

Abstract—The main evolutionary trends in the Permian ammonoids are traced, and the systematics of this group is revised at the ordinal, family, and generic levels. All Permian species and their stratigraphic and geographic ranges are listed. The phylogenetic relationships within all Permian ammonoid families are discussed. For a number of them, new phylogenetic reconstructions are made.

INTRODUCTION

The Permian completed the Paleozoic phase in the evolution of the biosphere and terminated in a vast biotic crisis. This coincided with a fundamental change in the evolution of ammonoids, one of the most important groups of marine organisms of the Permian. A comprehensive study of this fossil group not only allows the recognition of major evolutionary trends in the ammonoid evolution, but it also has wider implications for our understanding of the biotic changes that took place at this critical boundary.

The vast quantity of data accumulated over 150 years by several generations of workers on the morphology, composition, phylogeny, and distribution of the Permian ammonoids requires an updated analysis. More than 40 years have passed since V.E. Ruzhencev, an excellent and meticulous researcher, published his fundamental studies in this field. Since that time, the knowledge of the Permian ammonoids has greatly developed and new approaches have appeared in systematics, paleobiogeography, and biostratigraphy. The concept of morphological diversity has changed considerably, and the number of described genera and species has almost doubled. Numerous new localities have been discovered and ammonoid faunas in northeastern Russia; the Far East; northern Russia; Central Asia; the Canadian Arctic; Nevada; Central America; Japan; Indo-China; and, particularly, China have been studied anew. The existing classifications and settled views on the evolution of the higher ammonoid taxa do not always correspond to the modern state of knowledge. Therefore, I had to revise the systematics of Permian ammonoids based on the phylogenetic reconstructions of their families and orders using updated information.

The study was based on large collections of Permian ammonoids from the territory of the former Soviet Union. Primarily, these collections were from the Permian of the southeastern Pamirs and Darvaz and included more than 8000 specimens representing over 140 species of 70 genera and 20 families. Most of this material was collected by myself during field trips in 1973, 1974, 1986, and 1987. Part of the material was donated by other workers: V.Yu. Dmitriev, T.A. Grunt, E.Ya. Leven, S.V. Ruzhencev, V.L. Leleshus, and B.M. Gushchin. I also used ammonoid collections from other regions, both those housed in the Laboratory of

Mollusks of the Paleontological Institute of the Russian Academy of Sciences (from the Southern and Central Urals, northeastern Russia, Novaya Zemlya, Texas, and Nevada) and those received from Russian research institutes and the geological survey as well as from colleagues from abroad. I studied the collections of Permian ammonoids housed in the TsNIGR Museum, the Paleontology Department of the St. Petersburg State University, and the Mining Institute (all in St. Petersburg); Early and Late Permian ammonoid collections from China in the Nanjing Institute of Geology and Paleontology of the Chinese Academy of Science in 1992; Early Permian ammonoids of Nevada and Idaho (Boise State University, Idaho, in 1995); Early and Late Permian ammonoids of Texas, New Mexico, Mexico, Timor, and Sicily (University of Iowa, in 1995, 1996, 1998, and 2000); and Early and Late Permian ammonoids of western Australia and Malaysia (Deakin University, Melbourne, Australia, in 1997). A small collection of Late Permian ammonoids was collected during a field trip to southern China (near the town of Laibin) in 1999. I used my own generic and species databases, including data on the geographic and stratigraphic distribution of Permian ammonoids, for the revision of the systematics and for the analysis of evolutionary patterns in this group.

The publication of this study is planned as two volumes, the first of which will treat the systematics and phylogeny, and the second will cover the biogeography and biostratigraphy of Permian ammonoids.

Main Principles of Classification and Phylogenetic Reconstruction

The fundamental principles of the ammonoid taxonomy and the general system of the modern ammonoid classification were developed by Schindewolf (1954) and Ruzhencev (1957). These principles were essentially different from those of preceding systems in that they were based on the studies of the sutural ontogeny. These workers believed that the earliest Devonian ammonoids (group Agoniatitina of Schindewolf or the order Agoniatitida of Ruzhencev) gave rise to two lineages: Prolecanitina of Schindewolf or the order Agoniatitida of Ruzhencev with a U-type sutural ontogeny and Goniaticitina–Goniaticitida (A-type by Schindewolf or

L-type by Ruzhencev). Later, Ceratitida evolved from the U-type lineage, in turn giving rise to Ammonitida.

These principles are generally followed by most modern workers. Further studies were mainly concerned with the refinement of the systematics and taxonomy of individual groups.

The latest published classification of the subclass Ammonoidea (at ordinal level) was proposed by Bogoslovskaya *et al.* (1990) and is currently used by most Russian workers. Their classification represented an updated version of Ruzhencev's system, in which the Mesozoic fauna was comprehensively revised. As a result, the order Ceratitida included 10 suborders, whereas Ammonitida was subdivided into three orders; this classification indicates a trend toward the splitting of larger groups based on up-to-date taxonomic information.

In the Paleozoic part, the order Agoniatitida was subdivided into two orders: Anarcestida and Prolecanitida, following the opinions of Schindewolf (1954) and Miller and Furnish (1954). The taxonomy of the order Goniaticitida remained unchanged (three suborders), which is disputed in the present paper. The above system is inconsistent in choosing different classification criteria for different groups (Agoniatitida and Goniaticitida s.l.). The present paper tries to attain a more consistent system by using a uniform approach to the definition of the taxonomic rank of the characters.

I follow the widely accepted view that Ammonoidea represents a subclass of the class Cephalopoda (Basse, 1952; Teichert and Moore, 1964; Glenister and Furnish, 1980; and Bogoslovskaya *et al.*, 1990). The subdivision into orders is based on the following widely accepted taxonomic principles: (1) the mode of sutural ontogeny during the early ontogenetic stages and (2) the position of the siphuncle. Despite the fact that many workers recognize the considerable taxonomic importance of the position of the siphuncle (Zittel, 1895; Schindewolf, 1931, 1954; Ruzhencev, 1962; etc.), it is of little use in the classification of most groups except for Clymeniida, which is the order that is based on this character. The siphuncle and septal necks were among the major construction elements of the ammonoid shell; thus, the position of the siphuncle should be coequal with the type of sutural ontogeny in the taxonomy of ammonoid orders. The classification of suborders is largely based on the general patterns of sutural ontogeny and on the development of the major elements of the suture during the later ontogenetic stages. Virtually all Paleozoic ammonoid specialists agree that the most important criteria in the high-rank ammonoid taxonomy are those connected with the emergence and transformations of the primary lobes: the ventral (V) appeared earliest in the evolution; the umbilical (U) appeared third; the inner lateral (I), fourth; the dorsal (D), fifth; and the outer lateral (L) appeared sixth. The omnilateral lobe (O), which appeared second, is known only in archaic Early Devo-

nian Agoniatitina. During three periods of ammonoid evolution in the Paleozoic (Devonian, Carboniferous, and Permian), changes in all these lobes occurred repeatedly and not simultaneously. The ventral (most ancient) lobe was inherited from Bactritoidea and transformed earlier than other lobes; subsequently, this happened many times in different lineages. The umbilical lobe U also started to change in the Early Devonian, soon after its appearance, and, later, underwent transformations many times throughout the ammonoid evolution. The outer lateral lobe L, which appeared last (Middle Devonian), began its transformation later than all the other lobes, only in the mid-Carboniferous (Barskov *et al.*, 1994) (Tables 1, 2).

In the modern system of Paleozoic ammonoids (Bogoslovskaya *et al.*, 1990), major morphological changes in the lobes V, L, and U are evaluated differently. This system accepts that the archaic Anarcestida and the more advanced Prolecanitida are separate orders (both evolved following the U-type pattern, i.e., without evolving the primary lateral lobe L), as proposed by Miller and Furnish (1954), and in doing so, it accepts a high taxonomic rank of the changes in the primary umbilical lobe U. At the same time, the order Goniaticitida, which is much more diverse in its evolution than the order Prolecanitida, has retained its composition in the above classification; i.e., it includes three suborders that are united by a single feature in common, the presence of the outer lateral lobe L. Such taxonomy was justified when the remaining Paleozoic ammonoids were assigned indiscriminately to Agoniatitida. Following this logic, one should not only retain the composition of the order Agoniatitida but also extend it by adding Ceratitida and Ammonitida (if it is accepted that the two last groups evolved following the U-type pattern). In addition, there is no certainty which of the primary lobes (U or L) appears in the primary suture of Prolecanitida (Spinosa *et al.*, 1975; Zakharov, 1984; etc.); hence, the whole system loses its balance. Further refinement of the system should reduce the inconsistency in the classification of orders, primarily Agoniatitida and Goniaticitida.

Because data on the early sutural ontogeny are scarce and ambiguous, the taxonomic value of characters appearing during later stages increases. The order Goniaticitida showed fundamentally different trends in the evolution of the ventral (V), outer lateral (L), umbilical (U), and inner lateral (I) lobes. While in other orders, these characters are given considerable taxonomic weight, in Goniaticitida, they are underestimated by at least one rank. Therefore, the system of Paleozoic ammonoids is poorly balanced.

However, there are convincing reasons to consider Goniaticitida (in the original sense) to be a paraphyletic group based on both the sutural ontogeny and the position of the siphuncle.

For instance, the accepted system insufficiently refers to the fact that the ventral lobe (V), which is evo-

Table 1. Main diagnostic characters of Paleozoic ammonoid orders

Order	Position of the siphuncle	V	L and its derivatives	U and its derivatives	I and its derivatives	D	Type of sutural ontogen	Number of lobes
Ceratitida							V:UD→(V ₁ V ₁)L:(D ₁ D ₁) or VL:ID→ (V ₁ V ₁ LU ¹ U ² :I(O ₁ D ₁))	8-40
Goniatitida							VU:D→(V ₁ V ₁)LU:ID	8-60
Tornoceratida							VU:D→VLU:D	6-12
Praeglyphioceratida							VU:D→(V ₂ V ₁ V ₂)LU:ID	8
Prolecanitida							VU:D or VU:ID→VUU ¹ :ID	8-50
Clymeniida							VU:D or U:D	Not more than 12
Anarcestida	unstable				none		VO or YUD	up to 54 lobes

Table 2. Main diagnostic characters of Permian ammonoid superfamilies

Character Superfamily	Ventral lobe V	Lateral lobe L and its derivatives	Umbilical lobe U and its derivatives	Inner lateral lobe I and its derivatives	Dorsal lobe D	Position of the siphuncle
Prolecanitaceae		?				
Pronoritaceae		?		?		
Medlicottiiaceae		?				
Pseudohaloritaceae						
Agathicerarataceae						
Thalassocerataceae						
Neiocerataceae						
Somoholitaceae						
Shumarditaceae						
Marathonitaceae						
Cyclolobaceae						
Popanocerataceae						
Adrianitaceae						
Xenodiscaceae			reduced			
Otocerataceae						

lutionary older than the outer lateral lobe (L), is completely different in different suborders, both in its origin and development: in Tornoceratina, it is (in most cases) simple; in Goniatitina, it is always bipartite; and in Praeglyphioceratina, it is wide and tripartite.

The suborders Tornoceratina and Goniatitina have strikingly different positions of the siphuncle at different ontogenetic stages (there is no data on the siphuncle position in Praeglyphioceratina). The available material indicates that ammonoids possess three fundamentally different patterns of siphuncle position. These patterns are (1) the marginal-ventral position that persists throughout the ontogeny (Prolecanitida, Goniatitida s.s.), (2) the central position that subsequently shifts (at different times) ventrally (Anarcestida, Ceratitida, Phylloceratida, Lytoceratida, Ammonitida, Tornoceratina, and Agathiceratina) or the nonmarginal position that is close to the central or dorsal position throughout the ontogeny (Pseudohaloritina), and (3) the marginal-dorsal position with modifications (Clymeniida). It is clear that the position of the siphuncle is diagnostic for all ammonoid orders and only Goniatitida includes taxa with different modifications of this character.

By raising the taxonomic rank of Tornoceratina, Praeglyphioceratina, and Goniatitina to the ordinal level, both the evaluation of the taxonomic importance of major morphological changes in different lineages and the entire system of ammonoids become better balanced.

New Classification of Paleozoic Ammonoids

Subclass Ammonoidea Zittel, 1884

Order Anarcestida Miller et Furnish, 1954

Suborder Agoniatitina Ruzhencev, 1957

Suborder Auguritina Bogoslovsky, 1961

Suborder Anarcestina Miller et Furnish, 1954

Suborder Gephuroceratina Ruzhencev, 1957

Suborder Timanoceratina Bogoslovsky, 1957

Order Prolecanitida Miller et Furnish, 1954

Suborder Prolecanitina Miller et Furnish, 1954

Suborder Medlicottiina Zakharov, 1984

Order Praeglyphioceratida Ruzhencev, 1957

Order Tornoceratida Wedekind, 1918

Suborder Tornoceratina Wedekind, 1918

Suborder Pseudohaloritina subordo nov.

?Suborder Agathiceratina subordo nov.

Order Goniatitida Hyatt, 1884

Suborder Goniatitina Hyatt, 1884

Suborder Adrianitina subordo nov.

Suborder Cyclolobina subordo nov.

