THE STRUCTURE OF THE AMMONITELLA AND THE DIRECT DEVELOPMENT OF AMMONITES

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ABSTRACT: The development of ammonites, like that of all recent cephalopods, proceeded without a larval stage. The embryonic shell of the ammonitella, which emerged from the egg, consisted of a protoconch and a smooth planispiral whorl with prismatic wall microstructure. The ammonitella possessed a caecum and a prosiphon that attached its body to the wall of the protoconch. The protoconch was separated by one, less frequently two septa with prismatic microstructure. During the infant stage of the postembryonic period the ammonitella lived a planktonic mode of life, forming a nepionic ridge with nacreous microstructure; the nepionic line was located in front of the ridge. The end of the infant stage (ammonitella) and the beginning of the adolescent (neanic) stage are recorded by the construction of a shell with a new wall microstructure, by the appearance of sculpture and a different type of coiling in the heteromorphs.

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Paleontologists have long concerned themselves with changes in the ontogeny and phylogeny of the suture line, and in the morphology and sculpture of the shell in ammonites. These changes have been used as a basis for their biological interpretation and for the periodization of ontogeny. In the last ten years the scanning electron microscope has provided new data on ontogenetic changes in the structure of the shell wall, the septa and the septal necks. These data have instigated a new discussion on the early stages of ontogeny. Let us briefly consider some of the structural features of the shell before discussing the problem as formulated.

Ammonites had an external monomorphous or heteromorphous shell. What is understood by a monomorphous shell is any type of planispiral shell consisting of closely contacting whorls, differing in the degree of involuteness; lying in the same plane and not altering their structural plan in the course of ontogeny. All types of shells that deviate from monomorphous are customarily classified as heteromorphous; such shells, which alter their structural plan in the course of ontogeny, include planispiral shells with non-contacting whorls, straight shells consisting of one shaft or two-four contacting or non-contacting shafts connected by geniculate margins, cochlespiral shells, glomerulate shells (Nipponites) and other types of shells (criocones, ancyclocones). The majority of ammonites had a monomorphous shell, a minority had a heteromorphous shell. The latter included the first Early Devonian ammonites, which had a heteromorphous shell in the initial period of the establishment of the entire ammonite trunk, a few Late Triassic and Jurassic ammonites and the more varied and numerous Cretaceous ammonites during the period of their flourishing, their major divergence and their adaptation to various ecological niches.

Irrespective of their shape, monomorphous and heteromorphous shells consisted of two unequal parts, a living chamber housing the body of the mollusc, and the hydrostatic chambers. The first chamber, which differed from the others in that it was spherical or ridge-shaped, has become known as the protoconch, or the initial chamber. Both names are admissible and are equally employed, but the first is used more often, because it is shorter. All the other chambers constitute the hydrostatic apparatus, or phragmocone. The protoconch is hermetically separated from the phragmocone by the first septum, or proseptum. The siphuncle, a special process of the posterior part of the body, the function of which was to release and absorb liquid and gas in the chambers in the construction of the currently forming septum or in vertical migrations of the mollusc, extended through all the chambers of the phragmocone, from the protoconch to the beginning of the living chamber.

The initial part of the shell in all the Jurassic and Cretaceous ammonites, whether monomorphous or heteromorphous, consisted of a protoconch and a planispiral whorl surrounding it, in the

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Translated from Stroeniye ammonitelly i pryamoye razvitiye ammonitov, Paleont. Zhur., 1977, no. 2, p. 57-69.

Paleont. Jour. 1977, no. 2

ISSN 0031-0301/77/0200-0188 $ 07.50/0

final quarter of which there was the nepionic ridge, accompanied by the nepionic line. The nepionic ridge was a thickening of the nacreous layer that was sometimes 1.5-3 times the normal wall thickness. A series of appreciable transformations is to be noted in the following parts of the shell; there are changes in wall structure and in the architectonics of the whorls, and sculpture appears. Some students therefore relate the end of the larval period to the nepionic ridge, while others relate the beginning of the postembryonic period to it.

In most Cretaceous ammonites the living chamber occupied approximately 3/4 of the final whorl. In the course of growth the body of the mollusc enlarged, new portions of shell were constructed around the aperture, and at some point the body was drawn forward and cut off from the phragmocone by the next septum to be formed. There is some uncertainty as to how this process took place and how frequently septa were constructed. Let us assume that one septum was constructed in a lunar month (Ivanov, 1971; Ivanov and Stumbur, 1975).

Among the modern cephalopods Nautilus might serve as a model for comparison; like the ammonites it has an external shell, but it differs from ammonites in the anatomy of the soft parts, in lacking a prosiphon and a segregated caecum and in the median position of the siphuncle. Another model that might be employed is Spirula, which has an endogastrically coiled internal shell consisting of 2.5 whorls. The shell of Spirula is similar to that of ammonites in having a spherical protoconch, a caecum and a prosiphon; as in Late Devonian Clymenia the siphuncle occupies an internal marginal position. The periodicity in the construction of new septa has not been established.

We know that when modern cephalopods (Nautilus, Spirula, Sepia) construct a septum they fill the newly created hydrostatic chamber with a fluid, the salt composition of which is similar to that of seawater, but which has a different concentration of ions and cations. When construction of the new septum is complete the fluid is partly eliminated from the chamber cavity, giving way to gas (Bidder, 1962; Denton and Gilpin-Brown, 1966; Denton, Gilpin-Brown and Howarth, 1967).

