattern of the ammonoid radula has persisted unchanged at least from the Carboniferous (Closs 1967) to the Jurassic (Lehmann 1967, 1972). It is indistinguishable from that of the Coleoidea (Saunders and Richardson 1979). This suggests that a similar radula must have occurred also in the Bactritidae, the common ancestors of the ammonoids and coleoids. This constancy in structure of the cephalopod radula is surprising when compared to its diversity in the Gastropoda (Hickman 1980).

Belemnitida

Lobobactrites supposedly give rise to *Bactrites*, the latter genus being characterized by its circular cross section and less longiconic shell than most bactritids. A relative of *Bactrites* is *Eobelemnites caneyense* from the Chesterian (Namurian) of North America, the earliest representative of the subclass Coleoidea (see Flower and Gordon 1959). The boundary between the Bactritidae and Belemnitida is indicated with the appearance of the mantle covering the shell. The origin of this outer mantle cannot be precisely dated.

If the Bactritidae were attributed to the Ammonoidea (Erben 1960), the Coleoidea should be formally considered as descendants of the latter. However, the belemnites resemble closely the ammonites in structure of their radula and phragmocone. The Carboniferous belemnites already have ten

arms, with hooks (onychites) and beak-like jaws (Johnson and Richai l-son 1968; Donovan 1977; Saunders and Richardson 1979). The shell must have lost its protective function prior to its covering with the manɔle; hence, it is not surprising that the jaws ceased to function as an oper-culum.

Nautilida

The family Uranoceratidae has been attributed to the Tarphyceratida. However, the stratigraphic sequence of the uranoceratids does not corro-borate that hypothesis. The first known undoubted uranoceratid species is *Centrocyrtoceras vagrans* from the Lower Caradocian of Canada (Wilson 1961). It has a loosely coiled shell with a subcentral siphuncle, both feat-ures being typical of the family. The Upper Ordovician (Mutvei 1957) and Silurian species of *Uranoceras* are better known. They display a longitud-inally striated shell surface and inflated connecting rings. The morpho-logical gap between *Centrocyrtoceras, Uranoceras,* and the pre-Cara-docian Tarphyceratida is too wide to allow their phylogenetic inter-relationship. In turn, the Uranoceratidae can easily be derived from exo-gastric, longitudinally striated Orthoceratina. There are in the Silurian of Bohemia nautiloid species that may be assigned to the Orthoceratina as well as to the Uranoceratidae.

The primitive Uranoceratidae display a strongly developed pedal re-tractor scar at the ventral side of shell, resembling in this respect other exogastric nautiloids (e.g. *Choanoceras, Billingsites, Discoceras*). There is a complete morphologic transition to the lateral retractor scar character-istic of the Upper Silurian *Lechritrochoceras (Kosovoceras)* (Turek 1975). Until the Upper Givetian the latter genus maintained its shell shape and ornamentation with ventro-lateral tubercles, transverse ribs, and longitud-inal striae. There are no data on the Frasnian to Famennian descendants of *Lechritrochoceras (Kosovoceras)* but, nevertheless, this form appears to be ancestral to the most primitive Lower Carboniferous Nautilida, namely the group of *Chouteauoceras* and *Rineceras.* In addition to the affinity in shell shape, ornamentation and siphuncle position, the pattern of retractor scar is the same in *L. (Kosovoceras)* (Turek 1975) and in the Lower Carboniferous Nautilida (Mutvei 1957).

