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# Main Morphological Events in the Evolution of Paleozoic Cephalopods

**I. S. Barskov*, M. F. Bogoslovskaya*, F. A. Zhuravleva*, G. N. Kiselev**, L. F. Kuzina*, T. B. Leonova*, V. N. Shimanskii*, and S. V. Yatskov***

**Institute of Paleontology, Russian Academy of Sciences, Profsoyuznaya ul. 123, Moscow, 117647 Russia*
***Department of Paleontology, St. Petersburg State University, 16-ya Liniya 29, St. Petersburg, 199178 Russia*

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**Abstract** – New morphological features in shell structure, which were the starting points of cephalopod diversification into taxa of high ranks (subclasses, orders, superfamilies), are considered as phylogenetic events. Main morphological innovations in the evolution of nautiloid cephalopods; the formation of endosiphuncular and cameral deposits, shell coiling, truncation of the phragmocone's apical end, and contracted aperture, which originated to make the relative shell positioning in the water more efficient. Changes in the lobe line structure and various types of complications in the primary lobes (ventral, umbonal, and lateral) were the most important morphological innovations in convolute ammonoids. The functional significance of these changes remains unclear, but recognition of equally significant changes in primary lobes requires a review of the Paleozoic Ammonoidea taxonomy at the suborder level.

This paper is a continuation of a study whose first results have been published (Barskov *et al.*, 1993). The original materials are supplemented by T.B. Leonova's revised data on the Permian Ammonoidea and data of V.N. Shimanskii, F.A. Zhuravleva, and G.N. Kiselev on Carboniferous, Devonian, and Silurian non-ammonoid cephalopods (Fig. 1). General conclusions from the previous paper on the dynamics of generic diversity and interpretation of relevant changes remain valid. The evolution of non-ammonoid cephalopods was analyzed in a number of works (Barskov, 1989; Zhuravleva, 1972; *Osnovy Paleontologii*, 1962; Shimanskii, 1989; Shimanskii and Zhuravleva, 1961; *Treatise on Invertebrate Paleontology*, 1964; Teichert, 1967).

This paper presents an analysis of morphological innovations, which were the starting points of new trends in the evolution of the group (phylogenetic events). This is reflected in the taxonomy of high ranking fauna groups, from superfamilies to subclasses.

The events of primary importance are: (1) the appearance of the Cephalopoda as an independent molluscan class; (2) the appearance of the Ammonoidea; (3) the acquisition of an internal shell, which probably occurred more than once and is most likely characteristic of various taxa ranks. This problem is not considered here.

Formation of the cephalopod structural style began when primary benthic and creeping forms, similar in organization to monoplacophoran molluscs, acquired a phragmocone, which is a functional adaptation to regulate buoyancy. This provided for their transition into new pelagic zone environments. At the first stage, before appearance of the Ammonoidea, main morphological innovations were intended to improve the regulation of the buoyancy process and to support in various ways its relative position in the water. Only indirect evidence to judge how the buoyancy was intensified exists. Morphological changes such as the thinning of the siphuncle hard envelope and decrease of its diameter seem to reflect the specialization of the posterior phragmocone-related part of the animal body, which was transformed into a special organ, supporting the phragmocone function as a gas-liquid float. This morphological trend is clearly seen in all cephalopod groups when their early and late forms are compared. It is likely that there was another, extensive way of improving the siphuncle pumping activity at the expense of increasing its epithelium surface. Morphologically, it was the formation of a radial structure of the siphuncle. This adaptation was repeatedly used in cephalopod history (orders Oncocerida, Discosorida, and others).

Various morphological features, supporting the shell's relative position in the water, became the starting points that really determined cephalopod diversification at a high taxonomic rank. One can distinguish several ways of shell and body stabilization in orientated position: (1) formation of deposits inside the siphuncle envelope; (2) formation of deposits inside the phragmocone camerae. Both ways are especially effective for those forms with an orthocone shell, though they are also favorable for endogastric and, to a lesser degree, for exogastric forms. (3) Coiling of the shell into flat spiral, which is one of the most effective solutions to the problem of shell stabilization. It occurs through the convergence of buoyancy and gravity centers, when an animal is constantly under indifferent equilibrium and occupy any position relative to the bottom or water surface with minimal energy loss;