Order Clymeniida Hyatt, 1884

Suborder Gonioclymeniina Ruzhencev, 1957

Suborder Clymeniina Hyatt, 1884

Order Ceratitida Hyatt, 1884

Suborder Paracelitina Shevyrev, 1968

Suborder Otoceratina Shevyrev et Ermakova, 1979

In this scheme, the orders Anarcestida, Prolecanitida, Clymeniida, and Ceratitida are accepted according to the classification by Bogoslovskaya *et al.* (1990). Considering the above reasons, the rank of the suborders Goniatitina, Tornoceratina, and Praeglyphioceratina is raised to the ordinal level, with the previous diagnoses retained.

The major purpose of ranking Praeglyphioceratina as an order was the separation of the true goniatites from all the other groups that lack the major diagnostic characters of this order. Ruzhencev (1957) established the suborder Praeglyphioceratina, containing two Late Devonian genera (*Lagowites* and *Praeglyphioceras*), and one Tournaisian genus, *Karagandoceras*. This small group of ancient ammonoids was given such a high taxonomic rank (Ruzhencev, 1957; Bogoslovsky, 1971) because of the quite peculiar structure and ontogeny of the ventral lobe. In contrast to Tornoceratida and Goniatitida, Praeglyphioceratida have a tripartite ventral lobe (Fig. 1). Although recent studies have extended the specific composition of this group, the taxonomic and phylogenetic problems are far from being resolved (Bogoslovskaya *et al.*, 1999). This paper is concerned with Permian ammonoids and, therefore, does not discuss the phylogeny of Praeglyphioceratida, and the taxonomic rank of this group is discussed only from the point of view of the separation of the true Goniatitida. Hence, I propose to treat Praeglyphioceratida as an order rather than a suborder and to retain the diagnosis by Ruzhencev (1957, 1960) and Bogoslovskaya *et al.* (1990).

The rise in the taxonomic rank of Tornoceratida is based on the fundamentally different ontogeny of the ventral lobe and the unstable position of the siphuncle. While in the true goniatitids, the ventral lobe is primarily bifid, in most tornoceratids, it is undivided. In ancient Tornoceratida, the position of the siphuncle was unstable; there are a few Devonian genera with a non-ventral siphuncle (*Kirsoceras*, *Discoclymenia*, and *Sporadoceras*). In Permian Pseudohaloritidae, the subcentral position of the siphuncle is typical. The recognition of Tornoceratida as a separate order was previously proposed by Popov (1979, 1983), who also referred to the development of the bifid ventral lobe in this group. According to his concept, the "earliest goniatites are included in the order Tornoceratida, whereas the goniatites considered in the new, narrower sense begin with the suborder Goniatitina" (Popov, 1983, p. 8).

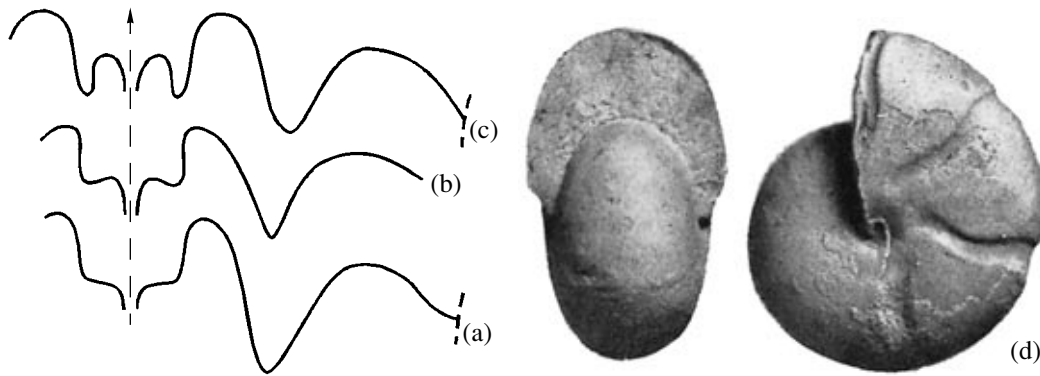


Fig. 1. Order Praeglyphioceratida. Sutures and shell shape: (a) *Lagowites rhipaeus* Bogosl.; (b) *L. niwae* (Sobol.); (c, d) *Praeglyphioceras pseudosphaericum* (Frech); Famennian (Bogoslowsky, 1957).

Since reliable data on the occurrence of Tornoceratida within a considerable interval from the end of the Early Carboniferous to the end of the Middle Carboniferous (Serpukhovian and Bashkirian) are lacking and the characters of the early (Devonian and Early Carboniferous) and late (Middle Carboniferous–Late Permian) tornoceratids are strikingly different, it seems logical to divide them into two suborders, Tornoceratina (VLU : D) and Pseudohaloritina (VLU : ID).

The above conclusions raise another problem in the taxonomy of agathiceratids that deals with the part of the family Agathiceratidae that presently includes only two genera, *Agathiceras* and *Gaetanoceras*, which have a central siphuncle during the early and intermediate ontogenetic stages. The study of cross sections of representatives of the phylogenetic lineages *Goniatites* → *Dombarites* → *Proshumardites* and *Agathiceras* → *Gaetanoceras* has shown that they cannot be interpreted as members of a single lineage because of the different position of the siphuncle in the early whorls. In the first group, the siphuncle is subventral beginning from the first whorl (Boiko, 2001); in the second group, it is central in the first four whorls. This suggests that agathiceratids should be assigned to Tornoceratida. On the other hand, they have a bifid ventral lobe, a character that distinguishes them from all other tornoceratids. This suggests a unique position. Clearly, this group should be treated as a suborder, although it is not clear to which of the two orders, Tornoceratida or Goniatitida, it should be assigned. The data on agathiceratids are not sufficient to draw a positive taxonomic conclusion.

Thus, the proposed order Goniatitida s.s. is identical in composition to the suborder Goniatitina of the previous schemes (excluding the aforementioned part of the family Agathiceratidae) but has much more distinct diagnostic features including the stable (ventral) position of the siphuncles, the presence of the bifid ventral lobe, and a L-type sutural ontogeny.

Because of the fundamental differences in the sutural ontogeny, i.e., of the primary L and U lobes, three suborders (Goniatitina, Adrianitina, and Cyclolobina) are proposed within the order Goniatitida s.s.

The suborder Goniatitina has the suture formula VLU : ID, with eight lobes that persisted virtually throughout the history of the group. The only exception is the Carboniferous superfamily Schistocerataceae (apparently paraphyletic) with a suture in which only the umbilical lobe U is subdivided following the pattern: $U \rightarrow (U_1U_2) \rightarrow U_1 : U_2 \rightarrow U_1U_{2.2}U_{2.1} : U_{2.2}$. This group shows the first morphological change in the goniatite suture (Middle Carboniferous), which led to the further development of the eight-lobed suture. In most *Goniatitina*, the increase in sutural complexity was achieved by the change in width and depth of major lobes and, more rarely, in the development of denticles on the major lobes without forming new elements. Usually, the lobes and saddle remained entire. The suborder includes 13 Carboniferous superfamilies, of which only four continued into the Permian: Goniolobocerataceae (until the Asselian–?Sakmarian), Somoholitaceae (until the mid-Artinskian), Thalassocerataceae (until the Wordian), and Neiococerataceae (until the end of the Permian). The latter superfamily includes seven families, of which five evolved following the above pattern. These were Paragastrioceratidae and Pseudogastrioceratidae, representing the major taxonomic diversity of the group throughout the Permian; the initial family Neiococeratidae (the genus *Eoasianites* existed at the beginning of the Permian); and two small families, Atsabitidae and Aulacogastrioceratidae. Two families, Metalegoceratidae and Spiroleoceratidae, which emerged at different times (the former at the beginning of the Permian from the neiococeratid genus *Eoasianites*, and the latter in the mid-Permian from the paragastrioceratid genus *Paragastrioceras*), increased the suture complexity by the division of the primary umbilical lobe as in Schistocerataceae, but they followed a differ-

ent pattern. Advanced representatives of this family had up to 12–16 lobes in their suture. This complexity was first achieved by the partial and then complete subdivision of the umbilical lobe into three lobes.

The suborder Adrianitina, including a single superfamily, shows a complex suture, which was formed in a specific way. Ruzhencev (1950) suggested (this observation was later confirmed) that, in contrast to all other suborders, the new umbilical lobes emerged at the top of the umbilical saddle and were shifted onto the inner and outer side of the whorl following the pattern: $(V_1V_1)LU : ID \rightarrow (V_1V_1)LUU^2 : U^1ID \rightarrow (V_1V_1)LUU^2U^{n+1} : U^nU^1ID$. Neither the outer lateral lobe nor the inner lateral lobe were subdivided. Both of them remained entire. This group evolved from Goniatitina by the beginning of the Late Carboniferous, but its major evolution occurred in the Permian.

The suborder Cyclolobina shows a primarily tripartite and, in some taxa, a more complex subdivision of the third outer lateral lobe: $L \rightarrow (L_2L_1L_2) \rightarrow L_2L_1L_2$. The inner lateral lobe (I) and umbilical lobe (U) in different families also underwent subdivision into two or three lobes, and in different lineages, these changes followed different patterns. In addition, all groups show the development of numerous denticles and petals on the lobes and saddles. This suborder includes superfamilies with very complex sutures: Cyclolobaceae, Shumarditaceae, Marathonitaceae, and Popanocerataceae.

Phylogeny. Phylogenetic reconstructions of all groups are used to develop a system for the Permian ammonoids. The completeness of the analysis of the major evolutionary trends and phylogenetic relationships of Permian ammonoids varies with the material available for different families. This analysis was based both on the original material (prolecanitids, thalassoceratids, marathonitids, cyclobaceans, perrinitids, adrianitids, metalegoceratids, popanoceratids, and agathiceratids) and on the literature (pseudohaloritids, paragastriceratids, and ceratids).

Phylogenetic patterns and modes. Ammonoids are classic subjects of onto-phylogenetic studies, which were applied to this group as early as the 19th century by Branco (1880–1881), Karpinsky (1890), Smith (1899), Hyatt (1900), etc. Ruzhencev (1940a, 1957, 1960) summarized these studies based on the phylogenetic-embryonic theory of Severtzov (1939). For instance, he elucidated the difference in the phylogenetic importance of changes during early, intermediate, and late ontogenetic stages (archallaxes, deviations, and anabolies) and formulated the major principles of phylogenetic systematics. Ruzhencev's principle of the "main cluster, a dominating type of essentially new physiological and associated morphological transformations" (Ruzhencev, 1960, p. 99) has an important place in this system.

The present paper performs a step-by-step analysis of the phylogenetic patterns and modes in the system of Permian ammonoids in an attempt to reconstruct the phylogenetic structure of higher taxa (orders, families, and subfamilies). Genera (as the most definitive and entire unit) are used as main units in these reconstructions, although it is noteworthy that the phylogenetic structure of some genera is quite complex.

Methodological aspects of phylogenetic reconstructions. Three groups of characters used in phylogenetic reconstructions, i.e., suture outline, shell shape, and ornamentation, play different roles in the substantiation of phylogenetic links between the ammonoid genera and suprageneric taxa, depending on the mode of the phylogenetic transformations. The classical phylogenetic reconstructions of ammonoids were mainly based on so-called orthogenetic sequences in the evolution of the suture, where each succeeding stage represented a direct continuation of the preceding stage, with the same evolutionary trend retained. To avoid the contentious issue of genetic mechanisms of orthogenetic evolution, I use the term orthogenesis to designate persistent trends in the evolution of characters (especially the ammonoid suture or its elements) remaining constant over a long time. Up to now, orthogenetic lineages form a core of ammonoid phylogeny. They form as anabolies over late ontogenetic stages; therefore, the relationships between the ancestors and derived forms can be easily determined from the persistence and developmental stage of the character. Thus, the taxa in a lineage represent more or less distinct stages of the channeled evolution (aromorphosis). A typical case of orthogenetic evolution is an increase in the number of lobes in the suture (in the lineages *Crimites* → *Neocrimites*, *Juresanites* → *Metalegoceras* → *Pseudoshitoceras*, and many others) and in the number of sutural elements, e.g., the increasing complexity of the external saddle in the lineage *Artinskia* → *Medlicottia* → *Syrdenites*, the increasing complexity of the lobe in the lineage *Almites* → *Suakites* → *Eohyattoceras*, etc. The increasing sutural complexity very often manifests itself both in the increasing number of lobes and in the increasing subdivision of the suture elements: *Demarezites* → *Waagenoceras* → *Cyclolobus*; *Properrinites* → *Metaperrinites* → *Perrimetanites*, etc.

Although classic reconstructions were mainly based on the trend toward increased sutural complexity, the same approach may be used in situations of gradual simplification in the framework of phylogenetic regression. Examples of such evolution may be traced in the lineages *Vanartinskia* → *Synartinskia* → *Prosicanites* → *Sicanites*, *Pamiritella* → *Palermites* → *Sizilites* → *Doryceras*, and others.

