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Paleozoic Ammonoids: Historical Pathways of the Development of Morphological Diversity

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Abstract—The history of Paleozoic ammonoids can be subdivided into two large intervals: Devonian and Carboniferous–Permian. There were two major evolutionary pathways: changes in the external shell morphology and changes in the suture, a character observed only in cephalopods. Almost all major shell types and ornamentation appeared at early stages of the evolution of the subclass Ammonoidea (archaic diversity). The suture in ancient taxa in this group was represented by virtually all known types, except for the complexly dissected suture lines of the "Mesozoic type" that appeared only at the end of the Paleozoic. During the time of the subclass's existence, Devonian morphotypes recurrently appeared in different orders. The senile diversity was associated with the diversification of exotic taxa at the end of the Ammonoidea evolution.

Keywords: Ammonoidea, Paleozoic, shell morphology, suture patterns

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INTRODUCTION

The first ammonoids appeared at the end of the early Devonian, ca. 400 million years ago, and having existed for more than 330 million years, became extinct at the Cretaceous–Paleogene boundary. The morphological structure of these fossil cephalopods is determined by a spirally coiled shell, a complex suture and the presence of a protoconch. The shell had a complex architecture and consisted of a body chamber (from 0.5 to 1.5 whorls) and a multi-chambered phragmocone, divided by complexly bent septa. The chambers were connected with a siphuncle, and represented a complex hydrostatic apparatus. Since the shell constantly built itself around the protoconch, each subsequent revolution retained a certain stage of individual development. This factor is successfully used to reconstruct the morphogenesis of groups of different systematic rank.

RESULTS AND DISCUSSION

External morphology. Ammonoids most commonly had a planispiral shell with different ratios of height and width and varying whorl overlap degree. The very first representatives of the subclass (*Anetoceras, Erbenocerasas, Mimosphinctes*) which appeared at the end of the early Devonian (Lower Emsian) had uncoiled or loosely coiled shells. It is noteworthy that this feature again appeared at the end of the evolution of the subclass in the Mesozoic heteromorphs (Figs. 1a, 1b). Shortly after their appearance, towards the end of the Emsian, the spiral shell became tightly folded, planispiral (Bogoslovsky, 1969, 1971; Nikolaeva and Bogoslovsky, 2005). This planispiral shell was the basis for all known morphotypes. Representatives of the Devonian orders Anarcestida (suborders Agoniatitina, Auguritina, Anarcestina, Gephuroceratina, Timanoceratina), Tornoceratida (suborder Tornoceratina), and Clymeniida (suborders of Gonioclymeniina and Clymeniina) have shells of all known morphotypes. In whorl overlap degree, the shells varied from completely evolute to hyper-involute shells, in the ratio of the whorl height and width the shells were ophioconic (Fig. 1c), platyconic (Fig. 1f), discoconic (Fig. 1k), pachyconic (Fig. 1h), cadiconic (Fig. 1e), and spheroconic (Fig. 1n), with the umbilicus from closed to very wide (Figs. 1c–1n) (terminology: Ruzhencev and Bogoslovskaya, 1971). The ventral side could be pointed or keeled (Figs. 1g, 1j), the flanks are flat (Figs. 1f, 1j) or convex (Figs. 1l–1n). In addition to the "regular" spirals, there were also shells with "irregular" triangular winding and lenticular ones (Fig. 1d). This means that for the entire subsequent history of the existence of the subclass, no fundamentally new ammonoid shell morphotype was formed. The only exceptions are heteromorphs with tangled-ball-shaped and other exotic shells. Thus, for an extremely short time (on a geological timescale) a single morphotype of half-uncoiled shells with non-contacting isometric whorls gave rise to all known types of the shell shape of this large group of cephalopods (Fig. 2).