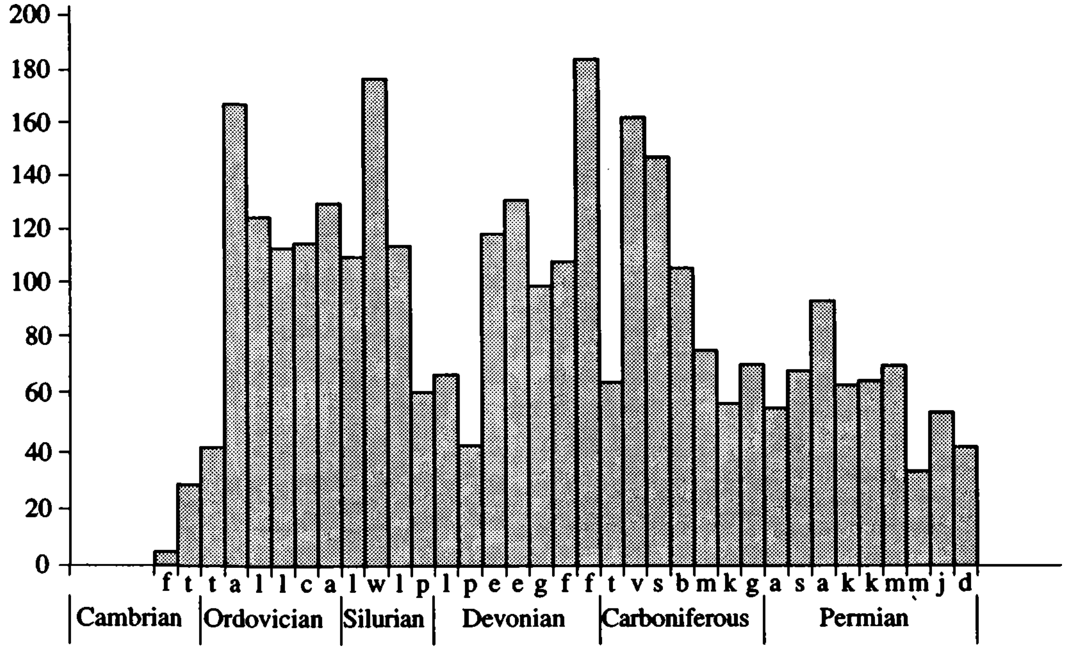

**Fig. 1.** Generic diversity of the Paleozoic Cephalopoda.

Y-axis – number of genera; X-axis – stages. Cambrian: f – Franconian and t – Trempealeanuan; Ordovician: t – Tremadocian, a – Arenigian, l – Llanvirnian, l – Llandeilian, c – Caradocian, and a – Ashgillian; Silurian: l – Llandoverian, w – Wenlockian, l – Ludlovian, and p – Przidolian; Devonian: l – Lochkovian, p – Pragian, e – Emsian, e – Eifelian, g – Givetian, f – Frasnian, and f – Famennian; Carboniferous: t – Tournaisian, v – Visean, s – Serpukhovian, b – Bashkirian, m – Moscowian, k – Kasimovian, and g – Gzelian; Permian: a – Asselian, s – Sakmarian, a – Artinskian, k – Kungurian, k – Kubergandian, m – Murgabian, m – Midian, j – Julfian, and d – Dorashamian.

(4) truncation of the back part of the phragmocone, which brings together the gravity and buoyancy centers; and (5) formation of a contracted or constricted aperture, an adaptation of forms that orientate in a hypostome position and use their shell as a passive float. The various ways of shell stabilization are shown on Fig. 2. One more feature of shell stabilization in different representatives of the ancestral order Ellesmerocerida (cephalopods) resulted in diversification of taxa at the order rank.

*The first morphological event* was the formation of the order Endocerida, characterized by the appearance of endosiphuncular deposits (endocones) equilibrated to the back end of the long-cone straight shell, providing buoyancy in a horizontal position with the ventral side directed downward.

*The second morphological event* resulted in the shell coiling into spiral plane and the formation of the order Tarphycerida.

*The third event* was the near simultaneous diversification of Ellesmerocerida into a number of high-rank taxa, each of which realized its own type of shell stabilization. The appearance of the order Actinocerida is related to the formation of endosiphuncular deposits. This was a new stage in siphuncle specialization as a buoyancy regulator as compared to Endocerida. It was expressed morphologically in different structures of the siphuncular envelope, namely, in its thinner and convex connective rings. Actinocerida also produced the cameral deposits, but the main function of stabilization was undoubtedly controlled by endosiphuncular deposits.