This hypothetical phylogeny of the Nautilida can be much more com-pletely documented in the fossil record than a derivation from the Onco-ceratida. The Trochoceratidae with subventral siphuncle may have branch-ed in the Devonian from the main evolutionary lineage linking the Urano-ceratidae and Trigonoceratidae.
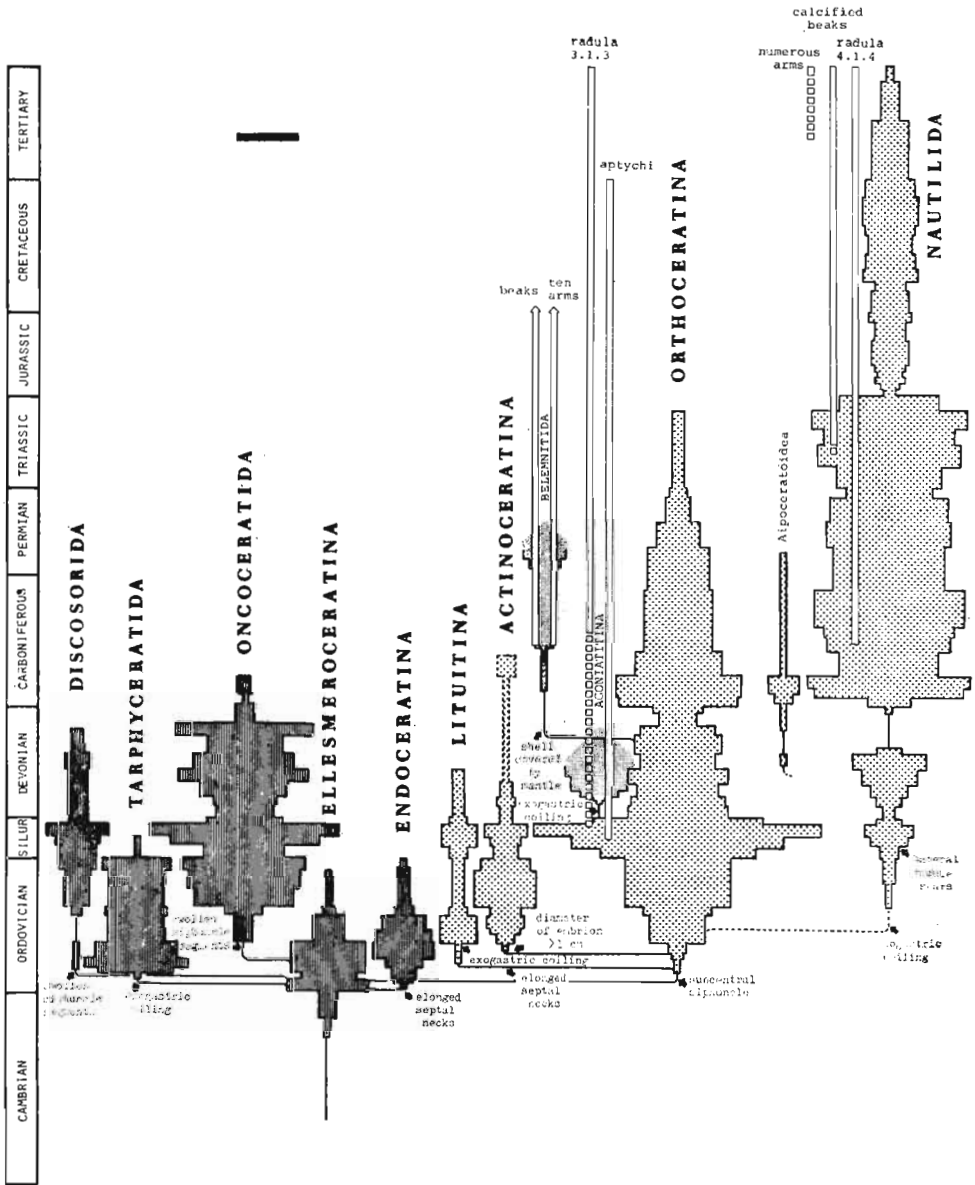
Fig. 10. Phylogenetic relationships among large groups of the Nautiloidea and their relation to the other cephalopod subclasses. Width of a branch reflects the species richness at a time plane (bar scale — 10 monospecific evolutionary lineages) with only unquestionably distinct species taken into account. Blank vertical bars indicate the fossil record of particular body structures (hypothetical occurrences marked by dashed lines). Black arrows indicate evolutionary events which permit definition of taxa. The derivatives of Orthoceratida, originally with subcentral siphuncle, are dotted, derivatives of Ellesmeroceratina, originally with ventral siphuncle, are hachured, early evolutionary stages of the Ammonoidea and Coleoidea are shaded grey.