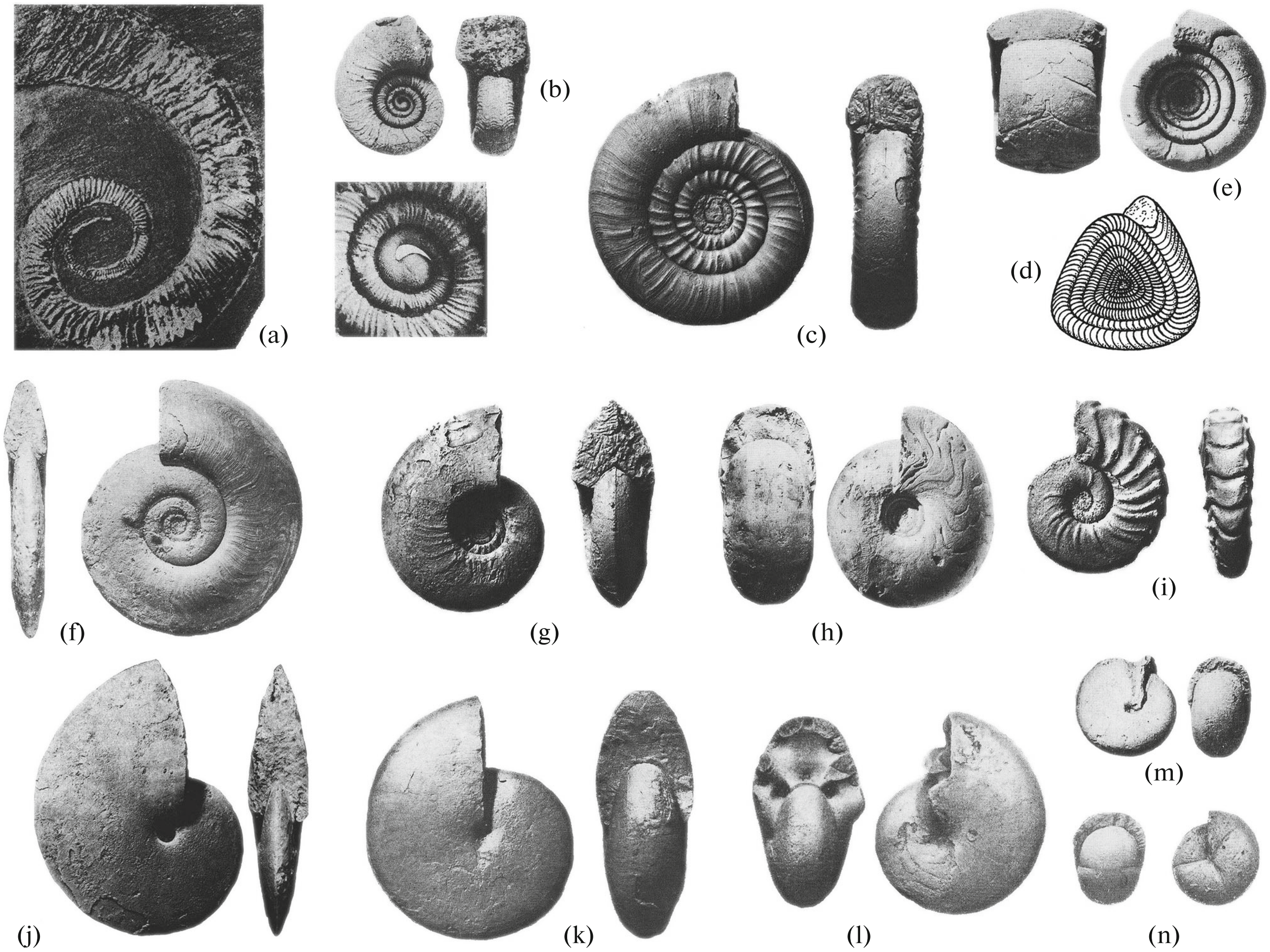

Fig. 1. Shell shape of Devonian ammonoids: (a) Agoniatitina, *Anetoceras arduennense* (Steininger), D_1, Emsian; (b) Agoniatitina, *Mimagoniatites obesus* Erben, D_2, Eifelian, the first whorls with protoconchs are enlarged; (c) Clymeniina, *Platyclymenia annulata richteri* Wedekind, D_3, Famennian; (d) Gonioclymeniina, *Soliclymenia paradoxa* (Münster), D_3, Famennian; (e) Anarcestina, *Cabrieroceras rouvillei* (Koenen), D_2, Givetian; (f) Gephuroceratina, *Ponticeras tschernyschevi* (Hopzapfel), D_3, France; (g) Clymeniina, *Rectoclymenia lyrata* Nikolaeva et Bogoslovsky, D_3, Famennian; (h) Anarcestina, *Werneroceras altaicum* Bogoslovsky, D_2, Eifelian; (i) Clymeniina, *Pricella tuberculata* (Kind), D_3, Famennian; (j) Gephuroceratina, *Carinoceras menneri* G. Ljaschenko, D_3, France; (k) Tornoceratina, *Sporadoceras semiflexum* Schindewolf, D_3, Famennian; (l) *Sporadoceras posthumum* Wedekind, D_3, Famennian; (m) *Prionoceras sulcatum* (Münster), D_3, Famennian; (n) Anarcestina, *Prolobites delphinus* (Sandberger et Sandberger), D_3, Famennian. After: Bogoslovsky, 1969; 1971; 1981; Ruzhencev, 1960; Nikolaeva and Bogoslovsky, 2005.

The shells of ammonoids were either smooth, or variously ornamented. The main types of ornamentation are transverse, spiral and reticulate (Table 1). Barskov (2017, 2018) reviewed the history of the ornamentation of non-ammonoid cephalopods. Ammonoids, as like other cephalopods, first had transverse ornamentation. The earliest forms (genera *Anetoceras, Erbenocerasas, Mimosphinctes*) had a transversely ribbed shell, apparently inherited from ancestral bactrites. Simple transverse ribs in a short time became very diverse: they could be fine and coarse, flat and convex, long and short, straight and bent. In addition to simple ribs, there appeared complex ribs, including dichotomous, branching, or fasciculate (collected in bunches) ribs. Ammonoids with smooth shells (genus *Taskanites*) appeared at almost the same time, at the very beginning of the existence of the subclass (the end of the Emsian). Shortly after the appearance of this morphotype, it had become one of the most common. Out of 41 families of Devonian ammonoids, representatives of 40 had a transverse sculpture, and 34 had a smooth shell. One family often included genera with different types of ornamentation.

The predominance of these two morphotypes was preserved in the subsequent history of the subclass. The analysis of 63 of Carboniferous-Permian families also shows that these two types of shell ornamentation (smoothened and transversely-ribbed) are most commonly found in the orders Goniatitida, Prolecanitida, and Ceratitida (Fig. 3). In the first two they included