More complex situations occur when the onto-phylogenetic trends change during the early and intermediate ontogenetic stages. Forms emerging as a result of these processes often give rise to progressive and

regressive lineages, which in turn branch off to form a complex system of higher taxa, which include a considerable proportion of the Permian ammonoid diversity. However, the problem of phylogenetic connection of the apical taxa in these lineages with their ancestral forms demands a somewhat different approach toward phylogenetic reconstructions than the approach used in the case of orthogenetic development, because the evolutionary trend can cease or change, thus preventing morphological continuation between successive forms. In these situations, there are no transitional forms in the accepted sense of the term that represent intermediate evolutionary stages. Mosaic [heterobathmic in the terminology of Takhtajan (1970)] forms, combining conservative and rapidly evolving structures, quickly act as connective links. Structural mosaics appear as a result of heterochronies, the ontogenetic acceleration in the development of some organs and retardation in others. Mosaics may be displayed in the development differently directed in different elements of the suture, e.g., in the case of two phylogenetic trends existing within the family Popanoceratidae: *Propanoceras* → *Popanoceras* and *Propopanoceras* → *Pamiropopanoceras*. In other cases, mosaic development may occur in the combination of sutural character, shell shape, and ornamentation. These groups of characters were apparently controlled by different genetic and ecological factors, because in many representatives of the families Adrianitidae, Cyclolobidae, Popanoceratidae, etc., the sutural characters evolved rapidly, with very little change in either shell shape or ornamentation. The deviation in the suture outline giving rise to a new diverse ammonoid group may go well together (at least during early stages) with the retention of the ancestral shell form, which occurs in *Juresanites* → *Metalegoceras* → *Pseudoschstoceras* and *Almites* → *Suakites*.

Mosaic forms combining a conservative shell morphology (ornamentation) and deviated sutural morphology are used as connective links in the reconstruction of the phylogenetic relationships between the subfamilies of Medicottidae: Uddenitinae and Medicottinae, Uddenitinae and Propinacoceratinae.

The opposite situation, when a conservative suture is combined with deviated shell morphology, occurs far less frequently, although it is observed in the families Agathiceratidae (*Agathiceras* → *Gaetanoceras*), Adrianitidae (*Crimites* → *Metacrimites*), Paragastrioceratidae (*Svetlanoceras* → *Synuraloceras* and *Svetlanoceras* → *Bulunites*), etc.

Modes of phylogenetic transformations. The most widespread and, formerly, the only accepted mode of phylogenetic transformation is related to orthogenetic evolution and operates through a progressive increase in structural complexity, of the suture in particular, by anabolies superimposed over the late stages of the ancestral ontogeny. Divergences from the ancestral ontogeny that give rise to side branches result from

ontogenetic events such as archallaxes or deviations. As mentioned above, such events produced many progressively evolving evolutionary lineages of Permian ammonoids (e.g., the emergence of the denticulation of the ventral and lateral lobes in *Eothalassoceras* gave rise to the new family Thalassoceratidae; the tripartite subdivision of the outer lateral lobe in *Aktubites* initiated the development of the diverse and highly advanced superfamily Shumarditaceae, etc.). At the same time, it seems useful to delineate different phylogenetically deviated situations leading to different evolutionary scenarios.

Progressive deviated lineages. Iteration. The derived lineage, or a sequence of derived lineages, that branches off the continuing ancestral lineage may develop either idioadaptively (without an increase in the level of organization) or arogenetically (with an increase in the level of organization). The evolution of the families Paragastrioceratidae → Pseudogastrioceratidae provides an example of the first mode; the genera in the two families differ in the presence or absence of a ventral sinus. Examples of the second mode include the evolution of the lineage *Crimites* → *Pamirioceras* and many other lineages.

Radiation. The ancestral group gives rise to two or more divergent lineages, as in *Subkargalites* → *Kargalites* and *Marathonites*; *Eoasianites* → *Svetlanoceras* and *Juresanites*; and *Properrinites* → *Metapererrinites*, *Shyndoceras*, and *Parapererrinites*.

Regressive deviated lineages. Trends toward simplification occur in many lineages of Permian ammonoids. Some workers (Glenister and Furnish, 1988a) consider these changes anomalous. They were often described as degeneration and neoteny (Ruzhencev, 1949a; Leonova, 1988a, etc.). Such an interpretation is not always sufficient or adequate. The modes that are sufficiently well documented are more likely to be interpreted as follows.

Reduction. The decrease in the level of the organization of the ancestral group occurs through the simplification of morphological structures or some of their elements, for instance, the smoothening of additional lobes or ornamentation as in *Propinacoceras* → *Difuntites*, *Neopronorites skvorzovi* → *N. permicus* → *N. darvasicus* → *N. asianus*. In some cases, simplified structures approach those of the ontogenetic stages in the immediate ancestors (paedomorphosis) or those of the definitive stages in more distant ancestors [retroconvergency, Krassilov (1995)], for instance, in *Crimites* → *Veruzhites* → *Pseudoemilites*.

Paedomorphosis. Paedomorphic structures, often occurring in Permian ammonoids and sometimes inaccurately named neothenic, are the products of two processes, abbreviation and negative anaboly, which are similarly directed but have different rates and phylogenetic results. *Abbreviation* means the abbreviating of the latest ontogenetic stages at various levels of ontogeny and leads to a retention of the juvenile state of the

character (paedomorphic mode), thus resulting either in a blind lineage or in a new series of deviated forms. This mode occurs in the phylogeny of the subfamilies Sicanitinae and Artioceratinae: *Artioceras* → *Artioceratooides*, etc. In contrast, *negative anaboly* represents a gradual trimming of the terminal stages of ontogeny, which in the case of orthogenetic evolution, represent positive anaboly. Thus, this process represents regressive orthogenesis (devolution) gradually approaching the ancestral state (family Somoholitidae: *Andrianovia* → *Neoshumardites*). This process can also give rise to side branches developing either without changes in the level of organization or even with some increase. These situations are infrequent, but they do occur in the phylogeny of the genus *Almites* → *Pseudovidrioceras* and *Almites* → *Suakites* → *Eohyattoceras*.

Parallel evolution. Parallel evolution in one of the three above-mentioned major groups of characters (sutural structure, shell form, and ornamentation) accompanies phylogenetic changes through several of the above modes. The parallel development of orthogenetic lineages is observed in its general form as a trend toward increased complexity but can also have a more specific character of uniform subdivision and the analogous development of additional lobes, as in metalegoceratid of the subfamilies Metalegoceratinae, Eothinitinae, and Pericycloceratinae. Apart from the uniform development of sutures, parallel evolution shows itself in shell morphology and ornamentation. One of the best examples of such parallel development are the genera *Atsabites* and *Anatsabites* in the family Anatsabidae and *Eothinites* and *Epiglyphioceras* in the subfamily Eothinitinae. Parallel evolution occurs in Permian ammonoids inhabiting isolated or semiisolated basins, in which similar phylogenetic trends are induced by similar conditions of selection.

A more closely paralleled development may occur in derived lineages branching off the long-persistent conservative taxa through sequential iterations, e.g., in *Crimites* → *Nevadoceras*, *Crimites* → *Istycoceras*. This type of parallel development is typical of shallow-water taxa branching off a conservative deep-water lineage during the regressive phase of cyclic sea level fluctuations. These iterations can occur repeatedly following the recurring regressive-transgressive cycles (Zhou *et al.*, 1999); because of the similarity in genetic and environmental conditions, each subsequent iteration generally imitates the previous. Apparently, there is a possibility of the unification of such sequential iterations in a single species, which, in this case, will have a polychronic nature.

Of special interest is the parallel development of paedomorphic changes, e.g., in *Propinacoceras* → *Difuntites* and *Almites* → *Pseudovidrioceras*, it may be interpreted as an indication of the effect causing regressive trends in different phylogenetic lineages. It is possible that the reduction of ancestral ontogeny,

when the juvenile states of characters are fixed at a definitive stage, occurs under stress and is most frequent during ecological crises. Regression caused by a sequence of negative anaboly is most likely due to the gradual despecialization of species that may result either from the diversification of feeding habits or from entering an ecosystem with different and less intense trophic relationships. However, these suggestions need confirmation with reference to more extensive material.

Structure of higher taxa. As mentioned above, the phylogeny of higher taxa of Permian ammonoids is reconstructed based on the gradual change of characters in orthogenetic lineages and, in the case of deviated forms, through connective links with a mosaic structure, i.e., a combination of archaic and derived characters. The taxa of ordinal rank are distinguished from each other by those characters that appear during early stages of their ontogeny, e.g., the genesis and development of primary lobes and the position of the siphuncle. They change through archallaxes or early deviations. There is no known higher ammonoid taxa that evolved as a result of orthogenetic development, no matter how long this development may continue, especially as the orthogenetic series are usually restricted in time by two or three geological stages. The inadaptive nature of the distortions of ontogeny occurring under normal conditions suggests that the successful deviations giving rise to the new taxa of higher rank are related to an anomalous selective environment, in which they may give rise to divergent or orthogenetic lineages.

The structure of a higher taxon is determined by the phylogenetic modes characteristic of this taxon and their combinations. In typical cases, the structure of a monophyletic family (or subfamily) is defined by the main lineage, i.e., by an orthogenetic sequence of three; four; or, more rarely, five distinct stages identified as taxa of generic rank. During the time of its existence, the main lineage produces a few side branches [these may be shallow-water series branching off a sequence of deep-water taxa (Zhou *et al.*, 1999)], which evolve without increasing their level of organization. The concluding stages often show regressive trends leading to the appearance of paedomorphs.

This kind of typical structure can be observed in the families Pronoritidae, Thalassoceratidae, Marathonitidae, etc. Variations of this structure are mainly related to the number of orthogenetic stages and to the extent of divergence between the main lineage and its side branches. After a short period of deviated development, side branches may produce short orthogenetic series parallel to the stem series or repeating it regressively in the reverse order (e.g., in the subfamilies Aristoceratinae and Marathonitinae).

A more complex version of the family structure appears as a result of the radiation of the main cluster forming a bunch of radiating lineages, which show different evolutionary rates and terminate their develop-

ment at different stratigraphic levels (the families Cyclolobidae and Popanoceratidae and the subfamily Paraperrinitinae). Some lineages may be orthogenetic or branching; at some stages, their development is almost parallel.

The parallel development of successive iterations produces a lineage of morphologically similar taxa that might be united in a single family, which will have a polychronic structure (e.g., subfamilies Eothinitinae and Pericycloceratinae).

The role of a family in the ammonoid evolution depends on its complexity: families with a radiate structure and repeated iterations are more likely to be founders of new suprageneric groups than families with a relatively simple orthogenetic structure. The most phylogenetically productive arogenetic families show the most complex combination of phylogenetic modes, e.g., Medicottiidae, Cyclolobidae, Marathonitidae, and Adrianitidae.

The studies of the structure of the superfamily Medicottiaceae based on mathematical techniques (Bogoslovskaya *et al.*, 1996) have confirmed previous expert opinions. The analysis of the diversity dynamics and changes in the index of the geographic range and that of the duration of genera supported the subdivision of prolecanitids into two suborders, Prolecanitina and Medicottiina. However, it has become clear that the accuracy of the quantitative analysis should always be verified against the phylogenetic analysis of the group under study.

In the Permian, three ammonoid orders appeared at the Devonian–Carboniferous boundary: Tornoceratida, Prolecanitida, and Goniatitida. The fourth order, Ceratitida, appeared at the Lower–Middle Permian boundary.

Below, is a new system of Permian ammonoids, including the brief diagnoses of all groups from the ordinal to subfamily levels, with the lists of genera and their species composition and stratigraphic and geographic ranges. The classification of Ceratitida is given according to Shevyrev (1986) with small additions, mainly based on new data published by Chinese paleontologists. Phylogenetic reconstructions are made for most families under consideration.

SYSTEMATIC PALEONTOLOGY

Order Prolecanitida Miller et Furnish, 1954

Prolecanitida: Bogoslovskaya *et al.*, 1990, p. 74

General remarks. Permian Prolecanitida were completely unique in their evolutionary rate and the variety of phylogenetic changes they exhibit, although they included fewer taxa than Goniatitida and their populations were not as great (Ruzhencev and Bogoslovskaya, 1978, p. 37). Recent studies of their shell morphology and sutures that were carried out by mathematical methods (Saunders and Work, 1997; Saunders *et al.*, 1999) have shown the distinctness of this group from all other ammonoids and the high rates of an

increase in the suture complexity. Previous researchers have reached similar conclusions based on the method of expert opinion.

Views on the prolecanitid systematics have considerably changed over the time the group was under study. At present, most researchers regard this group as an order. In contrast, Zakharov (1983, 1984) treats this group as two separate orders, Prolecanitida and Medicottiida, based on the suture ontogeny of three medicottiid species: *Artinskia artiensis* (Grunewaldt), *Medlicottia intermedia* Ruzhencev (for these two species, the ontogeny of the first three sutures was published for the first time), and *Artioceras rhipaeum* (Ruzhencev) (Fig. 2) (for which the three first sutures had been previously published (Ruzhencev, 1949a, 1956). Zakharov concluded that the medicottiid suture developed following the VLU-pattern: U (one-lobed prosuture)—VUD (three-lobed primary suture)—VLU : ID (five lobed third suture) (Zakharov, 1984, p. 32). However, this conclusion remains unjustified, since the inner part of the primary suture was not studied and only the outer part of the primary sutures of the studied medicottiids were figured (Zakharov, 1984, text-fig. 1). He studied the entire outline of the primary suture (VU : D) only in *Neopronorites skvorzovi*, a species belonging to a different family, Pronoritidae. The extension of these data to medicottiids is disputable.