The embryogeny of the present-day Nautilus and Spirula are inadequately investigated. The Nautilus female lays large eggs up to 25 mm long and 16 mm in diameter. The nauta that emerges from the egg has an embryonic shell consisting of one whorl; the body structure of the nauta is little different from that of the adult animal. A small constriction to be seen at the end of the first whorl on the surface of the embryonic shell is known as the nepionic line. Subsequent accretion of the shell of the mollusk is halted on emerging from the egg; this is indicated by the nepionic ridge, which arises at the time of adaptation of the mollusk to conditions that are new to it. The reticulate sculpture disappears completely after the nepionic ridge in Nautilus and the cross-sectional shape alters (Shimanskiy, 1948, 1962). These morphological changes are used to establish the limits of the embryonic shell in extinct nautiloids. Young of present-day coleoids, newly emerged from the egg capsules, differ from the adult forms in body size and in the underdevelopment of some organs (reproductive system, fins etc.). The smallest Spirula, taken at a depth of approximately 1000 m, had a body measuring 6 mm and an internal shell consisting of a protoconch and five hydrostatic chambers (Chun, 1975). According to the data of Mutvei (1964) and Barskov (1973), the shell of Spirula consists of two semi-prismatic layers (outer and inner), between which there is apparently a thin layer of periostracum. The septa are constructed from a dorsal conchiolin membrane and a nacreous layer, while the long septal neck extending to the preceding septum has, in addition to the two layers indicated, a further semi-prismatic inner layer; where it joins the preceding septum there is a spherulitic-prismatic layer. The same layer is discovered around the mural part of the septum. The first septum is connected to the wall of the protoconch around the apertural margin and consists of two layers — nacreous and spherulitic-prismatic. The conchiolin sheath of the caecum is attached to the septal neck of the proseptum; an organic dorsal process extends from it to the wall of the protoconch. This process serves for attachment of the siphuncle and is homologous to the ammonite prosiphon. In Spirula (Chun, 1975) the siphuncle is surrounded by epithelium, which is underlain by connective tissue; an axial bundle of parenchymatous tissue, in which the arterial vessel and the venous lacunae (of which there are 12 to 13) are submerged, extends along the center of the siphuncle. There is a cavity between the connective tissue and the axial bundle, which may be treated as a coelomic cavity. The siphuncular epithelium is a direct continuation of the epithelium of the shell sac, but it is distinguished by the structure and shape of the cells.

The ammonite female, like the Spirula female, probably laid numerous small eggs. The ammonitella that emerged from the egg capsule had an embryonic shell consisting of a protoconch and the first whorl. In Jurassic-Cretaceous ammonitellae the living chamber occupied 3/4 of the first whorl and was separated from the protoconch by a proseptum or a proseptum and a second septum. The proseptum was constructed after the body of the mollusc had been drawn out of the protoconch; the second septum was possibly secreted behind it. The proseptum was inserted on the apertural margin of the protoconch and it compressed the posterior part of the body, forming the caecum (fig. 1). The prosiphon was formed from the outer layers of the mantle. The shell of the ammonitella reached a diameter of 1.5 mm, which signifies that the eggs laid by the ammonite female

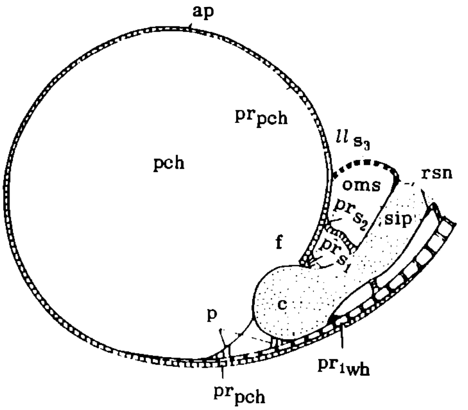


FIGURE 1. Structural diagram of the protoconch and the beginning of the phragmocone as exemplified by the genus Jauberticeras.

ap - apical part, f - flange, pch - protoconch, oms - organic membrane of siphuncle, p - prosiphon, ll_{s_3} - lamellar layer of third septum, pr_{pch} - prismatic layer of protoconch wall, pr_{1wh} - prismatic layer of wall of first whorl, pr_{s1} and pr_{s2} - prismatic layer of first and second septa, rsn - retrochoanitic septal neck, sip - siphuncle, c - caecum.

were probably small. No egg batches have as yet been discovered, although Wetzel (1959) has described ammonite "larvae" from Jurassic deposits in the FGR and a chitinous membrane 0.6 mm in diameter, similar to an egg membrane.

Information on the anatomy of the soft parts of the body and of the embryonic shells of extinct cephalopods may be found in works by Ruzhentsev and Shimanskiy (1954), Shimanskiy and Zhuravleva (1961), Ruzhentsev (1962) and Bogoslovskiy (1969). Comparatively little is known concerning the structure of the soft parts of ammonites. X-ray studies of pyritized ammonite remains carried out in recent years have shown that the appendages of the head consisted of eight to ten short arms (Zeiss, 1968). Remains of the preserved stomach filled with tests of foraminifers and ostracodes, remains of the upper and lower jaws, the ink sac and the radula, and impressions of the gills have been found in ammonite living chambers (Lehmann, 1971). The ammonite radula had seven teeth in each row, by comparison with the 13 in the present-day Nautilus. The ink sac, which was pyriform, and approximately 1/4 the length of the living chamber, had an aperture opening toward the anterior margin of the living chamber; we know that Nautilus lacks an ink sac. The existence of a small number of arms and of an ink sac, taken in conjunction with the structural type of the radula, indicate that ammonites were closer in the anatomy of the soft parts to coleoids than to nautiloids.