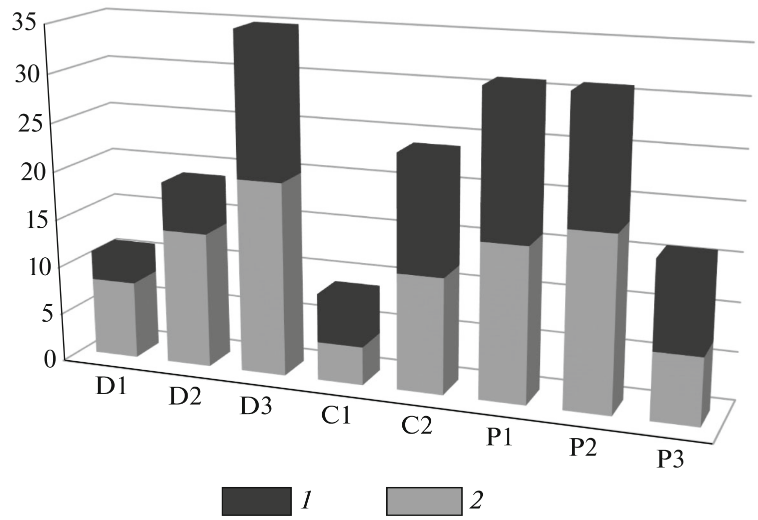

Fig. 2. Dynamics of variation in the diversity of Paleozoic ammonoids in shell shape and sutures. Explanations: (*1*) morphotypes of the shell shape; (*2*) morphotypes of sutures.

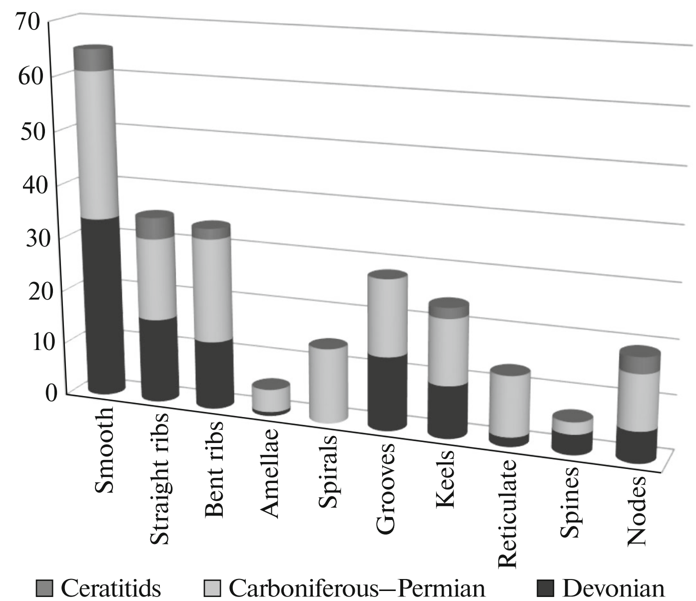

Fig. 3. Graph of the distribution of the main types of ornamentation in groups of Paleozoic ammonoids.

27 families (smooth) and 38 families (with transverse ornamentation), and in Ceratitida four and six, respectively. The very modest figures for the ceratites are due to the fact that at the end of the Paleozoic, the newly formed Ceratitida detachment (mostly Mesozoic) numbered only six families.

Variants of a combination of shell shape and typical morphotypes of sculpture could be very diverse: smooth shells of cadiconic, pachyconic, and oxyconic shape, etc. (Figs. 4a–4e); evolute shells with short ribs in the umbilical region or involute—with long ribs, shells of any shape with convex dichotomizing or branching ribs forming fascicles or carinae (Figs. 4f–4j). The second element of the transverse sculpture, lamellae (superimposed flattened thin plates) is known in a limited number of representatives of several suborders; they are most common in the Carboniferous-Permian suborder Cyclolobina (Fig. 4k).

Spiral ornamentation was less common in Paleozoic ammonoids. Keels and spiral grooves on the venter and ventrolateral shoulder (Figs. 4p–4r) are known from the beginning of the Middle Devonian (genus *Parentites*, Early Eifelian). Spirals, the most typical element of spiral ornamentation, appeared as an inde-

Table 1

Ornamentation type		Geological age	Examples (suborders, families)
Smooth shell		D_1–P_3	Gephuroceratina (Gephuroceratidae, Pharciceratidae Devonopronoritidae, Beloceratidae, Timanoceratidae), Agoniatitina (Agoniatitidae), Auguritina, Tornoceratina (Cheiloceratidae, Sporadoceratidae), Clymeniina (Clymeniidae, Rectoclymeniidae), Goniatitina (Muensteroceratidae, Homoceratidae, Thalassoceratidae), Prolecanitina (Prolecanitidae, Daraelitidae), Medlicottiina (Pronoritidae), Paraceltina (Paraceltitidae, Xenodiscidae), Otoceratina (Araxoceratidae, Anderssonoceratidae)
Transverse	Simple ribs	D_1–P_3	Agoniatitina (Anetoceratidae, Mimosphictidae), Gephuroceratina (Trianoceratidae), Tornoceratina (Tornoceratidae), Clymeniina (Cyrtoclymeniidae, Rectoclymeniidae), Goniatitina (Muensteroceratidae, Reticuloceratidae, Gastrioceratidae, Metalegoceratidae)
	Branching ribs	D_3–P_3	Clymeniina (Cyrtoclymeniidae, Rectoclymeniidae, Clymeniidae), Goniatitina (Homoceratidae, Decoritidae, Reticuloceratidae), Paraceltina (Paraceltitidae)
	Lamellae	D_3–P_3	Clymeniina (Cyrtoclymeniidae, Clymeniidae) Agoniatitina (Teicherticeratidae), Tornoceratina (Posttornoceratidae), Clymeniina (Cyrtoclymeniidae, Clymeniidae), Goniatitina (Stenoglaphyritidae, Bisatoceratidae), Cyclolobina (Marathonitidae, Vidrioceratidae, Cyclolobidae)
	Constrictions	D_2–P_3	Anarcestina (Prolobitidae), Tornoceratina (Cheiloceratidae, Prionoceratidae), Clymeniina (Rectoclymeniidae), Goniatitina (Muensteroceratidae, Homoceratidae, Reticuloceratidae, Metalegoceratidae), Cyclolobina (Popanoceratidae, Marathonitidae)
Spirals (spiral lirae)		C_1–P_3	Goniatitina (Goniatitidae, Girtyoceratidae, Nomismoceratidae, Neoglyphioceratidae, Cravenoceratidae, Agathiceratidae)
Reticulate		D_3–P_3	Clymeniina(Rectoclymeniidae), Tornoceratina (Sporadoceratidae), Goniatitina (Cravenoceratidae, Neoglyphioceratidae, Reticuloceratidae, Gastrioceratidae, Paragastrioceratidae), Adrianitina (Adrianitidae),
Exotic	Spines	D_2–P_3	Clymeniina (Cyrtoclymeniidae, Rectoclymeniidae), Adrianitina (Adrianitidae), Pseudohaloritina (Pseudohaloritidae)
	Keels, furrows	D_3–P_3	Agoniatitina (Mimoceratidae), Anarcestina (Prolobitidae), Tornoceratina (Tornoceratidae), Clymeniina (Clymeniidae), Goniatitina (Homoceratidae, Reticuloceratidae)
	Carinae	D_3–P_3	Clymeniina (Cyrtoclymeniidae), Goniatitina (Nomismoceratidae, Girtyoceratidae), Pseudohaloritina (Pseudohaloritidae)
	Nodes	D_3–P_3	Clymeniina (Cyrtoclymeniidae), Goniatitina (Muensteroceratidae, Gephuroceratina (Trianoceratidae), Clymeniina (Cyrtoclymeniidae), Goniatitina (Homoceratidae, Paragastrioceratidae), Medlicottiina (Medlicottiidae), Pseudohaloritina (Pseudohaloritidae), Paraceltina (Dzhulfitidae)