Leonova and Voronov (1989) showed that the primary suture of the typical medicottiid *Synartinskia* is not three-lobed VUD but four-lobed VU : ID. This suggests that medicottiids developed a suture following the $U \rightarrow VU : ID \rightarrow VUU^1 : ID \rightarrow (V_2V_1V_2)UU^1 : ID$ pattern (Fig. 3). Zakharov's conclusion that the outer lateral lobe L emerges in the primary suture is based on an unclear interpretation of a small incision on the top of the external saddle in a single specimen of *Medlicottia intermedia* (Fig. 4); this incision is absent in the second half of the same suture. Zakharov (1984, p. 31) stated that "*Medlicottia intermedia* apparently shows an emerging lateral lobe in the primary suture; it is suggested that this element transforms into a well-defined lobe within the third suture." It seems more likely that this incision resulted from mechanical damage to the edge of the suture of the specimen in question. Two other typical medicottiids, *Artioceras rhipaeum* and *Artinskia artiensis*, also studied by Zakharov (1984, text-fig. 1), have no incisions in the primary sutures that can be interpreted as emerging L-lobes.

One of the major questions is which pattern does the suture development follow in prolecanitids: VLU : ID or VUU¹ : ID. To interpret the lobe located between the ventral lobe and the umbilical saddle, Ruzhencev (1960, p. 183) used the concept of ontogenetic acceleration accompanied by the reduction of some intermediate stages. This explanation is credible, but it is not positively supported by the material. The results of the onto-phylogenetic reconstructions of the Sageceratidae used by Ruzhencev can hardly be used in this argu-

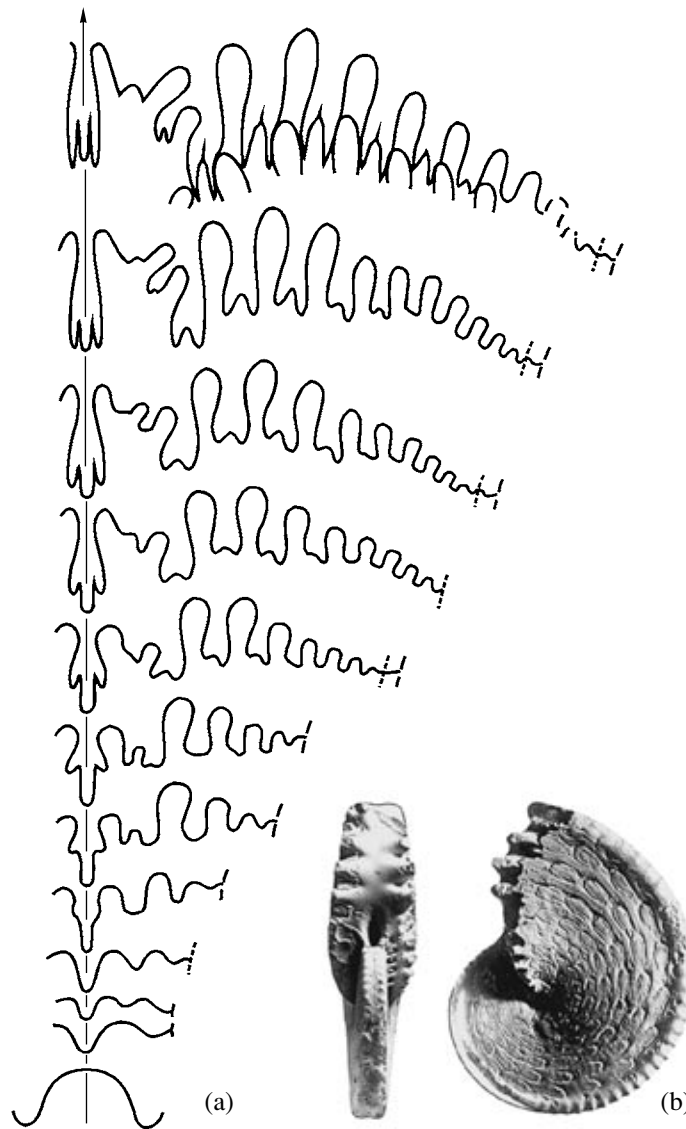


Fig. 2. *Artioceras rhipaeum* (Ruzhencev): (a) sutural ontogeny; (b) shell shape; Artinskian (Ruzhencev, 1949a).

ment, because subsequent workers excluded this family from the Prolecanitida and assigned it to Ceratitida (Popov, 1961; Tozer, 1971, Shevyrev, 1986, etc.). According to the latest classification of Shevyrev (Bogoslovskaya *et al.*, 1990), Sageceratina received the rank of a suborder in the order Ceratitida. The main evidence to support the hypothesis that the fifth lobe is U^1 is the ontogeny of *Merocanites asiaticus* (Fig. 5a) studied by Karpinsky (1896). Spinosa *et al.* (1975) published data indicating the presence of lobe L in Prolecanitida (Fig. 5b). It is noteworthy that all workers analyzing ontogenetic patterns in Prolecanitida used the same restricted set of data for the sutural ontogeny in this group but interpreted it differently. Unfortunately, at present, it is not possible to conclude positively which lobe, U^1 or L, emerges in the early ontogeny of Medlicottiina. It is necessary to obtain as much data as possi-

ble on the early ontogeny in this group, especially that of its earliest representatives. However, this is not yet possible because of lack of the material usable for such studies. In this situation, the use of the term *umbilical lobes* rather than *outer lateral lobes* is largely a matter of choice.

D i a g n o s i s. Shell from platyconic to discoconic, from evolute to involute. Whorl surface usually smooth or weakly ornamented. Siphuncle always ventral. Sutural ontogeny following VU pattern. Prosuture latisellate. Primary suture in ancient representatives three-lobed; VU:D; in geochronologically younger representatives, four-lobed; VU:ID (Figs. 3, 5). Ventral lobe changed in phylogeny from simple to wide tripartite (Prolecanitina) or narrow trifid (Medlicottiina). Suture complexity increased due to increase in umbilical lobe number: $UU^1 \rightarrow UU^1U^2U^3 U^4 \rightarrow$

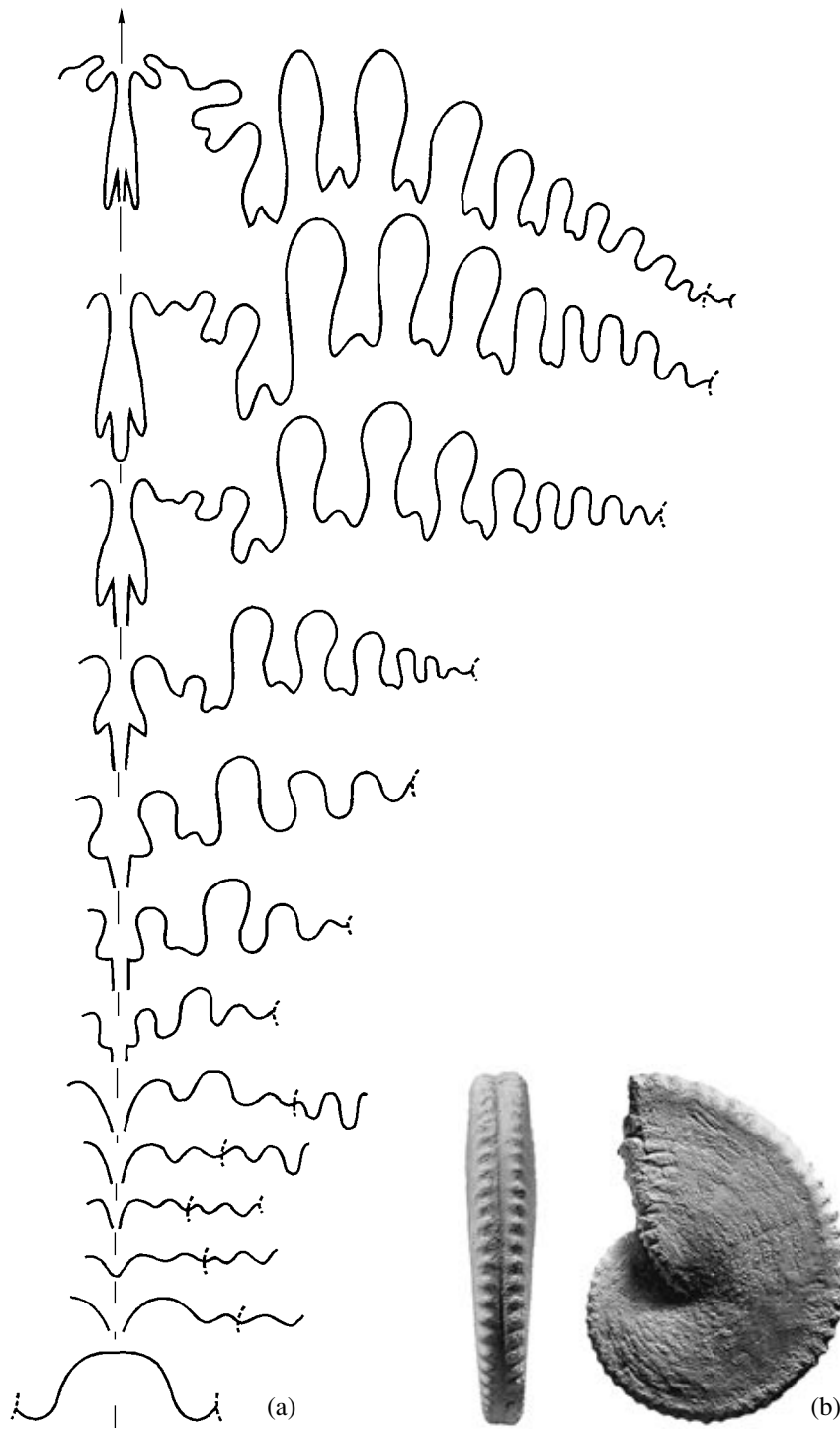


Fig. 3. *Synartinskia principalis* Ruzhencev, Sakmarian: (a) sutural ontogeny (Leonova and Voronov, 1989); (b) shell shape (Ruzhencev, 1952).

$UU^1U^2U^3U^4U^n \dots U^m : U^{m \pm 1} \dots U^{n \pm 1}$ (Ruzhencev, 1960), due to serration at the base and due to the formation of a bifid base and due to the development of several adventive lobes on the top of the external saddle (Medlicottiaceae). The dorsal lobe is deep, entire, or bifid. The total number of lobes varies from 8 to 50.

Comparison. This order differs from other orders in the mode of sutural development.

Composition. Two suborders.

Occurrence. Lower Carboniferous–Lower Triassic.

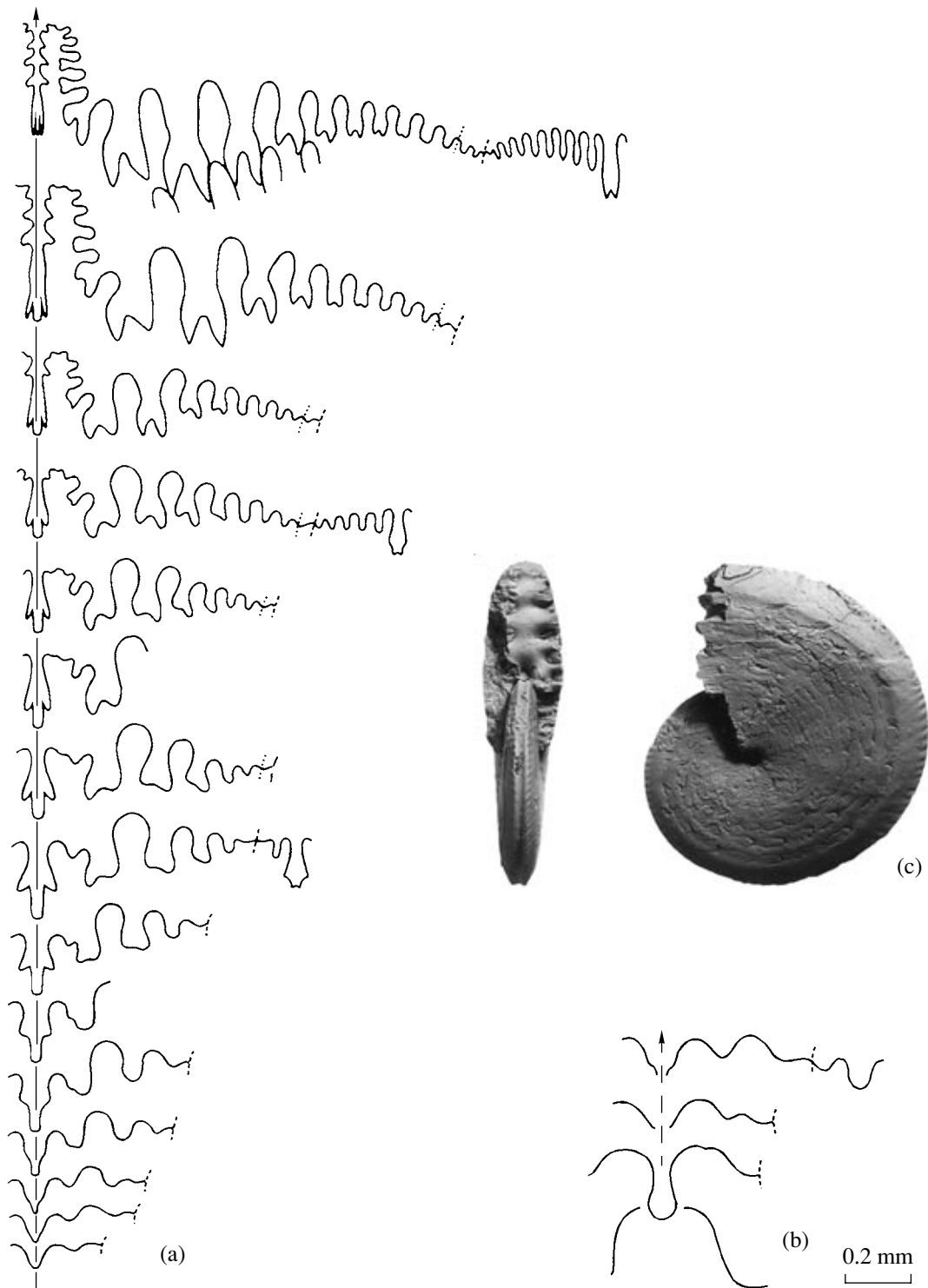


Fig. 4. Genus *Medlicottia*: (a) and (b) sutural ontogeny: (a) *M. orbignyana* (Vern.); Artinskian (Ruzhencev, 1949a); (b) *M. intermedia* Ruzhencev; Artinskian (Zakharov, 1984); and (c) shell of *M. basarensis* Toumanskaya; Kungurian (Leonova, 1985).