Information on the biology and anatomy of modern cephalopods and on their ontogeny, and data on the morphological changes to be observed in ammonite and Nautilus shells are used for the periodization of ontogeny, the history of which has been analyzed in detail by Ivanov (1971). We shall confine ourselves to an examination of embryogeny and of the earliest (nepionic) stage in the postembryonic life of ammonites. There are currently two points of view on ammonite development. The adherents of one view consider that ammonites, unlike the present-day cephalopods, had a larval stage (Shimanskiy, 1954; Erben, 1964). The present authors are of the other point of view, which assumes that ammonites developed directly, without metamorphosis (Drushchits, 1956; Drushchits and Khiami, 1969, 1970; Ivanov, 1973; Drushchits, Doguzhayeva and Mikhaylova, 1973; Mikhaylova, 1976a).

In arguing the direct development of ammonites we shall consider below the morphology and structure of the protoconch and the first whorl, the microstructure of their wall studied in a scanning electron microscope, the nature of changes in the suture line in early ontogeny, the structure of the primary varix and the changes to be observed in the shell after the nepionic line. Attention is concentrated on the structure of the embryonic shell and on the first (nepionic) stage of postembryonic development, during which formation of the shell of the ammonitella was completed, a process the duration of which corresponded to the formation of the primary varix. The following, neanic stage is defined by the construction of the shell after the nepionic line. Irrespective of the shape of the shell in the adult animal, the ammonitella of Jurassic and Cretaceous ammonites had a shell consisting of a protoconch and a first planispiral whorl. Its apertural margin was defined by the position of the anterior edge of the primary varix. The shell diameter of the ammonitella ranges between 0.7 and 1.4 mm in Cretaceous ammonites.

Three types of protoconchs have been established in Cretaceous ammonites: spherical, in which $W - D \leqslant 100\mu$ (where W is the width of the protoconch, D is its diameter), ridge-like, in which $W - D = 101 - 200\mu$, and fusiform, in which $W - D \geqslant 201u$ (Drushchits and Khiami, 1969). Protoconch diameter ranges 0.22 and 0.80 mm, width between 0.33 and 1.00 mm; on average a diameter of 0.3-0.6 mm and a width of 0.4-0.7 mm predominate. The largest protoconchs have been found in members of the family Placenticeratidae (Mikhaylova, 1974a: D = 0.75 mm, W = 1.00 mm). The smallest protoconchs are found in different groups: in the Berriasian genus Ptychophylloceras among the Phylloceratidae (D = 0.22-0.28 mm), in the Middle Jurassic genus Eurystomiceras (D = 0.32-0.39 mm) and the Aptian Ptychoceras (D = 0.28-0.29 mm) among the Lytoceratidae, and in the genus Aconeceras among the Ammonitidae (D = 0.20-0.35 mm). Among the genera investigated (more than 40) only Euphylloceras, Submartinoceras and some of the

Desmoceratoidea had a spherical protoconch; in all the others the protoconch was ridge-like. The protoconch wall is formed of a single prismatic layer (pl. V, illus. 1a-e). Slender aragonite crystals assembled in long prisms are oriented perpendicular to the protoconch wall. This layer peters out at the beginning of the first whorl (pl. VI, illus. 3c, 3d). The prismatic layer that forms the wall of the first whorl appears in the last 1/4 of the protoconch and gradually replaces its prismatic layer (pl. VI, illus. 3a, b; figs. 1, 2).

Birkelund and Hansen (1968, 1974) observed two layers in the protoconch wall of two Late Cretaceous ammonites (Sakhalinites and Scaphites); an inner prismatic layer and an outer subprismatic layer; the latter was distinguished by irregularly oriented crystals submerged in an organic matrix. The wall of the first whorl before the primary varix was constructed of prismatic crystals arranged, as in the protoconch, perpendicularly to the surface of the whorl (pl. V, illus. 1f, g). The protoconch was jointed to the beginning of the phragmocone by a slitlike aperture, through which the soft body of the mollusc was drawn out. This process probably took place slowly and gradually in the course of the construction of the first whorl.

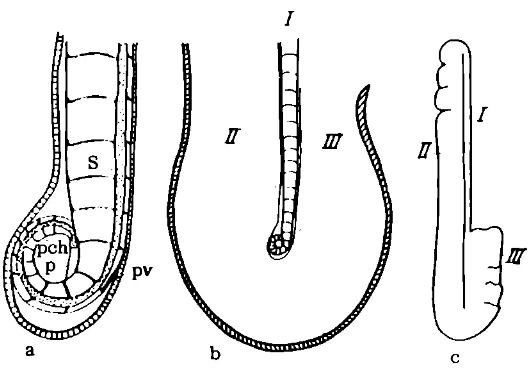


FIGURE 2. Shell structure in the genus Ptychoceras: a - protoconch, planispiral whorl, beginning of first shaft, surrounded by the dorsal wall of the second and third shafts (x 175), b - relationship of the planispiral whorl and the three shafts (x 35), c - general appearance of shell (x 1).

pv - primary varix, s - septum, I-III - serial numbers of shafts; otherwise as on fig. 1.

In Jurassic and Cretaceous ammonites the primary varix is at an angle of 270-340° to the proseptum. In shape the varix varies from elongated lenticular to swollen lenticular with an asymmetric steep anterior margin (pl. V, illus. 1h, i). The thickness of the varix is 1.5-3 times the wall thickness of the first whorl. The structural plan of the primary varix is simple; a nacreous layer, the thickness of which increases gradually or very rapidly, appears in the final quarter of the first whorl. As this layer thickens the prismatic layer tapers away; the point at which it finally peters out corresponds to the apertural margin of the embryonic shell. The primary varix is followed by the nepionic line.