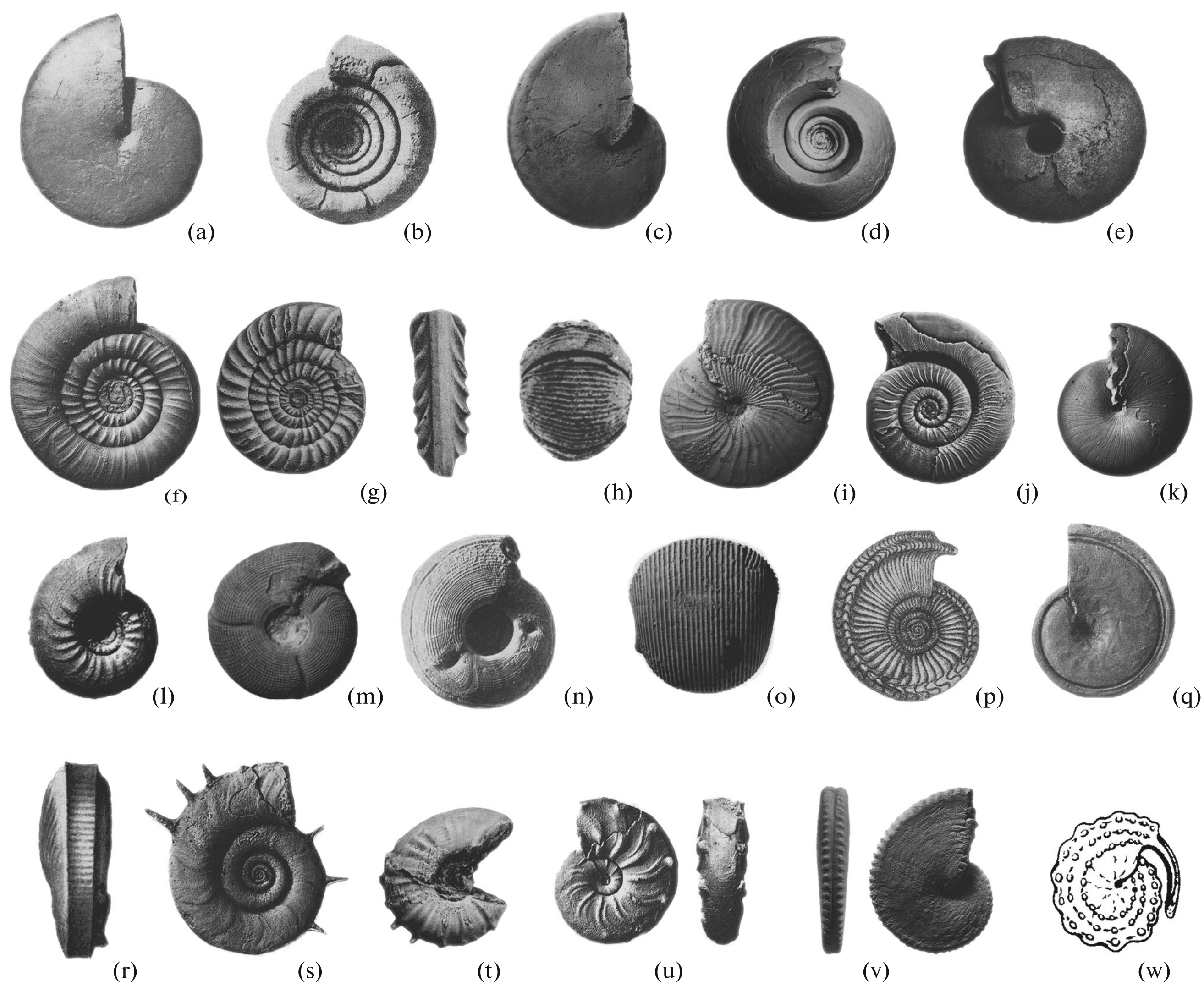

Fig. 4. Ornamentation of Paleozoic ammonoids. Smooth shells: (a) Tornoceratina, *Sporadoceras semiflexum* Schindewolf, D_3, Famennian; (b) Anarcestina, *Cabrieroceras rouvillei* (Koenen), D_2, Givetian; (c) Medlicottiina, *Parasicanites meridionalis* Leonova, P_1, Kungurian; (d) Goniatitina, *Juresanites karakhorum* Ruzhencev, P_1, Sakmarian; (e) Cyclolobina, *Waagenoceras mojsisovicsi* Gemmellaro, P_2, Wordian. Transverse ornamentation: (f) Clymeniina, *Platyclymenia anulata richteri* Wedekind, D_3, Famennian; (g) Goniatitina, *Anatsabites multiliratus* (Plummer et Scott), P_2, Wordian; (h) *Changhsingoceras meishanense* Chao et Liang, P_3, Changhsingian; (i) *Pamiropopanoceras meridionale* Leonova, P_1, Kungurian; (j) Paraceltitina, *Paraceltites elegans* Girty, P_2, Roadian; (k) *Almites invariabilis* Ruzhencev, P_1, Artinskian. Reticulate and spiral ornamentation: (l) Clymeniina, *Rectoclymenia lyrata* Nikolaeva et Bogoslovsky, D_3, Famennian; (m) Adrianitina, *Adrianites elegans* Gemmellaro, P_2, Wordian; (n) Goniatitina, *Ferganoceras elegans* Librovitch, C_1, Visean; (o) Adrianitina, *Epadrianites timorensis* (Boehm), P_2, Amarassian. Exotic ornamentation: (p) Goniatitina, *Entogonites grimmeri* (Kittl), C_1; (q) Goniatitina, *Aristoceras chkalovi* Ruzhencev, C_3, Gzhelian; (r) Medlicottiina, *Episageceras