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Mrs. Elżbieta Radzikowska took the photographs mounted on fig. 6c, d.

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POCHODZENIE GŁOWONOGÓW

Streszczenie

Panująca w literaturze paleontologicznej teoria pochodzenia głowonogów (Yochelson *et al.* 1973) opiera się na trzech przesłankach: (1) najstarsze głowonogi pełzały po dnie, (2) rozwój prosty wewnątrz osłonek jajowych był właściwy pierwotnym głowonogom, (3) organizacja anatomiczna głowonogów cechuje się pierwotną metamerią, podobną jak u dzisiejszych jednotarczowców. Konsekwencją przyjęcia tych przesłanek jest teza, że głowonogi powstały z jednotarczowców o stożkowatej muszli, przy czym septa głowonogów odpowiadają diafragmom w wierzchołku muszli tych jednotarczowców. Przemiany ewolucyjne prowadzące do powstania głowonogów odbywały się w strefie bentosu, zaś swobodny tryb życia głowonogów miałby być późniejszym ich osiągnięciem. Podstawowym brakiem tej teorii jest to, że nie wyjaśnia przyczyn powstania syfonu i wykształcenia hydrostatycznych funkcji fragmokonu, struktur najbardziej charakterystycznych dla gromady głowonogów.

Krytyczny przegląd danych paleontologicznych i analiza funkcjonalna muszli najstarszych głowonogów wykazuje niesłuszność wymienionych przesłanek. (1) Pełzanie po dnie najstarszych głowonogów byłoby sprzeczne z występowaniem u nich w pełni wykształconego fragmokonu. Trudno przypuścić, ażeby tak złożona struktura powstała przypadkowo bez ukierunkowanego nacisku selekcyjnego i była pozbawiona funkcji. (2) Z wielkości najmniejszych fragmentów muszli pierwszych głowonogów (poniżej 1 mm średnicy) wynika, że miały one larwy podobne do larw późniejszych ortocerasów i amonitów, tzn. przechodziły w rozwoju kuliste stadium embrionalne a po wykluciu z jaja stadium planktonicznej larwy. Moment metamorfozy zaznacza się w zmianie ornamentacji muszli (fig. 1). (3) Metameria przyczepów mięśni retraktorów powstała wtórnie w wielu grupach łodzików i nie jest pierwotną cechą głowonogów. Układ przyczepów retraktorów pierwotnych głowonogów nie jest podobny do umięśnienia dzisiejszych jednotarczowców (fig. 5). Pod tym względem, jak również pod względem przebiegu rozwoju larwalnego (Fig. 2) i pokroju muszli, głowonogi zbliżają się raczej do wymarłej grupy Coniconchia obejmującej hyolity i tentakulity.

Przyjmuję, że funkcje hydrostatyczne poprzedziły strukturalny rozwój fragmokonu u najstarszych głowonogów. Pierwotnie mógł je wypełniać pęcherzyk płynu o mniejszej od wody morskiej gęstości. Analogię stanowić tu może płyn coelomiczny dzisiejszych kalmarów Cranchiidae o gęstości 1010 kgm^{-3} (gęstość wody morskiej — 1030 kgm^{-3}). Mechanizm powstawania tego rodzaju płynu o obniżonej gęstości jest zbliżony do przemian płynu komorowego we fragmokonie głowonogów, mianowicie polega on na usuwaniu jonów Na$^+$ przez pompę jonową. U nieosłoniętych muszlą Cranchiidae konieczne jest zrównoważenie ciśnienia osmotycznego, co następuje w wyniku dopływu jonów NH$_4^+$. Wydaje się, że usuwanie jonów Na$^+$ z pęcherzyka płynu w apikalnej części muszli larwalnej mogłoby być wystarczające dla uzyskania odpowiedniej wyporności, jeśli się weźmie pod uwagę małą gęstość ciała larwy i słabą

