

its differentiation as well, as in the mature animal.

Thus, the start of ammonid shell formation occurs comparatively early, before mantle formation and differentiation, and before formation of the main internal organs of the mature individual type.

The hypothesis of larval development is more preferable than that of direct development. The stages of metamorphosis easily come into harmony with structural reconstruction (forming of the primary constriction). The protoconch-bearing initial parts of bacteritids and orthocerids have a similar construction. As was supposed formerly (Shimansky, 1962, and others), the development of the latter groups proceeds with "incomplete metamorphosis" and with a veliger-like larva. This larva was not a true veliger, because its planktonic behavior was warranted by a hydrostatic apparatus of the shell, but not by the velum.

Complex structural changes take place in early stages of the belemnite skeleton (Barskov, 1974). Belemnites had early deposition of the shell; their larvae apparently had an internal shell and so they can hardly be compared with veligers.

I propose the following scheme for the evolution of the cephalopod ontogenesis. The primary cephalopod larva (protocerella, non-planktonic) had a large conic shell with an apical opening (as Starobogatov postulated in 1974 for the larvae of molluscs with a dorsal visceral sac), no more than 1 chamber and no separated siphonal division. This construction resembled *Nanno* (Endocerida) and *Kochoceras* (Actinocerida). During the succeeding evolutionary tendency for direct development, the hatching individual (seminauta, nauta) acquired a conic or voluted conch with a 1-6 chambered phragmocone and body chamber, with the siphonal division formed. The relict apical opening was a cicatrix. The structure of the shell wall was analogous to that of the mature shell. Both hatching and mature individuals had a swimming behavior. This development type has succeeded in the cephalopod branch by Nautilida (orders Ellesmerocerida, Tarphycerida, Oncocerida and Discosorida) and partly by Orthocerida and Pseudorthocerida, and later by Endocerida and Actinocerida.

In the phyletic branch of the ammonids, belemnites and Recent Dibranchiata, a delay in development evolved. Such a delay was expressed in the protoconch's separation in the embryonal shell, the wall of which consisted of unique microstructure layers. Then a secondary planktonic larva, the deuterocerella (nautella, ammonitella, teutella), developed. The direct development of Recent teuthids is the latest evolutionary acquirement.

Thus, I suggest the existence of the following trends in evolution of cephalopod ontogenesis: from a primary larval development to a direct one (Ellesmerocerida, Endocerida and Actinocerida); from direct development to a secondary larval one (within Orthocerida, from Ellesmerocerida – or from Orthocerida – to Bacteritida); from secondary larval to "secondary direct development" (from Belemnitida to Teuthida; from Bactritida – or from Phragmoteuthida – or from Aulacocerida – to Sepiida).

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THE STRUCTURE OF THE SKELETAL ELEMENTS OF EARLY CRETACEOUS AMMONITES AND THEIR SYSTEMATIC IMPORTANCE

V. V. Drushchits and L. A. Doguzhayeva

*Zoological Institute, Academy of Sciences
Leningrad, U. S. S. R.*

Abstract

The introduction of the scanning electron microscope into the practice of paleontological research has made it possible to study the texture, microstructure and ultrastructure of the skeletal elements of cephalopod mollusks and to clarify their significance in systematics. To pursue this study the shells of 20 genera of early Cretaceous ammonites belonging to 3 orders (Phyllocerata, Lytocerata and Ammonitida) were studied.

The protoconch of all the ammonites studied was either globular or roller-like in form, with a diameter ranging from 0.25 to 0.8 mm. Its wall consists of 1 prismatic sublayer in the apical portion, and 2 prismatic sublayers in the region where the prosepium is attached to the ventral wall. The wall of the 1st whorl consists of 1 prismatic layer.

The primary varix, which is a thickening of the shell wall, is located at the end of the 1st whorl; its position is defined by "the angle of the primary varix," the size of which ranges from 225 to 340 degrees. It is formed at the expense of the nacreous layer which appears immediately before it or somewhat earlier, remaining very thin at some distance from the primary varix. The primary varix is usually of an ir-

belinia sp. In regard to the trematodes, metacercariae of didymozoids (type *Torticaecum*; 12.5%), *Hirudinella ventricosa* (1.05%) and a single mature didymozoid trematoda (0.09%) were found.