Suborder Prolecanitina Miller et Furnish, 1954

Prolecanitina: Bogoslovskaya et al., 1990, p. 75.

Diagnosis. Shell discoconic, from evolute to moderately evolute, and smooth. Initial sutural formula

VUU¹ : ID (Fig. 5). During phylogeny, ventral lobe transformed from simple and narrow to wide and tripartite. Dorsal lobe transformed from simple to bifid, umbilical lobes progressively increasing in number. In

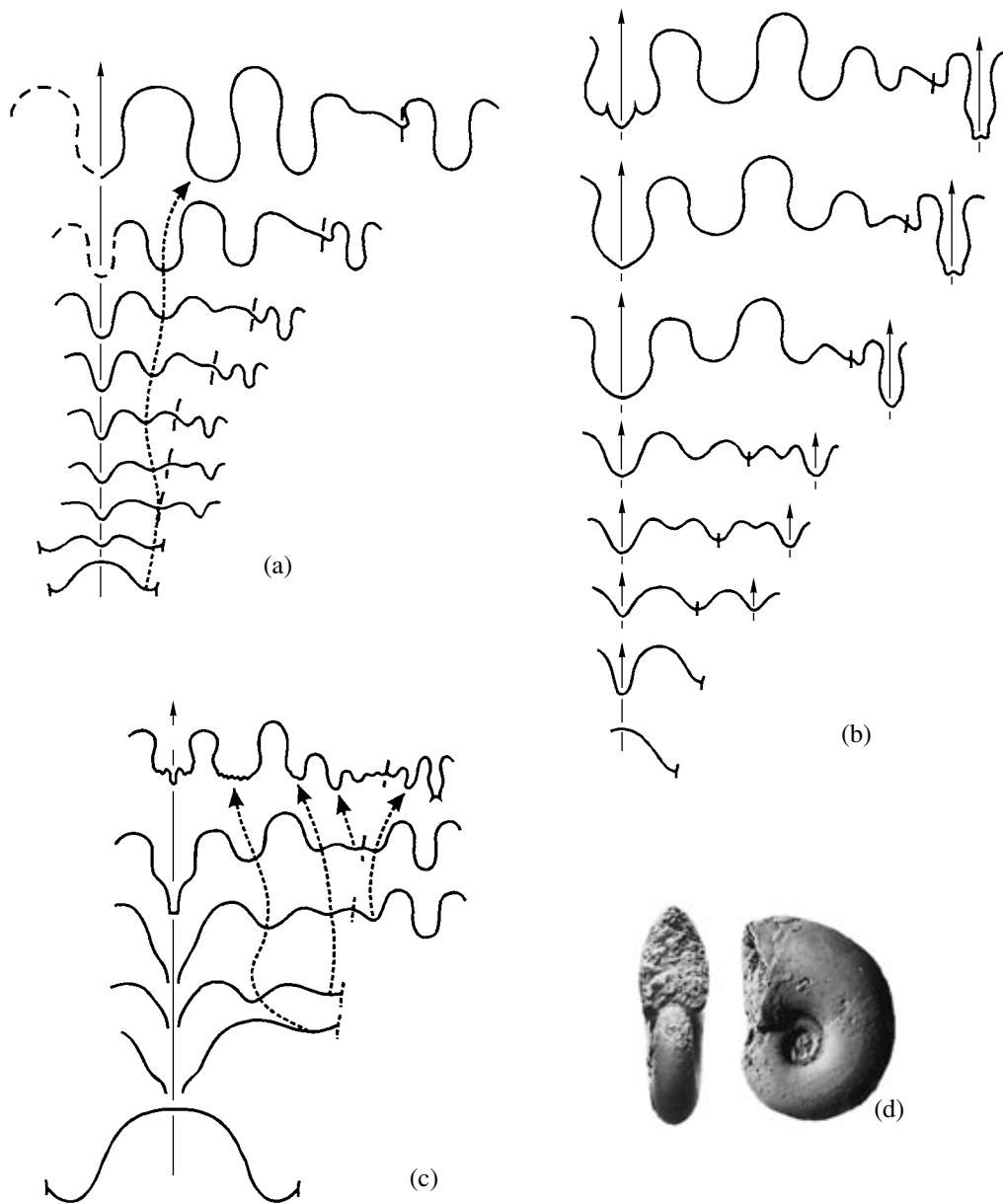


Fig. 5. Superfamily Prolecanitaceae: (a–c) sutural ontogeny: (a) *Merocanites asiaticus* (Karp.); Viséan (Karpinsky, 1896); (b) *Epicanites loeblichii*, Mississippian (Spinosa *et al.*, 1975); (c) *Boesites primoris* Ruzh.; Gzhelian (Ruzhencev, 1950); and (d) shell of *Draelites pamiricus* Toumanskaya; Kungurian (Leonova and Dmitriev, 1989).

later representatives, bases of external lobes are serrated. Suture composed of 8–22 lobes.

Comparison. This suborder differs from Medlicottiina in the presence of the simple first umbilical lobe.

Composition. One superfamily.

Occurrence. Lower Carboniferous–Middle Permian (Tournaisian–Wordian).

Superfamily Prolecanitaceae Hyatt, 1884

Prolecanitaceae: Ruzhencev, 1960, p. 184.

Diagnosis. The same as for the suborder.

Composition. Two families: Prolecanitidae and Draelitidae.

Occurrence. Lower Carboniferous–Middle Permian.

Family Draelitidae Tchernov, 1907

Draelitidae: Ruzhencev, 1960, p. 185.

Diagnosis. Shell discoconic, moderately evolute, with moderately wide umbilicus, and smooth. Suture comprising 12–22 lobes. Ventral lobe tripartite; in phylogeny, all of its elements are widened. During

evolution, bases of ventral and umbilical lobes evolved with a "ceratite" appearance (Fig. 5).

Comparison. Differs from Prolecanitida in the presence of the wide tripartite ventral lobe and serrated bases of the outer lobes.

Composition. Four genera, two from the Permian.

Occurrence. Viséan–Wordian.

Genus *Boesites* Miller et Furnish, 1940

This genus includes ten species from the Middle Carboniferous (Moscovian) to the early Permian (Sakmarian); Western Europe, Urals, Kazakhstan, southern China, North America, the Canadian Arctic. The type species, *Boesites texanus* Bose, 1917 occurs in the Upper Carboniferous in Texas. The following species are recorded from the Permian.

- (1) *B. sp.* Ruzhencev, 1951 from the Asselian of the Urals;
- (2) *B. aktubensis* Bogoslovskaya et A. Popov, 1986 from the lower Asselian of the Urals;
- (3) *B. intercalaris* Ruzhencev, 1978 from the Upper Asselian and Sakmarian of the Pamirs (Tashkazyk Formation);
- (4) *B. serotinus* Ruzhencev, 1951 from the Asselian and Sakmarian of the Urals;
- (5) *B. eurinus* Leonova, 1992 from the Sakmarian of the Pamirs (Khoridzh Formation);
- (6) *B. kingi* Plummer et Scott, 1937 from the Sakmarian of the Texas (Wolfcamp Formation).

Genus *Daraelites* Gemmellaro, 1887

- (1) The type species *D. meeki* Gemmellaro, 1887 from the Wordian of Sicily (Sosio Beds) and Kurdistan (Qulqula Formation);
- (2) *D. elegans* (Tchernow, 1907) from the Artinskian of the Urals;
- (3) *D. submeeki* Haniel, 1915 from the Kungurian (Bitauni Beds) of Timor;
- (4) *D. leonardensis* Miller et Furnish, 1940 from the Kungurian (middle portion of the Leonard Formation) of Texas;
- (5) *D. vozginensis* Leonova, 1992 from the Artinskian (Yakhtashian) of the Pamirs;
- (6) *D. pamiricus* Toumanskaya, 1949 from the Kungurian (Bolorian) of the Pamirs.

Phylogeny. The lineage *Boesites* → *Daraelites* with slight modifications persisted over several geological ages and retained a flattened, moderately evolute shell. The suture complexity very slowly increased, mainly through the broadening of the ventral lobe and an increase in the number of umbilical lobes, which became slightly serrated at the bottom. This slow evolution generated many intermediate forms with characters intermediate between those of both genera, e.g., *Boesites kingi*, for which generic assignment is quite difficult (Moyle, 1963). Apparently, Permian

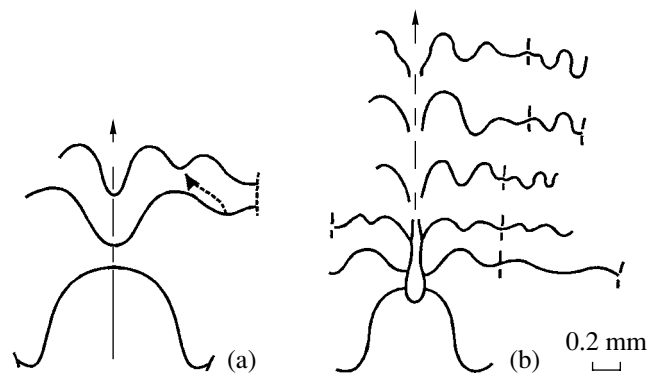


Fig. 6. Superfamily Pronoritaceae. Early sutural ontogeny of *Neopronorites*: (a) *N. permicus* (Tchern.) (Ruzhencev, 1949a); (b) *N. skvorzovi* (Tchern.), (Zakharov, 1984); both Artinskian.

daraelitids represented a relict stage in the evolution of a once diverse and successful group of Carboniferous prolecanitins. Most researchers believe that the first Ceratitida evolved from Prolecanitina in the mid-Permian (Ruzhencev, 1960, 1962; Shevyrev, 1968, 1986; Spinosa *et al.*, 1975; etc.).

Suborder *Medlicottiina* Yu. Zakharov, 1983

Medlicottiina: Bogoslovskaya *et al.*, 1990, p. 75.

Diagnosis. Shell platyconic, from moderately evolute to completely involute, smooth, or with thin transverse ornamentation. The initial sutural formula is $(V_2V_1V_2)(U_1U_1)U^1U^2U^3U^4 : ID$ (Ruzhencev, 1960). Ventral lobe narrow, deep, and trifid. First umbilical lobe bipartite (sometimes only in ontogeny). Dorsal lobe simple or bifid. The main phylogenetic trend was the development of adventive lobes at the top of the external saddle and the multiplication of umbilical lobes and the development of serrations at their bases. The total number of lobes is from 14 to 50.

Comparison. This suborder differs from Prolecanitina in having a bipartite first umbilical lobe and in including a number of groups that evolved a complex system of adventive lobes and saddles at the top of the external saddle.

Composition. Two superfamilies.

Occurrence. Lower Carboniferous–Lower Triassic.

Superfamily Pronoritaceae Frech, 1901

Pronoritaceae: Bogoslovskaya *et al.*, 1999, p. 93.

Diagnosis. Shell platyconic, from moderately evolute to involute, smooth. Ventral lobe moderately wide, trifid. Suture evolved by an increase in the number of umbilical lobes and appearance (or disappearance) of serrations at the base of lobes. The initial sutural formula is $(V_2V_1V_2)(U_1U_1)U^1U^2U^3U^4 : ID$ (Ruzhencev, 1960). First umbilical lobe wide and bipartite; external saddle simple (Fig. 6).

C o m p a r i s o n. In contrast to the Medlicottiaceae, the superfamily under consideration never developed adventive elements either on the sides or at the top of the external saddle.

C o m p o s i t i o n. Two families.

O c c u r r e n c e. Lower Carboniferous–Middle Permian.

Family Pronoritidae Frech, 1901

Pronoritidae: Bogoslovskaya *et al.*, 1999, p. 93.

D i a g n o s i s. Shell platyconic, from moderately involute to involute. Venter moderately wide and flattened. Flanks wide and flattened. Umbilicus from narrow to closed. Shell smooth. Ventral lobe tripartite, deep, from wide to moderately wide. First umbilical lobe subdivided into two broad digits almost equal in depth and size. Suture comprising 14–30 lobes.

C o m p a r i s o n. This family differs from Shikhanitidae in having a platyconic shell and completely developed ventral lobe.

C o m p o s i t i o n. Twelve genera, of which four are known from the Permian.

O c c u r r e n c e. Viséan–Wordian.