The stabilization function of cameral deposits is more evident in forms of the order Orthocerida, though some its families also had minor deposits inside the siphuncle. Yet it is precisely the cameral deposits that define the morphological peculiarity of the Orthocerida.

Endosiphuncular and cameral deposits are also typical of two other orders: Pseudorthocerida and Dissidocerida. The first, according to its morphology, is intermediate between the Actinocerida and Orthocerida, possessing (1) more evolved endosiphuncular deposits than in orthocerids, but comparable with those in actinocerids, and (2) a siphuncular envelope structure resembling that of the orthocerids. The shape of endosiphuncular deposits in the order Dissidocerida resembles, to a limited extent, the endocerids. However, the structure of its siphuncular envelope renders it more similar to pseudorthocerids.

Thus, at least four large taxa of a rank not lower than the order (actinocerids and endocerids are distinguished as subclasses) independently used the endosiphuncular deposits as the main regulator of shell stabilization. At the same time or somewhat later, we observe the first truncation of the posterior shell edge. The truncated apical end of the phragmocone in forms with a orthocone shell is a very effective way to converge the buoyancy and gravity centers. This resulted in the separation of the order Ascocerida from the orthocerids. A trend to be free of the phragmocone apical end occurs in the development of the orthocerids at least twice. However, the taxonomic rank of these transformations is considered to be lower (Sphooceratidae family in the Silurian and the Brachycycloceratidae family in the Carboniferous).

Another group of morphologically similar taxa consists of the Oncocerida and Discosorida orders, which appeared simultaneously. Initially, these forms are, having curved cyrtoceracone shell, exogastric in the first and endogastric in the second case. The curved shell is able to constructively support a positioning, which is close to the hypostome one, limiting the shell function of a more or less passive float. The development of additional mechanisms of shell orientation are rendered unnecessary, though they are present as endosiphuncular and cameral deposits in some forms of the discocerids, and as very rare cameral deposits in the oncocerids. However, it appears that the principle of shell morphology in these orders reveals their rejection of additional stabilization mechanisms. As a natural consequence, their shell had a predominantly hypostome orientation and their formation consisted of contracted and constricted apertures. This morphological tendency in both orders (more evident in oncocerids) was already realized in the Silurian, and may be considered independently as a *fourth morphological event*.

The *fifth morphological event* of the pre-ammonoid stage in cephalopod evolution is a recurring tendency of the shell coiling. This tendency was realized simultaneously in two phylogenetic branches and resulted in the formation of the Nautilida order from the exogastric cyrtoceracone oncocerids and the Ammonoidea subclass from the orthocone bactritids. This ends the search for an optimal shell shape, as regards its use as a gas-liquid hydrostatic apparatus.

Summarizing the pre-ammonoid evolutionary stage, the following should be emphasized. Practically all the morphological innovations were realized at the early stages of class evolution, i.e., in the early Ordovician or at the beginning of the middle Ordovician (Fig. 3). At that time, nine of the eleven generally accepted orders of non-ammonoid cephalopods; Endocerida, Orthocerida, Tarphycerida, Actinocerida, Discocerida, Pseudorthocerida, Dissidocerida, Oncocerida, and Ascocerida, came in to existence. The initial Ellesmerocerida order originated in the late Cambrian, and the Nautilida is the only post-Ordovican order. The Bactritida order is an ancestor of Ammonoidea, apparently having also originated in the early Ordovician.

The independent taxonomic status of the ammonoids is caused only by morphological acquisition, i.e., the formation of a planispiral shell. This was the third attempt in the evolution of cephalopods to use a morphological innovation favorable from the viewpoint of hydrostatics. But only this attempt became the most important event in the evolution of cephalopods, and resulted in the appearance of a group that outgrew all the earlier and later groups in its diversity. Significant phylogenetic success was predetermined, apparently, by ancestoral structural peculiarities and, probably, by their ecological specialization. The main feature of the bactritids is a thin siphuncle contiguous to the shell wall. As a result, the suture on the ventral side was interrupted, forming the neck lobe (termed the ventral lobe in the ammonoids), and an omnilateral lobe formed on the lateral sides of the shell. From here on,