mineralizację jej muszli. Jeśli odpowiednio szybko nastąpiło by odgrodzenie pęcherzyka płynu przez sztywną organiczną diafragmę, zneutralizowane byłoby działanie ciśnienia osmotycznego, które już po wytworzeniu kilku diafragm (septów) prowadzi do usuwania części płynu z komór za pośrednictwem syfonu. W warunkach obniżonego ciśnienia spowodowanego przez osmotyczny odpływ płynu następuje dyfuzja gazu z płynu komorowego (por. Gilpin i Denton-Brown 1966, 1973). Tego rodzaju proces wymaga sztywnej komory ciśnieniowej o półprzepuszczalnych ściankach, czyli komór powietrznych fragmokonu i rurki syfonalnej, i nie był możliwy przed uformowaniem fragmokonu. Istnieje zatem konieczność wprowadzenia hipotetycznego stadium rozwoju aparatu hydrostatycznego poprzedzającego wypełniony gazem fragmokon. Wytwarzany przez miękkie tkanki płyn wypycha je z wierzchołka muszli. Do wewnętrznej ścianki muszli embrionalnej przytwierdzony jest larwalny retraktor nogi (Crofts 1955). Wypchnięte mogą więc być jedynie tkanki nie związane z retraktorem a w miarę wzrostu rozmiarów pęcherzyka płynu w wierzchołku muszli pozostawałby jedynie sznur tkanek miękkich otaczających retraktor (fig. 3). Po wytworzeniu kilku diafragm jest to jedyna część miękkiego ciała kontaktująca się ze ściankami wcześniej utworzonych komór. Sądzę, że taki mógł być mechanizm powstania syfonu.

Drugą, oprócz fragmokonu, strukturą swoistą dla głowonogów są szczęki (fig. 7 i 9). Aptychy i anaptychy, stowarzyszone z muszlami amonitów i archaicznych łodzików (Turek 1978), pełniły funkcje szczęk i wieczek zamykających ujście muszli (Lehmann 1967, 1975). Szczególną cechą aptychów jest sposób ich powstawania — wytwarzane były przez sekrecję kalcytu od wypukłej, zewnętrznej strony (Farinacci et al. 1977). Te dwie pozorne antynomie można objaśnić przyjmując homologię aptychów z wieczkami muszli hyolitów i ślimaków. Podobnie jak dzisiejszych ślimaków Turbo czy Natica (fig. 6) aptych amonitów i łodzików zakładał się jako organiczna płytka sekrecjonowana od strony wewnętrznej (wklęsłej) (fig. 7). Wtórnie następowało pogrubienie aptycha w wyniku odkładania wapiennej zewnętrznej warstwy przez fałd ciała pokrywający go od zewnątrz. W trakcie wciągania ciała do wnętrza muszli jako pierwsze byłyby wnicowywane fałdy ciała umożliwiając zakrycie muszli przez mineralną powierzchnię aptycha (fig. 7). Koncepcja ta tłumaczy również dwuczęściowość aptychów.

Zbierając razem przedstawione powyżej koncepcje otrzymujemy obraz przodka głowonogów (fig. 8 i 10) jako planktonicznego mięczaka o wydłużonej stożkowatej muszli z organicznym operculum, o prostej organizacji rozmieszczenia mięśni pedalnych i złożonym rozwoju larwalnym. Wydaje się, że mięczaków o takiej organizacji należy poszukiwać w obrębie pierwotnej, słabo poznanej grupy kambryjskich hyolitów Circothecida.