Genus Metapronorites Librovitch, 1938

This genus includes nine species from the Middle Carboniferous–Early Permian. The following species are recorded from the Permian:

(1) The type species *M. timorensis* (Haniel, 1915) is recorded from the Sakmarian (Somohole Beds) of Timor and Asselian–Sakmarian of the Pamirs (Tashkazyk Formation);

(2) *M. angustus* Andrianov, 1985;

(3) *M. vladimiri* Andrianov, 1985; and

(4) *M. certus* Andrianov, 1985, all three above species are from the Asselian–Sakmarian of northeastern Russia;

M. sp. nov. Nassichuk, 1995 from the Asselian (Hare Fiord Formation) of the Canadian Arctic.

Genus Neopronorites Ruzhencev, 1936

This genus includes 15 species from the Upper Carboniferous–Lower Permian. Twelve species are recorded from the Lower Permian.

(1) The type species *N. permicus* (Tchernow, 1907) is recorded from the Artinskian and Kungurian of the Urals and northeastern Russia;

(2) *N. rotundus* (Maximova, 1938) from the Asselian of the Urals;

(3) *N. schucherti* Ruzhencev, 1938 from the Upper Asselian of the Urals;

(4) *N. shinini* Ruzhencev, 1938 from the Upper Sakmarian of the Urals;

(5) *N. tenuis* (Karpinsky, 1889) from the Asselian and Sakmarian of the Urals;

(6) *N. magnus* Maximova, 1938 from the Sakmarian of the Urals;

(7) *N. bakeri* Miller et Furnish, 1940 from the Sakmarian of Texas (Wolfcamp Formation);

(8) *N. praepermicus?* (Karpinsky, 1874) from the Upper Sakmarian of the Urals;

(9) *N. milleri* Ruzhencev, 1938 from the Upper Sakmarian and Artinskian of the Urals and Sakmarian of northeastern Russia;

(10) *N. skvorzovi* (Tchernow, 1907) from the Artinskian of the Urals and Kungurian of northeastern Russia;

(11) *N. darvasicus* Leonova, 1988 from the Artinskian (Yakhtashian) of the Pamir;

(12) *N. asianus* Leonova, 1988 from the Kungurian (Bolorian) of the Pamirs; and

(13) *N. sp.* from the Asselian (Hare Fiord Formation) of the Canadian Arctic (Nassichuk, 1995) and from the Artinskian–Bolorian (Longyin Formation) of southern China (Zhou, 1979).

Genus Sakmarites Ruzhencev, 1936

(1) Type species *S. vulgaris* (Karpinsky, 1889) from the Artinskian of the Urals;

(2) *S. asaphus* (Ruzhencev, 1938) from the Upper Asselian of the Urals;

(3) *S. ajdaralense* Ruzhencev, 1951 from the Upper Sakmarian of the Urals;

(4) *S. postcarbonarius* (Karpinsky, 1874) from the Upper Sakmarian of the Urals;

(5) *S. inflatus* Ruzhencev, 1951 from the Upper Sakmarian of the Urals; and

(6) *S. hanieli* Ruzhencev, 1949 from the Kungurian (Bitauuni Beds) of Timor.

Genus Parapronorites Gemmellaro, 1887

(1) Type species *P. konincki* Gemmellaro, 1887 from the Wordian of Sicily (Sosio Beds), Oman (Hamrat Duru Formation);

(2) *P. subitus* Leonova from the Sakmarian (Khoridzh Formation) of the Pamirs;

(3) *P. timorensis* Haniel, 1915 from the Kungurian (Bitauuni Beds) of Timor and, probably, Wordian of Tibet (Jiala Formation); and

(4) *P. rectus* Leonova, 1989 from the Kungurian (Bolorian) of the Pamirs.

P h y l o g e n y. Virtually all workers consider this family to be ancestral to Medlicottiaceae (Ruzhencev, 1949a; Glenister and Furnish, 1980; Leonova and Dmitriev, 1989; etc.). The main cluster in its evolution is the parallel development of both digits of the first umbilical lobe. During evolution, both digits first became deeper and strongly serrated at the base (*Metapronorites*), and, subsequently, in different branches of the family, this portion of the suture was transformed differently. In some pronoritids (genus *Parapronorites*), evolution continued in the same direction, toward the increased serration of the bases of the digits of the first umbilical

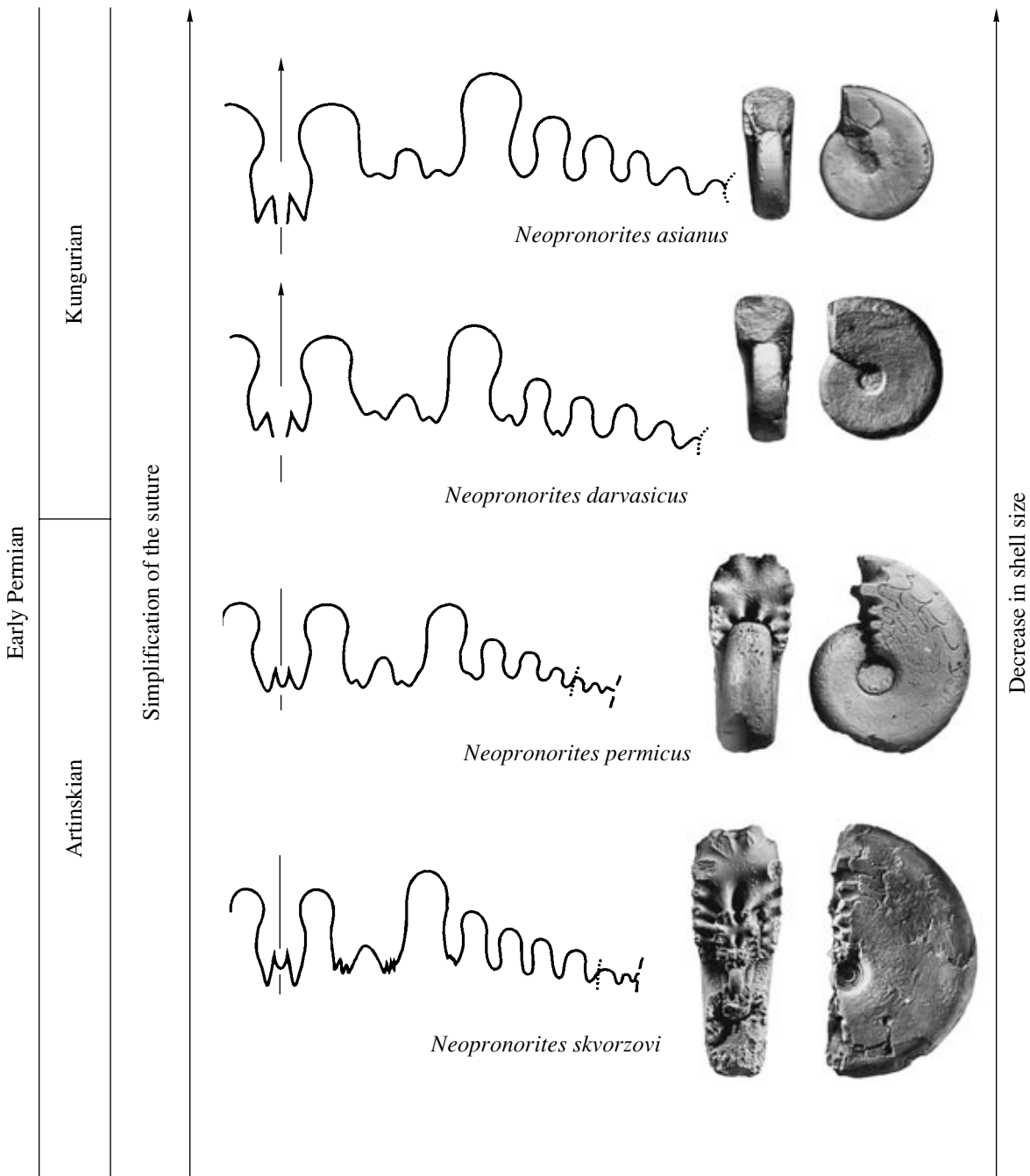


Fig. 7. Regressive lineage of *Neopronorites* species (Leonova, 1988a).

lobe and of other umbilical lobes, which also multiplied (orthogenetic lineage).

Other members of the family (*Neopronorites*, *Sakmarites*), beginning from the Artinskian, developed a trend toward increased shallowness of the first umbilical lobe and a decrease in the serration of the bases of its digits, i.e., showed signs of regression. This process was described in detail (Leonova, 1988) based on the genus *Neopronorites* (Fig. 7). The genus *Neopronorites* appeared in the middle of the Late Carboniferous and

progressively evolved and flourished in the Sakmarian. Then, beginning from the Artinskian, its evolution slowed down: the number of species considerably decreased, and a few Late Artinskian taxa showed signs of morphological regression. The first members of the phylogenetic lineage *N. milleri* → *N. skvorzovi* → *N. permicus* recorded from the Sakmarian and Lower Artinskian of the Urals showed a high level of morphological complexity. The second species, widely distributed in the middle of the Artinskian, became more

primitive compared to the first: the shell became more depressed, and the suture began to simplify. In the second half of the Late Artinskian, the third member of this group, *N. permicus*, appeared, which had the most simplified morphology (Ruzhencev, 1949a). According to Bogoslovskaya (1962), there is a considerable difference between the representatives of this species from the Central and Southern Urals; therefore, *N. permicus* from the Southern Urals should be regarded as a separate species and the fourth and most primitive member of the lineage of the Uralian *Neopronorites*. This species has a small shell; an angular outline of relatively wide whorls; a very primitive suture with a short, weakly differentiated first external umbilical lobe; and a smaller total number of external lobes. Having analyzed the evolution of the *Neopronorites* from the Urals, Ruzhencev (1949a, p. 90) concluded that the phylogeny in *N. permicus* showed signs of neoteny.

Leonova (1988) studied ammonoids from the Pamir and, for the first time, positively ascertained the presence of Tethyan species *Neopronorites*. Compared to *N. permicus*, the species from the Pamir represent a further stage in the regressive lineage under consideration. They have an even smaller shell: the diameter of the largest specimens (shell of six or seven whorls) does not exceed 20 mm. The suture of *N. darvasicus* and *N. asianus* is even more primitive than in *N. permicus* from the Southern Urals: a very short and wide first umbilical lobe with a very weakly serrated base and the ventral lobe with a long median digit (Fig. 7). Other *Neopronorites* species show a similar sutural outline at earlier ontogenetic stages (paedomorphosis). These dwarf species with a paedomorphic suture were apparently the last representatives of the evolutionary sequence of *Neopronorites*.

Family Shikhanitidae Ruzhencev, 1951

Sukhanitidae: Ruzhencev, 1951, p. 98.

D i a g n o s i s. Shell platyconic, involute, with very narrow and rounded venter and flattened flanks. Suture generally arched. Ventral lobe very short and weakly developed. First umbilical lobe wide, bipartite, without any adventive elements on external saddle, with the highest saddle being between second and third umbilical lobes.

C o m p a r i s o n. This family differs from Pronoritidae in the shell shape and in having an arched outline of the external portion of the suture.

C o m p o s i t i o n. One genus.

O c c u r r e n c e. Lower Permian (Asselian).

Genus *Shikhanites* Ruzhencev, 1938

This genus is based on a single species *Sh. singularis* Ruzhencev, 1938 from the Asselian of the Urals.

P h y l o g e n y. Judging from the similarity of their wide, bipartite first umbilical lobes and from the absence of any adventive elements on the external sad-

dle, this genus may be related to Pronoritidae. Generally, the suture is very primitive, which suggests that, after separation from Pronoritidae, this group evolved towards morphological regression. No positive conclusions can be drawn for lack of material.

Superfamily Medicottiaceae Karpinsky, 1889

Medicottiaceae: Bogoslovskaya *et al.*, 1999.

D i a g n o s i s. Shell platyconic, or discoconic, from moderately evolute to completely involute. Venter narrow, with nodes and keels, or flattened. Shell surface smooth or with thin transverse ornamentation. Ventral lobe trifid, deep, from moderately narrow to very narrow. During ontogeny, the first umbilical lobe was transformed into a complex system of adventive lobes and saddles following the formula $(U_1U_1) \rightarrow (U_1.U_1U_1.U_1) \rightarrow v^nsl^mU_1$ (Ruzhencev, 1960). Dorsal lobe deep and bifid. Suture has from 14 to 50 lobes.

C o m p a r i s o n. This superfamily differs from Pronoritaceae in the development of a system of adventive lobes and saddles at the top and on the sides of the external saddle.

C o m p o s i t i o n. Four families.

O c c u r r e n c e. Middle Carboniferous–Lower Triassic.

Family Medicottiidae Karpinsky, 1889

Medicottiidae: Ruzhencev, 1962, p. 352.

D i a g n o s i s. Shell platyconic, from moderately evolute to completely involute. Venter narrow, smooth, with two keels or with two rows of nodes. Umbilicus from moderately wide to closed. Ventral lobe narrow, deep, and trifid. System of adventive lobes and saddles developed at top and on sides of external saddle. Dorsal lobe bifid. Many of the umbilical lobes bifid at base. Suture has 20–50 lobes.

C o m p a r i s o n. This family differs from Episageceratidae in the normal development of the second umbilical lobe (its size is similar to or larger than the first umbilical lobe). Differs from Sundaitidae and Darvasiceratidae in the more complex outline of the external saddle.

C o m p o s i t i o n. Six subfamilies.

O c c u r r e n c e. Middle Carboniferous–Upper Permian.