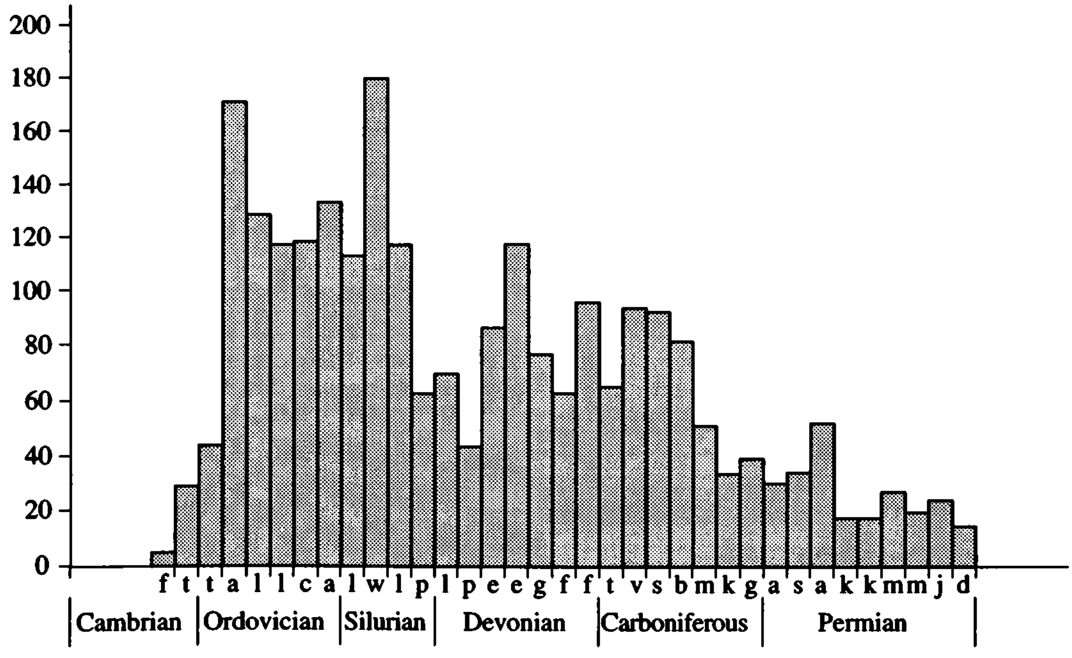

**Fig. 2.** Generic diversity of nautiloid cephalopods in the Paleozoic. See Fig. 1 for symbols.

we will use the terminology of elements of the lobe line and its formula after V.E. Ruzhentsev (1960).

Shell morphology of the Paleozoic Ammonoidea is quite diverse; encompassing practically all variants of the whorl expansion rate and the degree of overlapping discovered by D. Raup (1966, 1967). However, the main transformations, which provided for the rapid evolution and unusual diversity of the Ammonoidea in the Paleozoic, took place in the septum. The initial tendency of lobe line complication, namely the increasing number of lobes and their dismembering, formed the main evolutionary trend. Key moments of this tendency, which lead to principally new morphological changes and to important phylogenetic consequences (the genesis of high rank taxa of the modern Ammonoidea taxonomy), we term as morphological events. Their types (U-event, L-event, and so on) are defined with regard to those parts of the septum where changes occurred (Fig. 4).

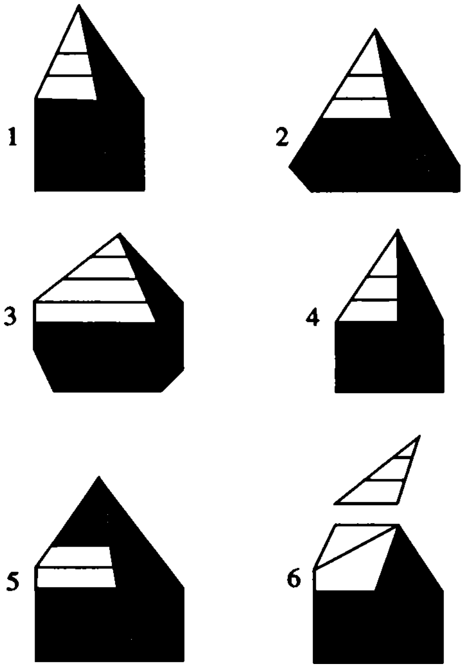

**Fig. 3.** Sketch images of main morphological events among nautiloid cephalopods.

1 – formation of endosiphuncular deposits; 2 – formation of short-conic shell (passive float); 3 – formation of contracted aperture; 4 – formation of phragmocone; 5 – formation of cameral deposits; 6 – truncation of shell apical end.