noetlilingi* Haniel, P_2, Amarassian; (s) Clymeniina, *Spinoclymenia aculeata* Bogoslovsky, D_3, Famennian; (t) Adrianitina, *Pseudagathiceras spinosum* Miller, P_2, Wordian; (u) Clymeniina, *Pricella tuberculata* (Kind), D_3, Famennian; (v) Medlicottiina, *Synartinskia principalis* Ruzhencev, P_1, Sakmarian; (w) Tornoceratina, *Elephantoceras nodosum* Zhao et Zheng, P_2, Roadian. After: Bogoslovsky, 1969; 1971; Ruzhencev, 1960; Nikolaeva and Bogoslovsky, 2005; Leonova, 2002; Furnish et al., 2009.

pendent morphotype in the Early Carboniferous (suborder Goniatitina, family Goniatitidae). There are indications (Bogoslovsky, 1971, 1981) that two Late Devonian (Famennian) genera had weak spiral elements, but they were accompanied by transverse elements, forming a reticulate pattern. It should be noted that the spirals are not as diverse as the transverse ribs, they differ in width, convexity, and also in the size of the gaps between them (Figs. 4n–4o). In the Paleozoic ceratitids, no spiral ornamentation has been observed.

Another type of "basic" sculpture is a reticulate pattern. It was fairly common in Paleozoic taxa, differing in the degree of intensity of longitudinal or transverse elements (Figs. 4l–4m). As mentioned, this type first appeared at the end of the Devonian in one genus

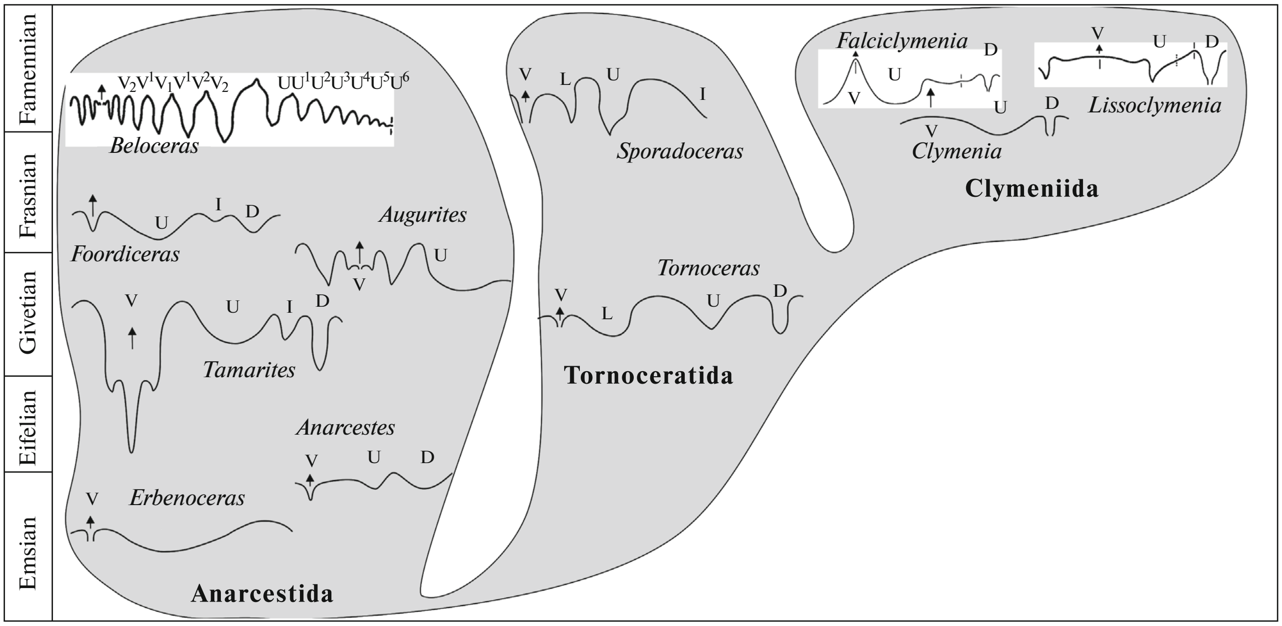

Fig. 5. Morphogenesis of the sutures of the Devonian ammonoids.