The embryonic period ended before the construction of the primary varix. Having left the egg capsule, the ammonitella transferred to a planktonic mode of life. In the course of the nepionic stage of the postembryonic period, which then began, the apertural margin of the mantle formed the nacreous layers of the primary varix. The ammonitella stage concluded with completion of the construction of the primary varix, and did not cover a further two whorls, as assumed by Ivanov (1971). The neanic stage began with the construction of a new part of the shell of the phragmocone, the wall of which was initially constructed from the outer prismatic and nacreous layers. Later, less frequently simultaneously, a third layer, the inner prismatic layer, appeared. This morphological boundary is recognized by all students although, as noted above, the biological interpretation of it varies. Various sculptural elements and growth lines may have appeared on the shell immediately after the primary varix.

In the study of heteromorphous ammonites, which has advanced appreciably in recent years, there is undoubted confirmation that the ammonitella on emergence from the egg capsule had a planispiral embryonic shell consisting of one whorl. It is now possible not merely to suggest, but to assert that all heteromorphs had a protoconch surrounded by a planispiral whorl. Any subsequent changes that led to the formation of a heteromorphous shell as such did not extend to this stage. Taken in conjunction with other characters, this specific nature of the structure of the first whorl indicates that the embryonic development of monomorphous and heteromorphous ammonites was of the same type (Bogdanova and Mikhaylova, 1975; Drushchits and Doguzhayeva, 1976; Atabekyan and Mikhaylova, 1976).

This conclusion is based on a study of a number of heteromorphs having the most varied shells in the adult state. In the Early Cretaceous genus Ptychoceras the first straight shaft was constructed after the planispiral embryonic shell, followed by the second and third shafts connected by two geniculate margins (fig. 2). The third shaft covered the embryonic shell and thus protected it against damage. In the Early Cretaceous genus Ammonitoceras the primary varix was followed by a short straight shaft, and then a gentle arc with an umbilical gape and contacting, weakly involute subsequent whorls (fig. 3). The initial part was of the same structural type in the genus