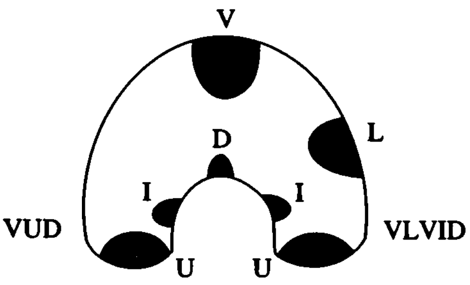

**Fig. 4.** Sketch image of the transverse section of a shell whorl of the Ammonoidea.

Symbols of main primary lobes: D – dorsal, I – inner, L – lateral, U – umbonal, and V – ventral. Locality of lobes and formula of the primary lobe line of L-branch (to the right), U-branch (to the left).

During their formation, the Ammonoidea inherited from their ancestors a lobe line with simple ventral and omnilateral lobes; according to accepted terminology their conditional formula is VO. The dorsal lobe (D) formed almost simultaneously because of contacting whorls, and the formula became VO : D. This was *the first event*, which resulted in the formation of the Agoniatitina suborder, the oldest in the Anarcestida order. Another new feature, apparently of the same time, the three-merous ventral lobe used as a diagnostic feature of the Auguritina suborder whose initial formula was $(V_2V_1V_2)O$ : D), did not result in significant phylogenetic consequences and did not develop further.

*The second event* (U-event) is a transformation of the wide omnilateral lobe of the Agoniatitina into an umbonal one, which gave rise to the Anarcestina suborder with the initial formula VU : D. Thus the U-branch, one of two main Paleozoic phyletic lines, came into being. Principle septum changes, which took place many times during evolution, formed various trends complicating the lobe line, which were used to distinguish large taxa (Fig. 5).

*The third event* (L-event) is the formation of the lateral lobe between the ventral and umbonal lobes. Taxonomically, this is used to define the Tornoceratina suborder, the most ancient in the Goniatitida order, with the primary formula VLU : D. If we accept the modern classification of the Ammonoidea, it starts the second phylogenetic line (L-branch) corresponding to the Goniatitida order. The septum transformations in this branch did not cause phylogenetic consequences as large as those in the U-branch, despite the fact that observed complications in the lobe line are sometimes more complex than in the latter branch.

Further, the septum complications in each of two main philogenetic lines (U-branch and L-branch) were rather similar, but occurred at different times and did not always cause equivalent taxonomic consequences.

*The fourth event* (3V-event) depicts the appearance of triseptate ventral lobe and separation of the Gephuroceratina suborder with the primary formula $(V_2V_1V_2)U$ : D). This disarticulation of the V-lobe gave rise to new elements in the lobe line: an inner lateral lobe (I) first, and subsequent umbonal lobes. Despite the high rate of evolution, which increased the number of lobes to 54, this trend was not continued.

*The fifth event* followed, notable in the U-branch as the 2V-event that generated the very limited Timanoceratina suborder with the formula $(V_1V_1)U$ : ID; this suborder existed briefly and disappeared without a trace.