An analysis of the species composition of helminths from ommastrephids has revealed 2 helminthocoenoses, coastal and oceanic. The main coastal forms are *Anisakis* sp. 1, *Phyllobothrium* sp. 1, *Dinobothrium* sp. and *Scolex pleuronectis*. The main oceanic forms are *Tentacularia coryphaenae*, *Nybelinia yamagutii*, *Phyllobothrium* sp. 1, *Anisakis* sp. 1, *Porrocaecum* sp. and metacercariae of the Didymozoidae. Such distinct differences in the species composition of the above helminthocoenoses refer not only to ommastrephids, but are a reflection of coastal and oceanic biocoenoses existing in the ocean.

A great specific variety of the helminths, and rather high indices of extensity and intensity of infection in the oceanic ommastrephids, are stipulated by their high ecological valence, as compared to the coastal representatives of this family.

The intraspecific and local variability in squid infection depends on the presence or absence of masses of parasites of ommastrephids, definitive hosts of helminths, and lastly on the historically formed trophic relations of the squid in a given region.

All helminths found in ommastrephids possess a wide specificity, and use for the same developmental stages many species of teleost fishes as intermediate hosts. The ancestors of ommastrephids "conquered" recent ecological niches on account of this or that group of teleost fishes, and acquired their helminths. Thus, the helminth fauna of ommastrephids is secondary in character and consists of typical "fish" forms.

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STRUCTURE OF THE SHELL AND EVOLUTION OF ONTOGENESIS IN THE CEPHALOPODA

I. S. Barskov

Moscow State University, Moscow, U. S. S. R.

Abstract

Unlike other molluscs, Recent cephalopods have no larval stages in their development. The shelled forms (e.g., *Nautilus*, *Sepia* and *Spirula*) have no morphological and structural differences in their embryonic and postembryonic skeletons (except in size and some allometric growth patterns). The embryonic shell seems to be secreted not only by the shell gland, but also by the mantle, the differentiation of which was identical to that of mature forms. The initiation of the secretion of the embryonic shell has been shifted to comparatively later stages of embryonic development. The fossil cephalopods, which were connected with the phyletic branch which evolved into the Recent Tetrabranchia, have the embryonic shell structure principally like that of Recent *Nautilus*. Thus, direct development with comparatively late embryonic formation of skeleton is an early evolutionary acquirement, and it may be the primary type of ontogenesis in this branch. There are great structural differences in the initial parts of the shell of fossil cephalopods which are related to the ancestors of the Recent Dibranchia. These differences are, for example, a known morphological and structural feature of the 1st whorl of ammonids and the initial part of belemnites', orthocerids' and bacteritids' shells.

There are opposite views on ammonid development, i.e., from a direct one to development with several larval stages and metamorphosis. These differences are caused by a different interpretation of the boundary between embryonic and postembryonic parts of the shell. Three possible variants of the place of this boundary have been presented: at the end of the protoconch (Erben, 1964, and others); at the end of the 1st whorl, excluding the primary ("nepionic") constriction (Drushitz, 1958, and others); and at the end of the 1st whorl, including the primary constriction (Ivanov, 1971; Kulicki, 1974).

The principal problem lies not in the position of the embryonic shell boundary, but in the explanation of the existing structural reconstructions. In the initial part of the ammonid shell, it is possible to distinguish 4 morphologically and structurally different regions, which correspond to 4 stages of early ontogenesis: 1) protoconch formation, 2) formation of the 1st whorl, 3) primary constriction formation, and 4) formation of the 2nd and the following whorls. The structural reconstructions occur between the 2nd and the 3rd, and the 3rd and 4th stages.

Thus, the existence of structural changes shows that physiological mechanisms responsible for secreting the shell have undergone changes. Structural monotony of the protoconch and 1st whorl layers shows their secretion to be produced not by differentiated epithelium but rather by the shell gland (or by the primary mantle roset as in the case of the veliger). The existence of nacreous layers in the primary constriction and in the shell wall of the following whorls testifies to the appearance of the mantle and to

regular lens-shaped form, with a gradual posterior and steeper anterior end. The prismatic layer of the 1st whorl in the primary varix wedges out or curves around its anterior portion. The primary varix is connected with the primary constriction, which is situated immediately beyond the varix, as a rule, and evidenced in various ways in the forms studied: from a hardly noticeable form to a sharply marked one. The height of the whorl usually changes after the primary varix. The primary varix is characterized by marked changes which had occurred in the ontogeny of ammonites; in the opinion of some scientists, it signifies the end of embryonic development (Birkelund, 1967; Ivanov, 1971; and others), while others contend that it stands for the transition from the larval to the postlarval stage (Erben et al., 1968b). We support the former viewpoint.