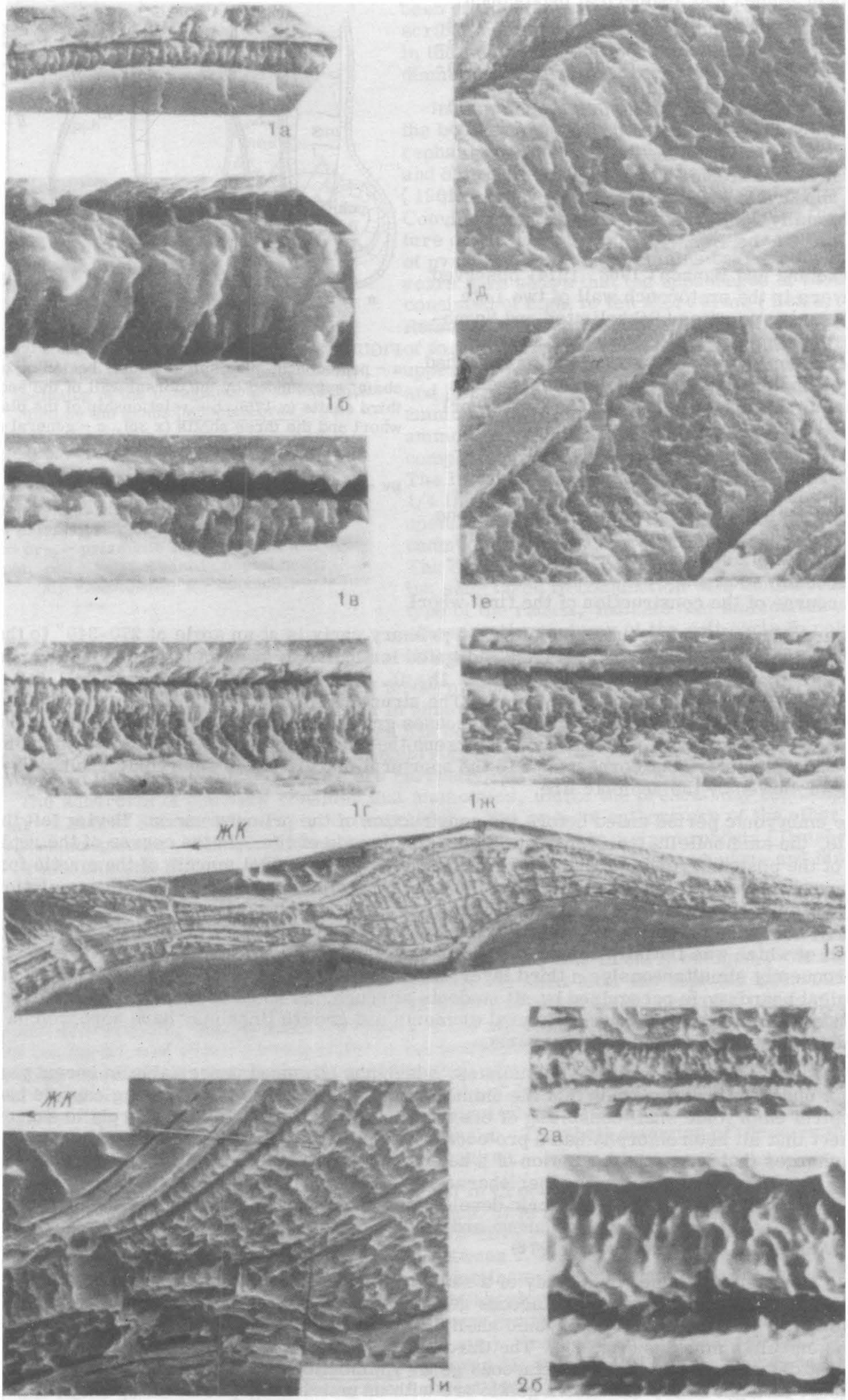


PLATE V

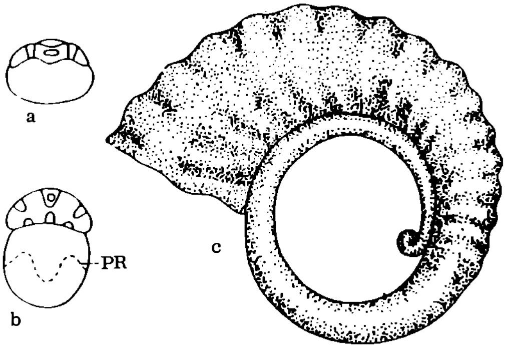


FIGURE 3. Shell structure in the genus Ammonitoceras (from Bogdanova and Mikhaylova, 1975): a - protoconch (x 22), b - first planispiral whorl (x 22), c - general appearance of shell (x 4).

pr - prosuture

Paraspiticeras (Wiedmann, 1969). In the Late Cretaceous genus Hypoturrilites, which had a turretiform adult shell, the embryonic shell also consisted of a protoconch and a first planispiral whorl approximately 1 mm in diameter (fig. 4, e-g). The protoconch had a diameter of 0.43 mm. The cochlespiral shell began after the primary varix. The shell tube straightens after the primary varix in the Late Cretaceous genus Baculites and becomes a straight shaft (fig. 4, a-e).

Smith (1901) depicted a shell belonging to the genus Baculites found in the Upper Cretaceous of North America; this shell consisted of a protoconch, one whorl, a proseptum and a preserved caecum, but lacked the primary varix. From our point of view, this shell may be treated as embryonic. The planispiral whorl of the Early Cretaceous genus Acrioceras (fig. 5, h, i) is reproduced by Branco (1879-1880). Dietl (1975) described the protoconch and the first planispiral whorl, followed by a straight shaft, in the Middle Jurassic genus Spiroceras.

The proseptum, or the first septum, differs fundamentally from the primaseptum, or second septum, and also from all subsequent septa in the trend of the corrugation in the plane of symmetry. This difference emerges with particular clarity in the outlines of the prosuture (first suture line) and the primasuture (second suture line): in the first case a ventral and a dorsal saddle are to be seen in the plane of symmetry, while in the second the place of the saddles is occupied by corresponding lobes present in all the following suture lines.

The fact that Jurassic and Cretaceous ammonites have a narrow ventral saddle prompted Branco (1879-1880) to term this prosuture angustisellate. There are two or three lobes on either side between the ventral and dorsal saddles. Ventral and dorsal lobes are added to these lobes in the second suture, and the total number of lobes is correspondingly five (counted only on one lateral side, with the addition of the ventral and dorsal lobes). Study of the interrelationships between the prosuture and the second suture is a fairly complicated matter that is not considered here (Schindewolf, 1929, 1968; Drushchits, 1956; Ruzhentsev, 1962; Mikhaylova, 1976a, b). All Early Cretaceous ammonites have six (Schindewolf, 1968), which indicates a shift in the late development stages of the suture lines to earlier stages of ontogeny.

According to the data of all investigators who have viewed it in the electron microscope, the proseptum has prismatic microstructure (pl. VI, illus. 1). This is apparently connected with the formation of the first septum before differentiation of the mantle and the start of the secretion of a substance with nacreous microstructure, i. e., during embryogeny. In some genera the microstructure of the second septum is prismatic (Erben, Flajs, and Siehl, 1969), while in others it is nacreous (Birkelund and Hansen, 1974; Kulicki, 1974, 1975). In the investigated genus Cadoceras (Drushchits, Doguzhayeva and Lominadze, 1976) the proseptum is of prismatic microstructure, the second septum of nacreous microstructure (pl. VI, illus. 1). To judge by its microstructure, the second septum was apparently secreted in the egg, in the first instance, and after emergence from it, in the second.

The proseptum was constructed in the egg capsule by the epithelium of the posterior part of the body, after the body had been drawn out of the protoconch. On the dorsal side it was attached to the protoconch wall at a varying distance from its margin (fig. 5). The first septum is similarly attached to the shell in Spirula (Mutvei, 1964; Chun, 1975). The second septum was attached to the phragmocone wall or to the proseptum on the dorsal side, which is reflected in the convergence and contacting of the second suture and the prosuture (Branco, 1879-1880, pl. 8, illus. 3; pl. 9, illus. 1, 3). Partial resorption of the prismatic layer and the lack of a conchiolin membrane covering the shell cavity on the inside are to be observed on the ventral side at the attachment site of the proseptum (pl. VI, illus. 2a, b).