Tornoceratida (*Sporadoceras*) and in one clymeniid genus (*Rectoclymenia*). The reticulate morphotype is most typical of the representatives of Carboniferous Goniatitina (families Cravenoceratidae, Neoglyphioceratidae, Reticuloceratidae, Gastrioceratidae, Rhymmoceratidae, etc.) and Permian Adrianitina (Adrianitidae) (Table 1). To date, no Paleozoic ceratitids with reticulate ornamentation have been found.

In a number of taxa, there are "exotic" types of sculpture, represented by combinations of the most diverse and often hypertrophied elements: thorns of different shapes and sizes (Figs. 4s–4t), transverse ridges with spirals ribs, spines, nodes of various sizes and shapes (Figs. 4u–4w). The maximum diversification of such exotic taxa usually coincides with the final stage of the evolution of the taxon. For Paleozoic taxa these are representatives of the suborders Clymeniina at the end of the Famennian, some Goniatitina at the end of the Early Carboniferous, Pseudohaloritina in the second half of the Permian (Late Paleozoic). In general, for the subclass, the maximum diversity of "exotic taxa" and heteromorphs is at the end of the Mesozoic, a decline stage in the group's evolution (Shevyrev, 2005).

As follows from the above examples, the bulk of the morphotypes of the shell and sculpture appeared in the early stages of the existence of the subclass, again confirming the validity of the hypothesis of archaic diversity. Having appeared in the Devonian, these morphotypes were repeated many times in various combinations in different groups (Leonova, 2016a).

Suture. A complex suture is the most specific character of ammonoids. In Paleozoic ammonoids, sutures are usually consistent within each taxon and serve as an important diagnostic feature. The suture type is determined by the structure of the primary suture formed by the larva emerging from the egg, and several of the following septa. The order of appearance of incipient lobes and the general plan for the structure of the suture characterize groups of the order rank, smaller details are important in identifying families, genera and species. The formation of a complex curved septum and dissected suture is the main cluster in the evolution of ammonoids (Ruzhencev, 1960). The functional significance of this process, mainly, consisted in optimizing the operation of the hydrostatic apparatus (Barskov, 1999; Barskov et al., 2008). Almost all morphotypes of the sutural outline were formed in the Paleozoic. The ratio of their diversity to the variety of shell shape is shown in Fig. 2. The graph shows that the number of sutural morphotypes exceeds the varieties of shape.

The earliest members of the subclass (Emsian Stage, end of the Early Devonian) had the simplest, bilobate suture inherited from bactritoids with a sutural formula VO (ventral and omnilateral lobes). Examples include the most ancient genera *Anetoceras, Erbenoceras, Teicherticeras*, etc. (order Anarcestida, family Anetoceratidae) (Fig. 5). The next stage: the appearance of the dorsal lobe, VO: D at the end of the Emsian (genera *Mimosphinctes, Talenticeras*, family Mimosphinctidae, etc.). At the Early-Middle Devonian boundary, the omnilateral lobe was replaced by the umbilical lobe (U) (family Anarcestidae, genera *Anarcestes, Cabrieroceras, Archoceras*, etc.), and hence, the sutural formula changed to VU: D (Fig. 5).

In the Givetian (Middle Devonian), an inner lateral lobe (I) first appeared (Gephuroceratina, genus *Tamarites*, etc.); such sutures are designated by the formula VU:ID. In another order, Tornoceratida, also on the Middle Devonian, the outer lateral lobe (L) emerged for the first time, at that time four-lobed lines (VLU:D) (genus *Tornoceras*, etc.) appeared. In the late Devonian (Famennian), five-lobed sutures (VLU:ID) of Sporadoceratidae (*Sporadoceras* and others) also appeared among the Tornoceratida (Fig. 5). All subsequent modifications of the suture occurred on the basis of these five main lobes, and their ratio determines the modern system of the subclass Ammonoidea (Leonova, 2017).

Among Anarcestida (Early Devonian (Emsian)—the end of the Devonian), it is practically possible to encounter all the possible morphologies of the septal edge (sutures) known for Paleozoic ammonoids (Fig. 5). Despite the fact that the Devonian has a truly archaic variety of lines in different, often small and short-lived groups, not all sutural types appeared within the same or similar time intervals. Some of the Devonian morphotypes never again occurred in any taxon of ammonoids.

These are very simple (three-lobed) and multilobed sutures with complex ventral and numerous umbilical lobes. The "ceratitic" and "ammonitic" sutures have not been found among the oldest representatives of the subclass. Morphotypes with dentate and multi-lobed lobes, apparently, were the product of a long evolution, and the first appeared at the end of the Carboniferous, but became more common in the Permian, at the very end of the Paleozoic.