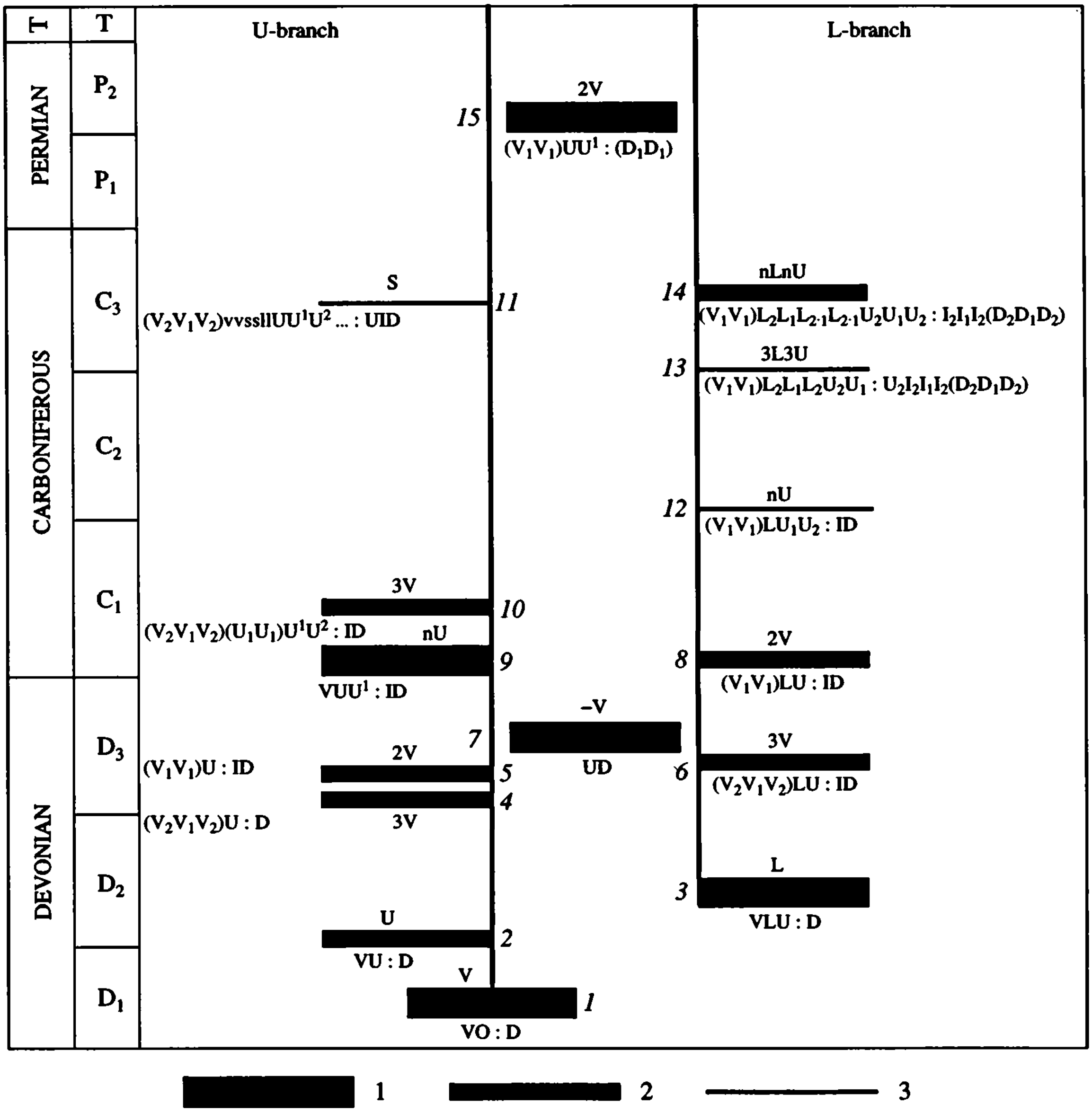

Fig. 5. Main morphological events in the history of the Paleozoic Ammonoidea.

1 – orders, 2 – suborders, and 3 – superfamilies; *1* - *15* – ordinal numbers of events.

*The sixth event* (3V-event) took place in the L-branch, and is characterized by the appearance of a triseptate ventral lobe. This event was similar to the fourth one in the U-branch, but did not develop further. The resultant Praeglyphioceratina suborder with the initial formula $(V_2V_1V_2)LU$ : ID developed slowly over a very short period.

*The seventh event* (V-event) was unprecedented. Morphologically, it manifested itself in the displacement of the siphuncle from the ventral to the dorsal side, and in a general reorganization of its septum. Taxonomically, this event resulted in the creation of the Clymeniida order. The ventral lobe disappeared first, and the lobe line formula became UD (Clymeniina suborde). Later, the V-lobe appeared again, but this time unrelated to the ventral position of siphuncle. It appears to be a resetting of the original lobe line of the Ammonoidea with the formula VU : D (Gonioclymeniina suborder). All the previously mentioned ways of V- and U-lobe complication occurred in this lobe line during a short period. Morphological simplifications of the ventral and dorsal lobes, including their full disappearance, also occurred. The clymeniids had a large diversity "boom" during the short period of their existence (the Famennian) and became extinct without descendants (Bogoslovskii, 1969).

*The eighth event* (2V-event) observed in the L-branch was one of the most important. The origin of the Goniatitina suborder with the initial formula $(V_1V_1)LU$ : ID is the key moment of this event. The double partition of the ventral lobe caused many changes in the septum, which at the first stage took place only in the initial eight lobes, and did not change the original formula. More principal changes resulted in the formation of additional lobes. Their partition occurred during subsequent events (Ruzhentsev and Bogoslovskaya, 1978; Kulmann, 1981).