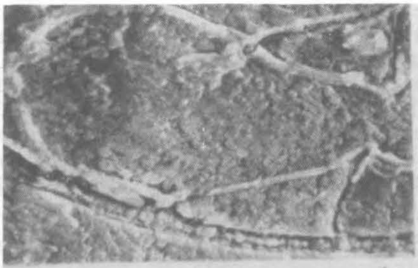
KEY TO PLATE V

Euphylloceras velledae Michelin:

1 - specimen 189/615: a) apical part of protoconch wall (x 1200), b) the same (x 7000), c) middle part of protoconch wall (x 2340), d) wall at end of protoconch (x 1270), e) the same (x 3500), f) shell wall at start of first whorl (x 2340), g) wall before primary varix (x 1400), h) primary varix (x 350), i) detail of varix (x 1000); Northwestern Caucasus, Khokodz' River; Upper Aptian.

Melchiorites sp.:

2 - specimen 189/840: a) wall at end of protoconch, one prismatic layer (x 1800), b) the same (x 6000); Northwestern Caucasus, Khokodz' River; Upper Aptian.



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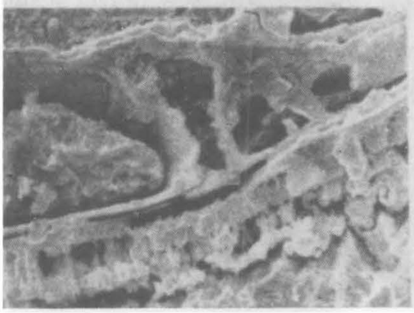

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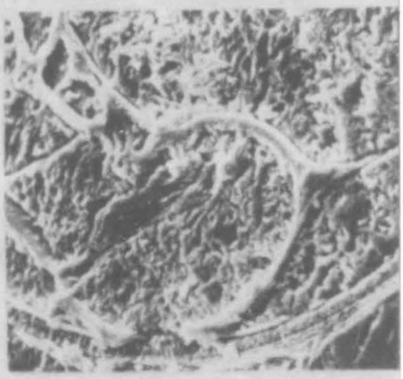

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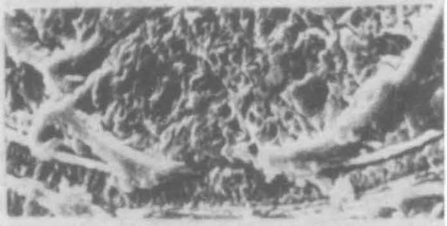

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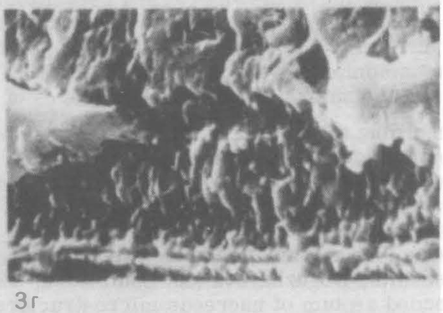

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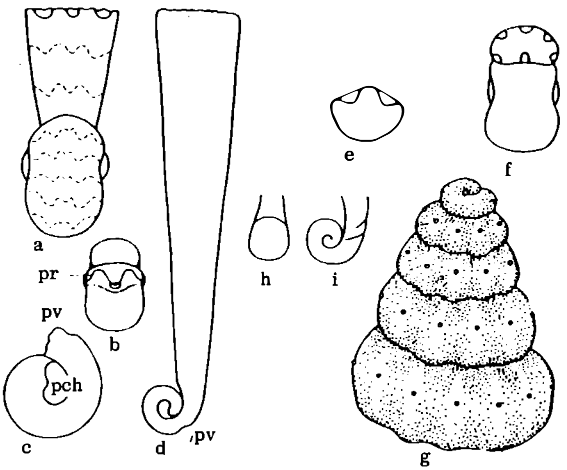

FIGURE 4. Shell structure in Baculites, Hypoturrilites and Acrioceras; a-d - Baculites: a - initial portion of shell (x 20), b, c - first planispiral whorl (x 20), d - general appearance of shell (x 7) (from Smith, 1901); e-g - Hypoturrilites: e - protoconch (x 22), f - protoconch and first planispiral whorl (x 22), g - general appearance of initial whorls (x 10) (from Atabekyan and Mikhaylova, 1976); h, i - Acrioceras, embryonic shell (x 15) (from Branco, 1879-1880). Key as in figs. 1-3.

membrane covering the shell cavity on the inside are to be observed on the ventral side at the attachment site of the proseptum (pl. VI, illus. 2a, b).

In the opinion of Kulicki (1975) the proseptum was formed before the caecum and the prosiphon. The proseptum and the protoconch were formed as follows. The protoconch was constructed in the egg, after which a subprismatic layer, from which the ventral part of the proseptum was formed, was secreted on the ventral side of the protoconch. The next stage in ontogeny was manifested in the further secretion of the inner prismatic layer of the protoconch, in the construction of the dorsal part of the proseptum and the flange in a deep fold and in secretion of the wall of the first whorl. The following data may be advanced in support: a) the dorsal part of the proseptum is separated from the protoconch wall by a distinct boundary, b) the proseptum appears to give way to the prismatic layer of the first whorl on the ventral side. We have considered this instance above and were of the opinion that the proseptum was attached to the ventral wall in the same way as all along its periphery. Were this not to be so, we should not see the type of prosuture to be observed in all ammonites. It is difficult to accept the opinion that it was only after formation of the proseptum that the body of the mollusc was drawn out of the protoconch cavity and that the prosiphon and caecum arose. This is contradicted by data on the interrelationship between these formations in ammonites and in Spirula.