At the end of the early Devonian, a wide tripartite ventral lobe appeared for the first time in the suborder Auguritina. Then, already in the Late Devonian, this character reappeared in representatives of the suborder Gephuroceratina. In some of the Gephuroceratina the suture reached a very high level of complexity due to the formation of additional ventral or umbilical lobes (up to 54 lobes around the whorl) (Fig. 5). In representatives of the suborder Timanoceratina, the ventral lobe was bipartite (Fig. 5). In general, the oldest ammonoid order Anarcestida is characterized by the VU:D sutural outline (Bogoslovsky, 1969).

Representatives of the order Clymeniida existed very briefly, during the Famennian only. They differed significantly from all other ammonoids. Instead of the ventral lobe, they formed a ventral saddle (Fig. 5), which was associated with a dorsal, rather than a ventral (as in most other groups), siphon. After the radiation of the "archaic diversity" of the Devonian ammonoids of the orders of Anarcestida with five suborders and Clymeniida with two suborders (Shevyrev, 2006), a serious biotic crisis occurred led to an extinction of almost all Devonian ammonoid taxa. The only exception was the order Tornoceratida, and the Devonian-Carboniferous boundary was crossed by a few taxa with a simple ventral lobe, and these gave rise to new large groups of ammonoids. At the very beginning of the Carboniferous, the taxonomic and morphological structure of the ammonoid community radically changed. Of the Devonian orders, only a few representatives of the tornoceratids continued to exist, but at this time two new orders of Goniatitida and Prolecanitida appeared, which constituted the main variety of ammonoids during the last two Paleozoic eras. Goniatitida as a whole was characterized by a bipartite ventral lobe, while in Prolecanitida this lobe was narrow, deep, and tripartite.

The order Prolecanitida was previously included in the Devonian detachment of Agoniatitida (Ruzhencev, 1960, Bogoslovsky, 1969, etc.), since it was believed that its original suture consists of three VU:D lobes. Studies of recent decades (Zakharov, 1984; Leonova and Voronov, 1989; Korn et al., 2002) showed that prolecanitids formed both a three-lobed (VU: D) and four-lobed (VU:ID), and in some cases even five-lobed (VLU:ID) sutures. The order is clearly subdivided into two morphological groups. One of them remained extremely conservative (suborder Prolecanitina) with a relatively wide ventral and a few lateral and umbilical lobes. The second group progressively evolved (suborder Medlicottiina). The main cluster of evolution in this suborder was the increasing complexity of the external saddle and the increase in the number of lobes on the flank up to 20, which became deeper and more strongly dissected (Fig. 6). Apparently, the first, non-specialized group of prolecanitids gave rise to the Mesozoic Ceratitida at the Early-Middle Permian boundary.

Three groups (at the rank of suborder) are distinguished in the composition of the Carboniferous-Permian order Goniatitida (Tournaisian–Changhsingian) on the basis of fundamental differences in the development of the primary lateral (L) and umbilical (U) lobes: Goniatitina, Adrianitina and Cyclolobina (Leonova, 2002). In Goniatitina, the total number of lobes around the whorl remained eight (with rare exception) almost throughout their entire history. In the vast majority of goniatitins, the complication of the suture was achieved by varying the width and depth of the main lobes, and much less commonly by the formation of serrations and projections on the main lobes, almost without the formation of new elements. As a rule, the lobes and saddles remained entire (Fig. 6). It should be noted that in all groups of ammonoids the umbilical portion of the suture possessed maximum plasticity. The suborder Adrianitina (Late Carboniferous, Kasimovian to Middle Permian,