*The ninth event* (nU-event) in the U-branch was nearly simultaneous with the eighth one in the L-branch. This was the origin of the Prolecanitida order with the initial formula $VUU^1 : ID$. The appearance of the second umbonal lobe in the initial lobe line determined, apparently, the main septum complication trend of, the increasing number of simple umbonal lobes, which migrated first, towards the outer side, and further towards the inner side.

*The tenth event* (3V/2V-event) in the U-branch gave rise to the Medlicottiina suborder with the primary formula $(V_2V_1V_2)(U_1U_1)U^1U^2 : ID$. The simultaneous appearance of a triseptate ventral lobe and a biseptate first umbonal lobe in the lobe line determined the suborder separation. The biseptate first umbonal lobe is typical of all specimens of this suborder, but sometimes only at the early stages of ontogenesis. In the first stage, the complication included an increase in the amount of umbonal lobe and the dissection of their base. The beginning of the second stage is indicated by *the eleventh event* (s-event), when principally new and earlier unknown ways of septum complication were recognized in the development of adventive lobes in the outer saddle. This gave rise to the successfully developed Medlicottiidae family, which has the primary formula $(V_2V_1V_2)\,vvssllUU^1U^2 \ldots : \ldots UID$.

*The twelfth event* (nU-event) is seen in the L-branch. For the first time in the history of the Goniatitina, changes in the septum went beyond the limits of eight lobes. The lobe multiplication occurred with the addition of umbonal lobes, a diagnostic feature of the Schistocerataceae superfamily, which has the initial formula $(V_1V_1)LU_1U_2 : ID$. Later, the Goniatitina multiplied their lobe number many times and in various ways. This occurred at various stages of general evolution, even being repeated sometimes. Relevant features were used to distinguish taxa lower than the suborder rank. It is reasonable to emphasize that among the variety of ways, the two ways of septum complication after the nU-event resulted in the creation of forms with the most complex lobe lines known for the Paleozoic Ammonoidea.

One of them, defined here as *the thirteenth event* (3L3U-event), determined a separation of the Maratonitaceae superfamily having the initial formula $(V_1V_1)(L_2L_1L_2)U_2U_1 : U_2(I_2I_1I_2)D$. A triple partition of the primary L-, U-, and I-lobes caused the complication of the lobe line via the significant dissection of all lobes without the appearance of new elements. *The fourteenth event* (nLnU-event) was morphologically similar. As a result, the Cyclolobaceae superfamily having the primary formula $(V_1V_1)L_2L_1L_{2\cdot1}L_{2\cdot1}U_2U_1U_2 : I_2I_1I_2(D_2D_1D_2)$ came into existence. In contrast to the thirteenth event, the last one tended to multiply all of the lobes. This resulted in the creation of new forms with 58 - 60 lobes with a degree of dissection equal to that of the complex-lobed Mesozoic Ammonoidea (Bogoslovskaya, 1990).

Finally, the appearance of the biseptate ventral lobe and the crenulated base of V- and U-lobes in the lobe line typical of the ancient prolecanitids was the *fifteenth event* in the Paleozoic history of the Ammonoidea. Taxonomically, it is a ramification of the most ancient Paraceltina suborder having the primary formula $(V_1V_1)UU^1 : (D_1D_1)$ from the Ceratitida order.

The most important morphological events in the Ammonoidea history are related to the appearance and transformation of primary V, U, and L outer lobes. Frequency and times of these transformations in primary lobes were directly dependant on the events of their appearance. Changes in the most ancient ventral lobe started before those in other types and were most frequent, having a recurrent character. The U-lobe begins to multiply soon after its appearance. Changes in the latest L-lobe, which was very conservative for a long time, characterize the beginning of the second stage in this evolutionary line. The taxonomic significance of the primary phylogenetic events under consideration as compared to the modern taxonomy of the Ammonoidea (Bogoslovskaya *et al.*, 1990) varies. Following the logic of the above distinguished phylogenetic events, providing them with a corresponding taxonomic significance, it is necessary to review the Ammonoidea classification at the order and suborder ranks. For example, the ramification of the Paleozoic Ammonoidea into the U- and L-branches must be reflected in the taxonomy. The events transformating the lateral lobe of the Goniatitina and the outer saddle of the Medlicottiina also seem to rate a higher taxonomic value.

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