The organ that regulated the regime of the hydrostatic apparatus in ammonites is the siphuncle, which extends from the posterior part of the body (figs. 5, 6). The siphuncle originates in the protoconch as a small swelling, that has become known as the siphonal caecum, but more often as the caecum. The caecum is situated in the protoconch cavity or partly in the first chamber. In cross-section the caecum is usually dorsoventrally compressed. After an abrupt narrowing associated with the presence of a narrow opening in the proseptum, the caecum gives way to the siphuncle proper (fig. 5). The caecum is usually closely pressed against the ventral wall of the protoconch (pl. VI, illus. 2a, 3b, 4; fig. 5) and it corresponds in its origin to the posterior part of the body of the ammonitella. A thin calcareous sheath surrounding the caecum, which was attached to the proseptum and which probably completely isolated the protoconch cavity from the other hydrostatic chambers, has been observed in one specimen of Tetragonites.

The caecum was attached to the wall of the protoconch as a distinct organic band, which has been named the "prosiphon". The length of the band varies. It may be short, equal in length to the diameter of the caecum, of medium length, equal to between one and two diameters of the caecum, or long; in the latter case its length is twice the diameter of the caecum. In phylloceratids and lytoceratids the prosiphon was represented by numerous short bands (Drushchits and Doguzhayeva, 1974, pl. IV, illus. 2c).

KEY TO PLATE VI

Cadoceras sp.:
1 - specimen 189/1131: a) commencement of siphuncle (x 400), b) flange, proseptum and second septum (x 1800), c) proseptum and second septum (x 2500); Oka River; Callovian.

Acanthohoplites sp.:
2 - specimen 189/1072: a) start of siphuncle (x 360), b) interrelationship between proseptum and ventral wall (x 1200); North Caucasus; Middle and Upper Aptian.

Acanthohoplites sp.:
3 - specimen 189/651: a) shell wall approximately at the third septum (x 1000), b) start of siphuncle (x 400), c) part of caecum, proseptum and shell wall (x 600), d) interrelationship between proseptum and shell wall (x 1800); Northwestern Caucasus, Khokodz' River; Upper Aptian.

Phyllopachyceras sp.:
4 - specimen 189/783, start of siphuncle (x 360); Northwestern Caucasus, Khokodz' River; Upper Aptian.

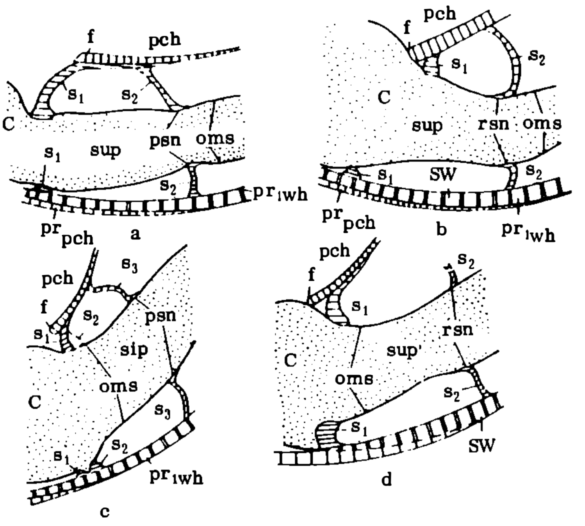

FIGURE 5. Structure of the initial part of the phragmocone in Melchiorites (a), Jauberticeras (b), Deshayesites (c) and Tetragonites (d) (x 250).

psn-prochoanitic septal neck, s_1, s_2, s_3 - first, second and third septa, sw - shell wall;, other symbols as on fig. 1.

At the start of the spiral the siphuncle occupies a central or subcentral position, but subsequently becomes ventromarginal or dorsomarginal in Late Devonian clymeniids. The authors have recently examined the alteration in the position of the siphuncle and in the structure of the formations accompanying the siphuncle in ontogeny and phylogeny (Drushchits, Bogoslovskaya, and Doguzhayeva, 1976).

In contrast to the point of view defended by the authors, Erben and his colleagues (Erben, 1964; Erben, Flajs, and Siehl, 1969) distinguish three periods in ammonite ontogeny; embryonic, larval and postlarval. A conchiolin mitriform shell was formed in the embryonic period. Layers of subprismatic microstructure arose successively at its apical end; they tapered off to either side of the apex. Following them the shell gland secreted fully prismatic layers that constructed the narrowed apertural part of the protoconch. Erben relates the "first change in the growth" of the shell and the end of the embryonic period with this constriction. The larva that emerged from the egg capsule had a protoconch and resembled a gastropod larva of the type of a veliger. Formation of the first whorl and what is referred to as the "proseptal layer", from which the proseptum was subsequently constructed, proceeded during the larval period. At this time the body of the larva freed the protoconch and attached itself by means of the prosiphon to the protoconch wall. The flange was constructed on the dorsal side of the protoconch. The authors cited were of the opinion that the flange was not the dorsal part of theprotoconch wall; it consisted of one or two prismatic layers that were attached inside to the "proseptal" layer, i. e., the flange was formed after creation of the proseptum. The function of the flange was unclear to the authors cited, but it was assumed that it might serve for attachment of the proseptum, or could be treated, as an ontogenetically more recent formation, as a secondary dorsal margin of the protoconch (the first dorsal margin of the protoconch petered out slightly earlier).

The larval period was concluded by the formation of 1-1/4 whorls of the shell (Erben reckoned from the apical part of the protoconch). The primary varix arose near it from the nacreous layer, a hiatus began in the construction of new parts of the spiral tube, and the second septum formed.