G e n e r a l r e m a r k s. The development of adventive lobes and saddles on the external saddle is the main feature characterizing the entire group of Medicottiidae. Although this feature developed to a different extent in different phylogenetic lineages within the family (deviations occurred during different ontogenetic stages), the way in which it initially developed from the external branch of the first umbilical lobe is definitive for all Medicottiidae (main cluster principle). Medicottiids showed extremely diverse modes of phylogenetic transformations: orthogenetic, progres-

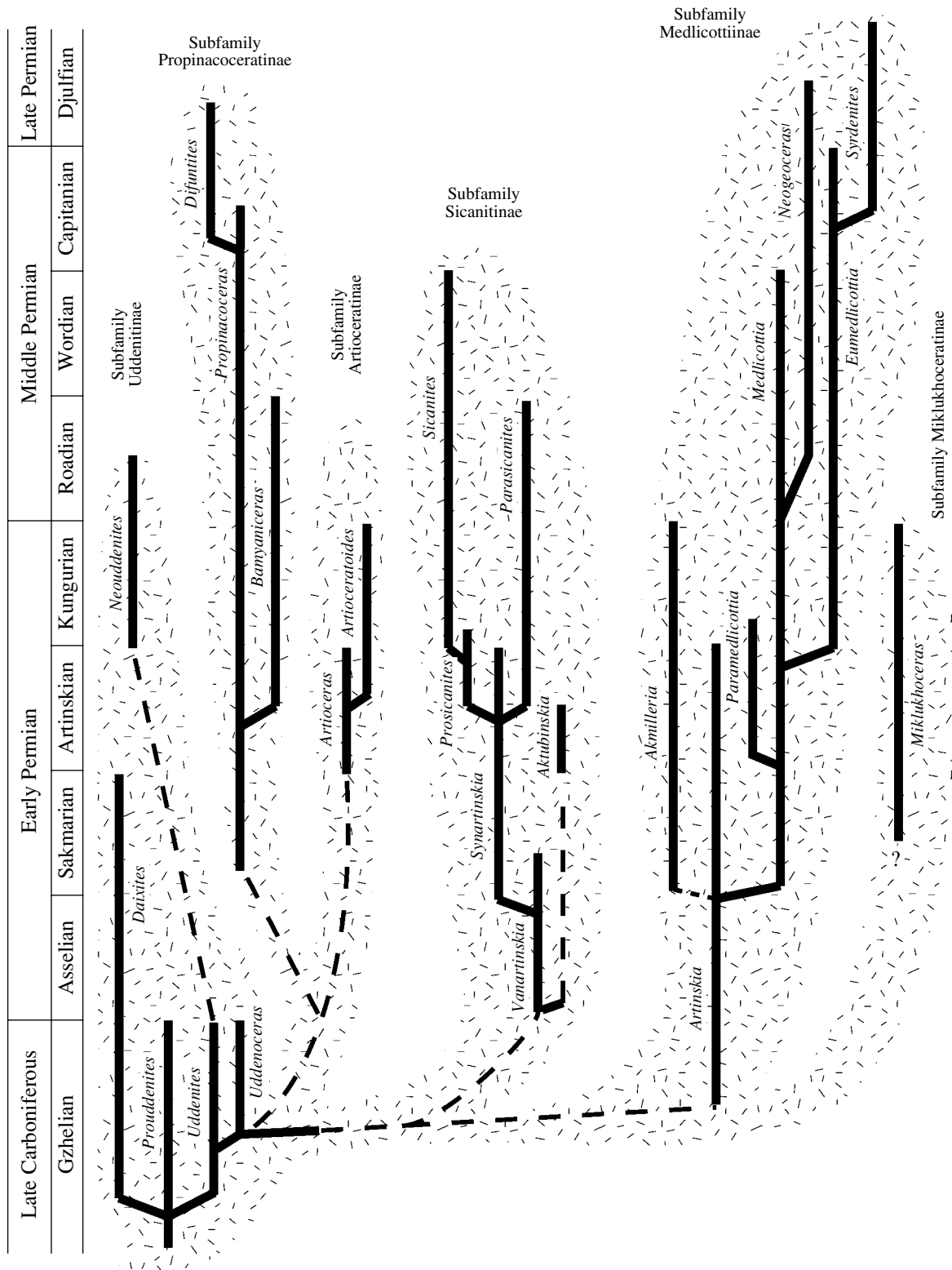


Fig. 8. Phylogenetic reconstruction of the family Medicottiidae (Leonova and Dmitriev, 1989; modified).

sive deviant, regressive deviant, parallel evolution, etc. (Fig. 8). The earliest primitive genera from the subfamily Uddenitinae were restricted to the Middle and Upper Carboniferous of North America, the Urals, and

Central Asia, whereas the geochronologically younger (advanced) medicottiids occur throughout the Permian beds but are particularly abundant in the deposits of the Permian seas of the Paleotethys Ocean.

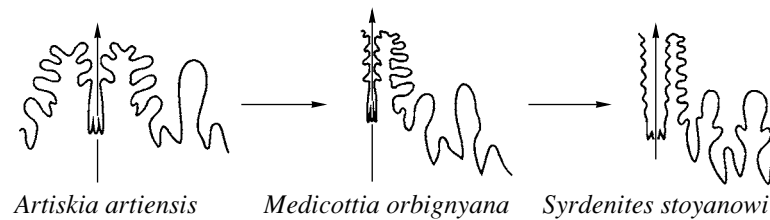


Fig. 9. Increased complexity of the external saddle in Medlicottiinae.

Subfamily Uddenitinae Miller et Furnish, 1940

Uddenitinae: Ruzhencev, 1962, p. 352.

Diagnosis. Shell platyconic, from moderately involute to completely involute. Venter smooth, flattened, with shallow ventral furrow. Umbilicus from moderately narrow to very narrow. Suture with tripartite ventral lobe, first umbilical lobe asymmetrically bipartite, remaining six or seven occurring on the outer side are simple. Dorsal lobe deep and simple. Suture has 20–24 lobes.

Comparison. This subfamily differs in the entire bases of the inner digits of the first and all other umbilical lobes.

Composition. Five genera: *Prouddenites*, *Uddenites*, *Uddenoceras*, *Daixites*, and *Neouddenites*. Two genera occur in the Permian.

Occurrence. Moscovian–Kungurian.

Genus *Daixites* Ruzhencev, 1941

This genus includes six species from the Gzhelian–Sakmarian. Three species are known to be from the Permian.

- (1) Type species *D. meglitzkyi* Ruzhencev, 1941 from the Gzhelian (Orenburgian) of the Urals;
- (2) *D. antipovi* Ruzhencev, 1941 from the Lower Asselian of the Urals;
- (3) *D. attenuatus* Ruzhencev, 1941 from the Upper Asselian of the Urals; and
- (4) *D. sp.* recorded by Leonova from the Sakmarian (Khoridzh) of the Pamirs.

Genus *Neouddenites* Ruzhencev, 1961

- (1) *N. andrianovi* Ruzhencev, 1961 from the Kungurian of northeastern Russia;
- (2) *N. caurus* Nassichuk, Furnish et Glenister, 1965 from the Artinskian and Kungurian of the Canadian Arctic and northeastern Russia; and
- (3) *N. orientalis* Bogoslovskaya, 1991 from the Kungurian of northeastern (Dzhigdal Formation) and southeastern Mongolia.

Phylogeny. The earliest and most primitive genus *Prouddenites* was found in the Middle Carboniferous of North America (Miller and Furnish, 1940). In contrast to all pronoritids and the supposed ancestral genus *Megapronorites* (Ruzhencev, 1949a), this genus

acquired a new pattern in the development of the first umbilical lobe: its outer part was subdivided into two lobes (archallaxis); this determined the subsequent evolution of the group. At the beginning of the Gzhelian, this genus almost simultaneously gave rise to *Daixites* and *Uddenites*; the latter, in turn, gave rise to the more advanced genus *Uddenoceras*. *Daixites* continued into the Permian (Asselian–Sakmarian). The phylogeny of the Kungurian *Neouddenites* is difficult to interpret. Its organizational level and morphology are close to those of *Uddenites*, and they are certainly related phylogenetically. However, at present, these relations cannot be determined, since these two genera are separated in time by three geological ages.

Subfamily Medlicottiinae Karpinsky, 1889

Medlicottiinae: Ruzhencev, 1962, p. 354.

Diagnosis. Shell platyconic, involute, with narrow venter, possessing two keels or two rows of nodes. Umbilicus from moderately narrow to closed. Suture complex, with system of adventive lobes on external saddle and several bifid umbilical lobes on outer and inner sides of whorl. During phylogeny, the complexity of external saddle increased (Fig. 9), whereas the depth of first umbilical lobe decreased compared to that of the second umbilical lobe.

Comparison. This subfamily differs from other subfamilies in the gradually increased complexity of the external saddle (from two to seven pairs of adventive lobes) during phylogeny and in the increasing subdivision of the bases of the umbilical lobes and the narrowing of the venter.

Composition. Seven genera.

Occurrence. Gzhelian–Djulfian.

Genus *Medlicottia* Waagen, 1880

- (1) Type species *M. orbignyana* (Verneuil, 1845) from the Artinskian of the Urals;
- (2) *M. vetusta* Ruzhencev, 1949 from the Sakmarian of the Urals;
- (3) *M. semota* Ruzhencev, 1951 from the Sakmarian of the Urals;
- (4) *M. intermedia* Ruzhencev, 1949 from the lower part of the Artinskian in the Urals;
- (5) *M. copei* White, 1891 from the lower part of the Artinskian of Texas (Clyde Formation);

(6) *M. arroensis* Plummer et Scott, 1937 from the Artinskian of Texas (Arroyo Formation);

(7) *M. chozaensis* Plummer et Scott, 1937 from the Kungurian of Texas (Choza Formation);

(8) *M. milleri* Plummer et Scott, 1937 from the Kungurian of Texas (Choza Formation);

(9) *M. costellifera* Miller et Furnish, 1940 from the Kungurian of Texas (Leonard and Bown Spring Formations);

(10) *M. jakovlevi* Toumanskaya, 1949 from the Kungurian (Bolorian) of the Pamirs;

(11) *M. basarensis* Toumanskaya, 1949 from the Kungurian (Bolorian) of the Pamirs;

(12) *M. busterensis* Toumanskaya, 1949 from the Kungurian (Bolorian) of the Pamirs;

(13) *M. tenuis* Leonova, 1985 from the Kungurian (Bolorian) of the Pamir;

(14) *M. postorbignyana* Bogoslovskaya, 1997 from the Kungurian (Talatinskaya Formation) of Pai-Khoy;

(15) *M. gansuensis* Liang, 1982 from the Kungurian of northwestern China (Shuangputan Formation);

(16) *M. orientalis* Liang, 1982 from the Kungurian of northwestern China (Shuangputan Formation);

(17) *M. aff. orbignyana* from the Roadian (Assistance Formation) of the Canadian Arctic (Nassichuk, 1970, 1995);

(18) *M. kingorum* Miller et Furnish, 1940 from the Wordian (Word Formation) of Texas; and

(19) *M. sp. nov.* from the Kungurian (Bitauini Beds) of Timor.

Genus *Artinskia* Karpinsky, 1926

(1) Type species *A. artiensis* (Grunewaldt, 1860) from the Artinskian of the Urals;

(2) *A. kazakhstanica* Ruzhencev, 1951 from the lower part of the Asselian of the Urals;

(3) *A. liliana* Miller et Youngquist, 1947 from the Asselian and Sakmarian of Texas (Bursum, Pueblo, and Wolfcamp formations);

(4) *A. nalivkini* Ruzhencev, 1938 from the upper part of the Asselian and Sakmarian of the Urals;

(5) *A. multituberculata* Ruzhencev, 1938? from the Sakmarian of the Urals;

(6) *A. separata* Leonova, 1992 from the Sakmarian of the Pamirs (Khoridzh Formation); and

(7) *A. timorensis* (Haniel, 1915) from the Kungurian of Timor (Bitauini Beds).

Genus *Akmilleria* Ruzhencev, 1940

(1) Type species *A. transitoria* (Haniel, 1915) from the Kungurian of Timor (Bitauini Beds);

(2) *A. adkinsi* (Plummer et Scott, 1937) from the Sakmarian of Texas (Admiral Formation, lower part of the Wichita Group);

(3) *A. huecoensis* (Miller et Furnish, 1940) from the Sakmarian of Texas (lower part of the Hueco Limestone);

(4) *A. whortani* (Miller, 1936) from the Sakmarian of Kansas (Big Blue series, Florena Shale);

(5) *A. electraensis* (Plummer et Scott, 1937) from the Artinskian of Texas (Clyde Formation); and

(6) *A. sp. nov.* from the Sakmarian of Nevada (Portuguese Springs) (Schiappa, 1993).

Genus *Paramedlicottia* Leonova, 1992

This genus includes only the type species *P. sauk-sayensis* Leonova, 1992 from the Artinskian (Yakhtashian) of the Pamirs (Chelamcha Formation).