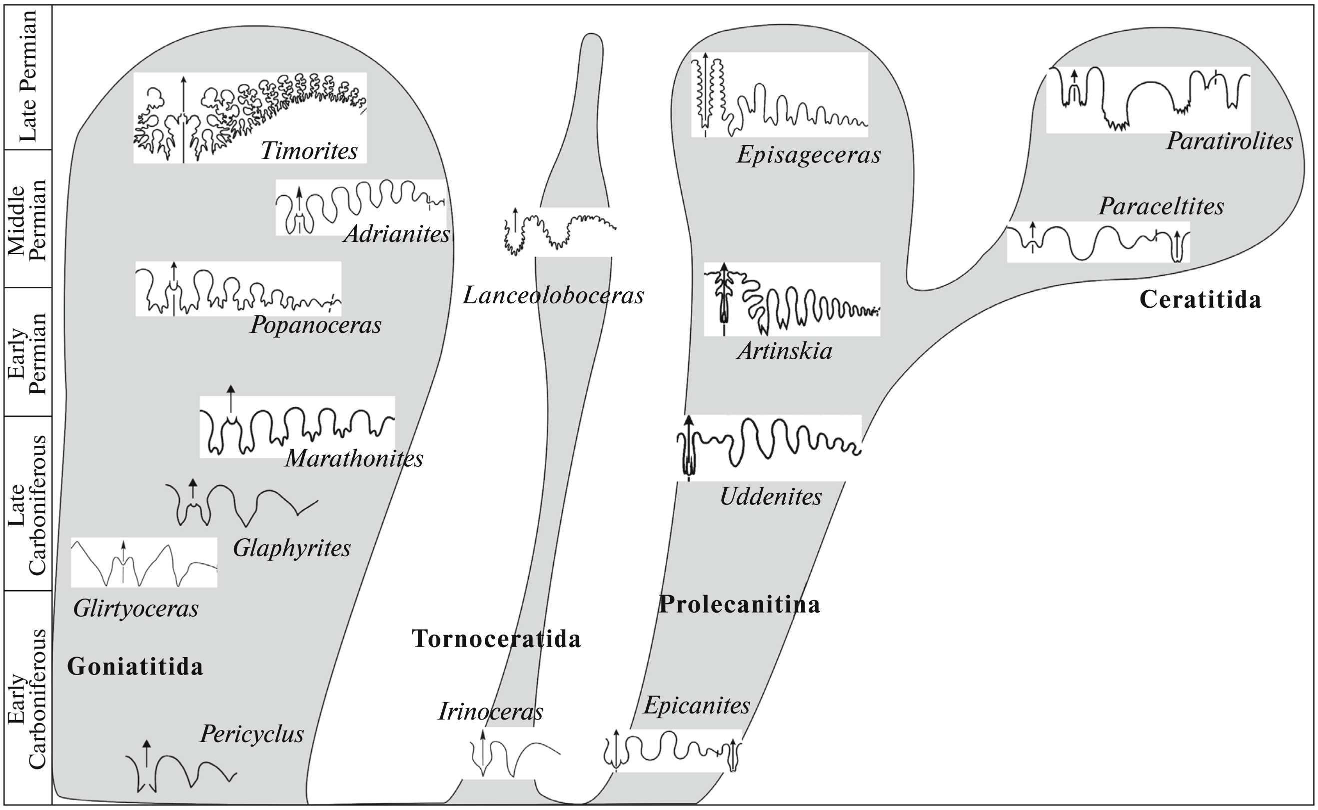

Fig. 6. Morphogenesis of the sutures of the Carboniferous–Permian ammonoids.

Capitanian) is characterized by a complex suture, formed in a very specific way: new umbilical lobes formed at the top of the umbilical saddle and alternately moved first to the inner and then to the outer side of the shell following the formula (V_1V_1) LU:ID → (V1V1) $LUU^2:U^1ID$ → (V_1V_1) LUU^2Un 1:UnU^1ID. At the same time, neither the outer nor the inner lateral lobes have ever divided. The number of lobes in different taxa could vary within wide limits, but all the lobes remained entire (Fig. 6). This group separated from goniatitins by the beginning of the Late Carboniferous, but it reached its maximum diversity in the Permian, where several branches of adrianitids were characterized by different evolutionary trends (Leonova and Boiko, 2015).

The most advanced of goniatitids, Cyclolobina (Late Carboniferous, Gzhelian to the end of the Permian, Changhsingian) reached maximum complexity of the suture. It is characterized primarily by a tripartite division of the lateral blade $L \rightarrow (L_2L_1L_2) \rightarrow L_2L_1L_2$, and in a number of groups by further subdivision the third external lateral lobe. The inner lateral (I) and umbilical (U) lobes in different superfamilies also underwent three- or two-partite division, and in different branches these transformations occurred in different ways. In addition, in all groups there are numerous denticles and petals on the lobes and saddles (Fig. 6). This suborder includes the superfamilies with the most complex sutures: Cycloloboidea (the total number of lobes in the suture was 60), Shumarditoidea, Marathonitoidea, Popanoceratoidea.

The first representatives of the Mesozoic order Ceratitida appeared at the beginning of the middle Permian (Roadian). They most probably evolved from Prolecanitina. For the ceratitds, the development of the three-lobed (in Permian Paraceltitina) primary suture VU:D to the five-lobed VLU:ID, then in ontogeny there is a loss of the umbilical lobe (VL:ID), and in the later stages there is an additional internal lobe (V_1V_1) $LII^1:(D_1D_1)$. The second Permian suborder Otoceratina is characterized by a four-lobed primary suture (VL:ID). Further increase in complexity is due to the formation of new umbilical lobes (V_1V_1) LU^1U^2:II (D_1D_1) (Fig. 6). This way of increasing sutural complexity fundamentally distinguishes Ceratitida from Prolecanitida and Goniatitida (Shevyrev, 1986).

Each of the above-considered lineages also contained many not so cardinal and often parallel changes of various elements of the suture (the number and shape of the lobes and saddles, the degree of their dissection). These characters are usually taken into account in the classification of taxa of lower rank: families, genera and species. Paleozoic forms are characterized by stability of the structure of the blade line within a single taxon, which manifests itself even in details. In this they differ from the Mesozoic ammonoids. Therefore, the characters of the suture, as a rule, are the most significant diagnostic characters of Paleozoic taxa.

Nevertheless, there are cases of asymmetrical development of lobes and saddles on different sides of the same shell, the formation of additional digits and small lobes in the umbilical zone (Leonova, 2016c). The study of the sutures provides broad possibilities for modeling various directions and mechanisms of morphogenesis: parallel development (synchronous and asynchronous), heterochrony, recapitulation, pedomorphosis, the emergence of mosaic forms (Leonova, 2015, 2016b). The combination of these with various trends in the development of ornamentation and the shell shape give abundant material for evolutionary reconstructions.

CONCLUSIONS

Thus, the formation of the morphological diversity of ammonoids resulted in the emergence of all known morphotypes of the shell shape and ornamentation as early as in the Devonian. The diversity of the morphotypes of the suture towards the end of this epoch was the maximum for all ammonoids, which corresponds to the principle of "archaic diversity." At the Devonian-Carboniferous boundary, a profound crisis resulted in the fundamental change in the morphological structure of the ammonoid communities and the Devonian orders practically died out. In the further history of ammonoids, the "Devonian" morphotypes repeatedly appeared in various orders. The next crisis, which led to a morphological reorganization ammonoid biota, was at the Permian-Triassic boundary. At the end of the existence of each large group, as a rule, numerous morphotypes appeared, showing the extreme expression of the main characters, the so-called "exotic taxa." The most pronounced senile diversity is associated with the diversification of similar taxa at the end of the existence of the subclass Ammonoidea at the end of the Cretaceous.

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