After the primary varix, the outer wall of the shell of all subsequent whorls consists of 3 calciferous layers (the outer prismatic, the middle nacreous and the inner prismatic layers) and 2 organic layers (the external periostracum and the fine layer lining the shell inside). The calciferous layers do not form at the same time. The outer prismatic and nacreous layers appear on the internal surface of the primary varix in its anterior part, forming the outer surface of the evolute part of the whorl. The inner prismatic layer appears either before the primary varix, or simultaneously with the 2 mentioned above, or on the 2nd whorl of the spiral. In structure, the dorsal wall (the involute part of the whorl) is sharply differentiated from the external (ventral and lateral). It is built out of 1 inner prismatic layer; the 2 other layers, comprising the external wall, wedge out in the area of the umbilical seam. The dorsal wall of the Phylloceratida and the Lytoceratida is thick; in thickness it is either as thick as the ventral wall or thicker by 50-400%. In the living chamber, it wedges out at a distance equal to the length of 1.5-2.5 hydrostatic chambers. The dorsal wall of the ammonites that have been studied was equal in thickness with the ventral wall or thinner; in the living chamber it did not wedge out, but merely thinned. In ammonites with a costate shell, the dorsal wall does not repeat the curves of the preceding ventral wall and forms a smoothed-out inner surface of the shell (*Colombiceras* and *Acanthohoplites*).

Assymetrical bulges, or varices, can be observed in many forms on the 2nd and following whorls, particularly in the Phylloceratida and the Lytoceratida. These varices, just as the primary varix, also develop at the expense of thickening, by 50-400% of the nacreous layer. There may be as many as 10-12 of these varices in the Lytoceratida. The external prismatic layer usually passes the varices without changing, while the inner prismatic layer thins in places of the maximum thickening of the nacreous layer and, quite possibly, wedges out.

A close study of ammonites revealed that the structure of the wall of the protoconch and of the 1st whorl, and the structure of the primary varix and the walls of the shell after it, are closely similar, and this testifies to the common origin of all groups of ammonites.

The first 2 septa – the proseptum and the primarseptum – are of prismatic structure, while the rest are built out of 1 nacreous layer and 2 layers of conchiolin. The mural part of the septa is directed towards the living chamber; at places where the septa are attached to the wall of the shell, a partial "erosion" of the wall takes place, providing for the secure attachment of the septa to the shell. It is fairly possible that, at the same time, a partial recrystallization of this area of the shell wall occurs, particularly marked where the proseptum and primarseptum are located. On the 1st whorl, the septal necks of the Phylloceratida and the Lytoceratida are retrochoanitic; at the beginning of the 2nd whorl they become prochoanitic. In ammonites, prochoanitic septal necks are developed from the 1st whorl.

Short septal necks are typical of the Phylloceratida; long septal necks are characteristic of the Lytoceratida; and short septal necks on the 1st 3 whorls and then short and long necks are typical of ammonites.

A characteristic feature distinguishing the Phylloceratida and the Lytoceratida are special formations – cuffs – encircling the siphuncle. The Ammonitida obviously lack such cuffs. The presence or absence of these cuffs, and the peculiarities of their structure, may be used in defining whether or not an ammonite in question belongs to a given order.

In all ammonites, the siphuncle begins in the protoconch as a drop- or globule-shaped caecum with a diameter from 0.07 to 0.13 mm. The caecum is attached to the wall of the protoconch by means of the prosiphon. The prosiphon consists of a beaker encompassing the caecum and 1 long or several short cords. A long prosiphon is typical of the Ammonitida (it is sometimes attended by several short ones); short prosiphons have been observed in the Phylloceratida and the Lytoceratida. The siphuncle occupies a central position in the 1st 2 septa and then moves to the ventral wall at different speeds. In the Phylloceratida, the siphuncle occupies a ventral-marginal position at the end of the 2nd or on the 3rd whorls; in the Lytoceratida it is in the 1st half of the 1st whorl; in the studied superfamilies of Ammonitida it is in the 2nd-3rd whorls. The change in the position of the siphuncle in the early stages of ontogeny is of systematic importance.