In accordance with our views, Erben's postlarval period coincides with the start of the nepionic stage. The idea developed by Erben and his colleagues had its predecessors. Smith, who studied the ontogenetic development of Baculites chicoensis, long ago (1901) distinguished the same three stages. According to Smith, the embryonic stage was concluded by construction of the protoconch and part of the first whorl housing the body of the young mollusc. The boundary of the living chamber of the embryo lay between the first and second septa and was expressed by a slight constriction (fig. 4, b). The diameter of the embryonic shell was 0. 53 mm. The first larval (or ananepionic stage was recorded by the construction of the first whorl, and by formation of the proseptum and caecum. The surface of the protoconch and the first whorl was granulated. The second larval stage (metanepionic) began with construction of the second septum, with alteration in the sculpture at the end of the first whorl, and with replacement of the granules by fine striae and costellae. It occupied the 1/4 of the second whorl after the nepionic line and a part of the straightened shell. Smith distinguished the end of the larval stage from the appearance of the ammonite suture line as such.

* * *

It is difficult to accept the opinion of those who propound the larval development of ammonites. The following facts are proof of the direct development of ammonites without a larval stage:

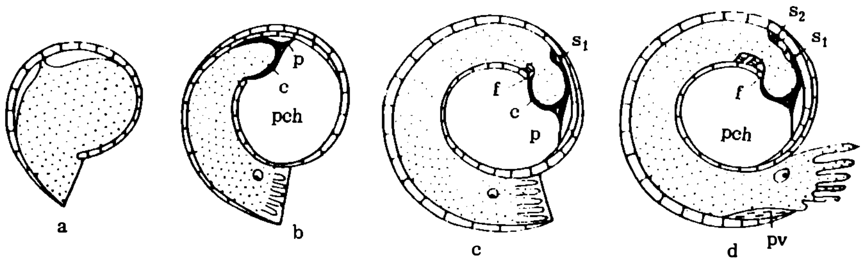

FIGURE 6. Embryonic and postembryonic periods in the ontogeny of ammonites: a - secretion of the protoconch, b, c - formation of the first whorl, d - shell of ammonitella. Key as in figs. 1, 2 and 5.

1. All ammonites, including the heteromorphs known to us (*Spiroceras*, *Ammonitoceras*, *Paraspiticeras*, *Hypoturrilites*, *Ptychoceras*, *Baculites*) have an embryonic shell constructed to the same plan and consisting of a protoconch and a planispiral whorl.

2. The living chamber of the ammonitella occupied 3/4 of a whorl and was separated from the protoconch by one, less frequently two septa. The shell of a dead ammonitella in which the living chamber was separated from the protoconch by a proseptum has been preserved in Upper Cretaceous deposits (Smith, 1901).

3. The wall of the protoconch, of the first whorl to the primary varix, the proseptum and in some instances the second septum have an identical prismatic microstructure, which is indicative of a common secretary mechanism.

The above arguments testify to the direct development of ammonites without a larval stage. On emerging from the egg the ammonitella lived a planktonic mode of life like the nauta and most of the present-day cephalopod "larvae". The term "larva" is incorrectly used by biologists when describing the ontogeny of Recent forms, since it does not reflect the true nature of the early stages of postembryonic development (Ivanov, 1971). The protoconch of the ammonitella, which was filled with gas and, possibly, partly with liquid, was a float of relatively large diameter (fig. 6). The ratio of protoconch diameter to the diameter of the embryonic shell is 1:2 or 1:2.5. This float maintained the young animal suspended in the water and enabled it to lead a planktonic mode of life for some time. Like the young nauta, the ammonitella constructed a primary varix in the apertural margin of the embryonic shell. Further accretion of the shell was temporarily halted in connection with adaptation to new conditions.

The end of the nepionic stage and the beginning of the neanic stage are expressed morphologically by the development of the nepionic line; after this the height of the whorl of planispiral shells is usually increased and a new type of shell appears in heteromorphous ammonites. In many forms the first sculptural elements develop after the primary varix, the wall microstructure is modified and it becomes two-layered or three-layered.

On the basis of all that has been said we distinguish two periods in ammonite ontogeny, embryonic and postembryonic. During the first period, which occurred in the ammonite egg capsule, as in present-day cephalopods, the embryonic shell was formed. The changes to be seen between the protoconch and the beginning of the phragmocone are manifested only in narrowing of the aperture and cannot be regarded as the boundary of a larval stage.

Consequently, ammonites developed directly, without metamorphosis, like present-day cephalopods. The shell of the ammonitella has the following characteristic features: a) the surface of the protoconch and the first whorl is smooth as far as the nepionic line, without any traces of sculpture; b) the boundary of the embryonic shell in ammonites is at the nepionic line, as in the present-day *Nautilus*, after which the shell surface and the shape of the whorls change their nature; c) like all the following septa, the proseptum was secreted by the posterior part of the mantle epithelium and it was attached to the phragmocone wall, as in the present-day *Nautilus* and *Spirula*; d) the prosuture, which reflects the corrugation of the peripheral margin of the proseptum, differs from all the subsequent suture lines in having ventral and dorsal saddles, which owed their origin to the presence of a caecum; e) the primary varix was formed in the apertural part of the embryonic shell after the mollusc emerged from the egg into the first (nepionic) stage of postembryonic development; it was formed by the nacreous layer during adaptation of the ammonitella to the new habitat and the associated interruption in accretion of the shell.

Significant changes in shell morphology occurred in ammonites after the primary varix, the morphological boundary between the embryonic and postembryonic periods: sculpture appeared, the wall became two-layered and subsequently three-layered, and the architectonics of the shell were modified in heteromorphs. The neanic stage begins with construction of the shell after the primary varix.

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