Genus *Eumedlicottia* Spath, 1934

(1) Type species *E. bifrons* Gemmellaro, 1887 from the Wordian of Sicily (Sosio Beds) and Oman (Hamrat Duru Formation);

(2) *E. whiteyi* Bose, 1917 from the Kungurian and Roadian of Texas (Leonard and Blaine formations) and Mexico;

(3) *E. subprimas* (Haniel, 1915) from the Kungurian–Lower Djulfian stage of Timor (Bitauini, Basleo, and Amarassi beds);

(4) *E. burckhardti* (Bose, 1917) from the Wordian of Texas (Word Formation) and Mexico;

(5) *E. verneuli* (Gemmellaro, 1887) from the Wordian of Sicily (Sosio Beds);

(6) *E. primas* Waagen, 1872 from the Capitanian–Djulfian of Salty Range (Wargal and Chhidru Formations) and Japan (Ochiai Formation); and

(7) *E. nikitini* Yu. Zakharov, 1986 from the Capitanian of Vladivostok region (Chandalazian).

Genus *Neogeoceras* Ruzhencev, 1947

(1) Type species *N. girtyi* (Miller et Furnish, 1940) from the Wordian–Capitanian of Texas (upper part of the Delaware Mountain Formation) and Mexico;

(2) *N. canavari* (Greco, 1935) from the Wordian of Sicily (Sosio Beds);

(3) *N. trautscholdi* (Gemmellaro, 1887) from the Wordian of Sicily (Sosio Beds), Tunisia (Bellerophon Limestone), Kurdistan (Qulqula Formation), and ?Roadian of Afghanistan;

(4) *N. marcoui* (Gemmellaro, 1887) from the Wordian of Sicily (Sosio Beds) and Oman (Hamrat Duru Formation);

(5) *N. glabrum* Bogoslovskaya, 1982 from the Wordian of Novaya Zemlya (Shadrinsk Formation);

(6) *N. boreale* (Tschernyschew) from the Permian of Novaya Zemlya;

(7) *N. smithi* (Miller et Furnish, 1940) from the Wordian of Timor (Basleo Beds);

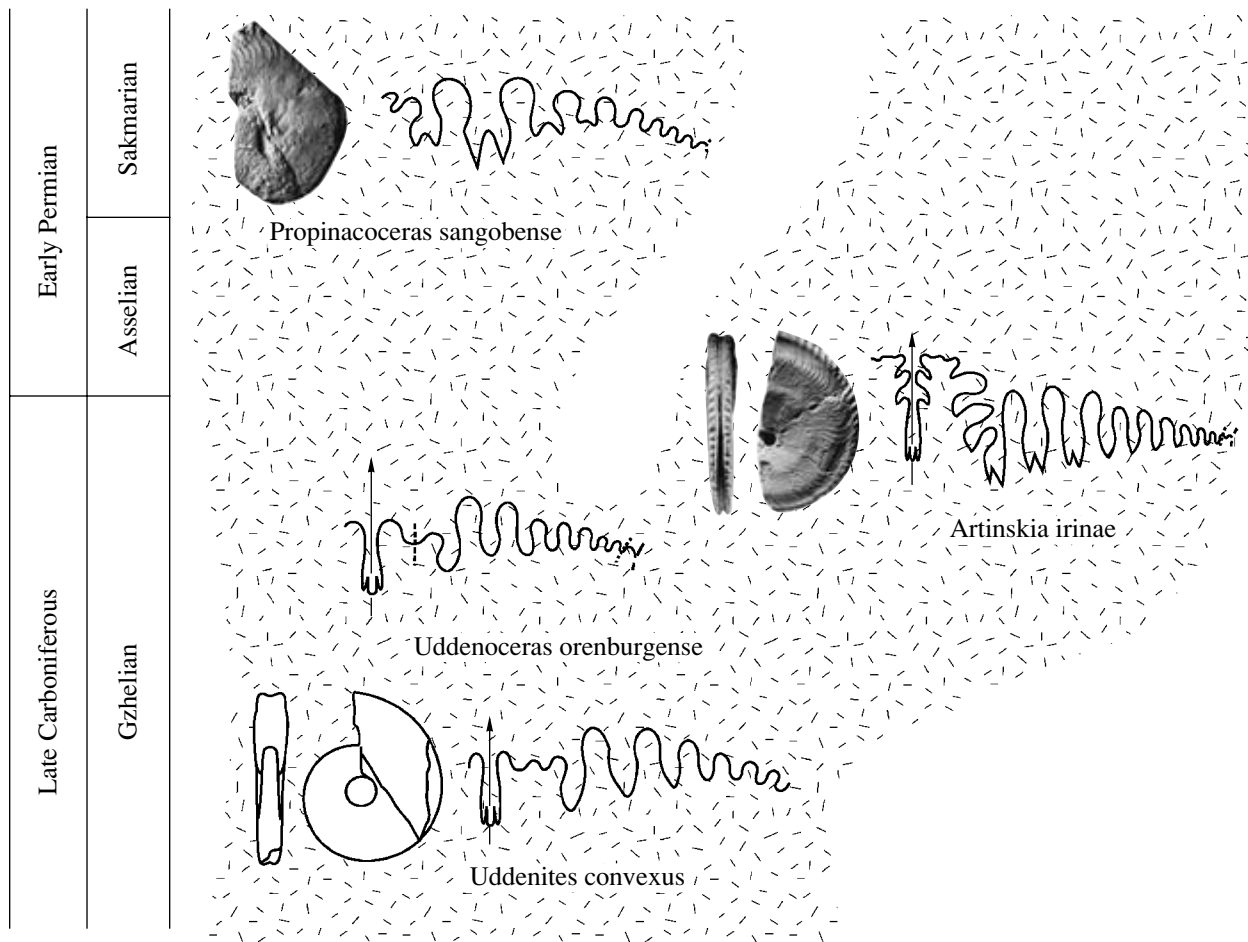


Fig. 10. Phylogenetic relationships of the subfamilies Uddenitinae, Propinacoceratinae, and Medicottiinae.

(8) *N. macnairi* Nassichuk, 1965 from the Wordian of the Canadian Arctic;

(9) *N. beishanense* (Liang, 1981) from the Wordian of northwestern China (Yushitan Formation);

(10) *N. tenue* Sheng et Liu, 1983 from the Wordian of Tibet (Jiala Formation);

(11) *N. malmqvisti* (Frebold, 1932) from the Capitanian–Djulfian of eastern Greenland (Martinia Beds);

(12) *N. thaumastum* Ruzhencev, 1962 from the Capitanian–Djulfian of Vladivostok region (Chandalazian Horizon); and

(13) *N. kitakamiense* (Bando et Ehiro, 1985) from the Djulfian of Japan (Senmatsu Formation).

Genus *Syrdenites* Nassichuk, Furnish et Glenister, 1965

(1) Type species *S. stoyanovi* Nassichuk, Furnish et Glenister, 1965 from the Djulfian of Transcaucasia, Timor (Amarassi Beds), and the ?Vladivostok region and

(2) *S. sp. nov.* (collection of the University of Iowa) from the Capitanian–?Djulfian (La Difunta Beds) of Mexico.

Phylogeny. The earliest genus of the subfamily, *Artinskia*, is apparently related to *Uddenoceras* (Fig. 10)

and appeared as a result of profound transformations during early ontogenetic stages, leading to the development of a system of adventive lobes at the top of the external saddle and bifid bases of the umbilical lobes (archallaxis). The further development of Medicottiina involved a progressive increase in sutural complexity (Fig. 9), especially in the ventral part of the suture, shortening of the first umbilical lobe, narrowing of the venter, development of two sharp keels, decreasing diameter of the umbilicus, and increase in the degree of whorl overlap. The four genera constitute the major orthogenetic lineage: *Artinskia* → *Medlicottia* → *Eumedlicottia* → *Syrdenites*. *Artinskia* has a shell with evolute initial whorls, a rather wide venter possessing two rows of prominent nodes, and a suture with two adventive lobes on the ventral side of the external saddle and three lobes on the inner side (two in pairs and one unpaired). The next genus, *Medlicottia*, has a significantly more complex outline of the external saddle (it possesses from three to six pairs of adventive lobes) (Fig. 11), a strongly narrowing venter with two keels, and gradual disappearance of nodes. The shell of the medicottiids remained involute throughout all stages of ontogeny. The genus *Eumedlicottia* represents

a new stage of morphological complexity. This genus was the most progressive of all medicottiids in having a smooth shell and suture that became more complex due to the appearance of digits on the sides of the main lobes. The following member of this lineage, *Syrdenites*, is close to Eumedlicottia in its level of organization. Without visible signs of regression, it became extinct in the Djulfian. Apart from the main branch, the family Medicottiidae contains another three iterative lineages: *Artinskia* → *Paramedicottia*, *Artinskia* → *Akmilleria*, and *Medlicottia* → *Neogeoceras*. The genus *Paramedicottia* resembles *Artinskia* in its moderately evolute early whorls, although its venter is considerably narrower and its suture possesses an additional (third) pair of adventive lobes approaching the sutural complexity of *Medlicottia*. *Neogeoceras* has a relatively wide, flattened venter and a characteristic shape of the first umbilical lobe. Some characters indicating regressive development; i.e., the smaller size of the adventive lobe on the external saddle and widening of the venter distinguish this genus from the ancestral *Medlicottia*.

The genus *Akmilleria* can be tentatively assigned to this subfamily. The shell shape of this genus and the nodular ornamentation on the venter are similar to those of Medicottiinae. The suture is quite archaic: a few bifid umbilical lobes and a relatively wide and shallow ventral lobe, with the first umbilical lobe always shallower than the second. The most significant distinction is the structure of the external saddle with a single adventive lobe on the ventral side and two lobes on the inner side. These differences may be explained by assuming that the genera *Artinskia* and *Akmilleria* diverged during very early stages and one pair of adventive lobes disappeared.

Subfamily Sicanitinae Noetling, 1904

Sicanitinae: Leonova and Dmitriev, 1989, p. 102.

Diagnosis. Shell platyconic, with two rows of subacute nodes, or flattened. Umbilicus from closed to moderately wide. Suture moderately complex, with one or two pairs of adventive lobes on the top of the external saddle, a hypertrophied unpaired adventive lobe, and a deeper first umbilical lobe (compared to the second).

Comparison. Sicanitinae differ from other Medicottiidae in having a very large first adventive lobe and deeper base of the first umbilical lobe and in the steady regressive development of the suture and the size and shape of the shell.

Composition. Six genera.

Occurrence. Asselian–Wordian.

Genus Vanartinskia Ruzhencev, 1978

Only the type species *V. asiana* Ruzhencev, 1978 from the Asselian–Sakmarian of the Pamirs (Tashkazyk Formation)

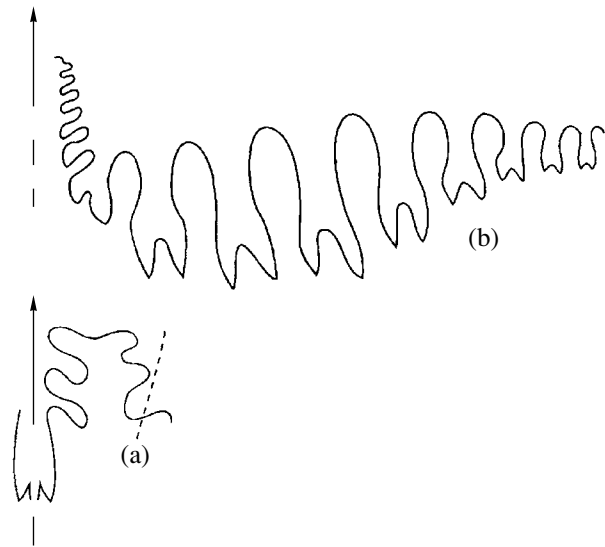


Fig. 11. Sutures of Medicottiina: (a) part of the suture of *Artinskia timorensis* (Haniel), specimen no. SUI 62210, ×3; (b) *Medlicottia timorensis* (?) Haniel, specimen no. SUI 12704, ×1.8; Timor; Kungurian, Bitauuni Beds.

Genus Synartinskia Ruzhencev, 1939

- (1) Type species *S. principalis* Ruzhencev, 1939 from the Sakmarian of the Urals;
- (2) *S. orientalis* Leonova, 1992 from the Artinskian of the Pamirs (Chelamcha Formation);
- (3) *S. sakmarae* Karpinsky, 1874 from the Sakmarian of the Urals (Kondurovskaya Formation). This species is poorly studied; and
- (4) *S. sp.* from the Sakmarian of the Pamirs (Khoridzh Formation).

Genus Prosicanites Toumanskaya, 1949

- (1) Type species *P. edelsteini* Toumanskaya, 1937 from the Artinskian (Yakhtashian) of the Pamirs;
- (2) *P. laxilectus* Leonova, 1992 from the Artinskian of the Pamirs (Zygar and Chelamcha formations);
- (3) *P. minutus* Leonova, 1992 from the Artinskian of the Pamirs (Zygar and Chelamcha formations); and
- (4) ?*P. papuanus* (Smith, 1927) from the Kungurian (Bitauuni Beds) of Timor.

Genus Sicanites Gemmellaro, 1887

- (1) Type species *S. schopeni* (Gemmellaro, 1887) from the Wordian of Sicily (Sosio Beds), Oman (Hamrat Duru Formation), and Kurdistan (Qulqula Formation);
- (2) *S. bactrianus* Leonova, 1985 from the Kungurian of the Pamirs (Kochusu Formation);
- (3) *S. evolutus* Leonova, 1985 from the Kungurian of the Pamirs (Kochusu Formation); and
- (4) ?*S. croaticus* (Vogl, 1913) from the ?Wordian of Croatia (Mrzla–Vodica Beds).

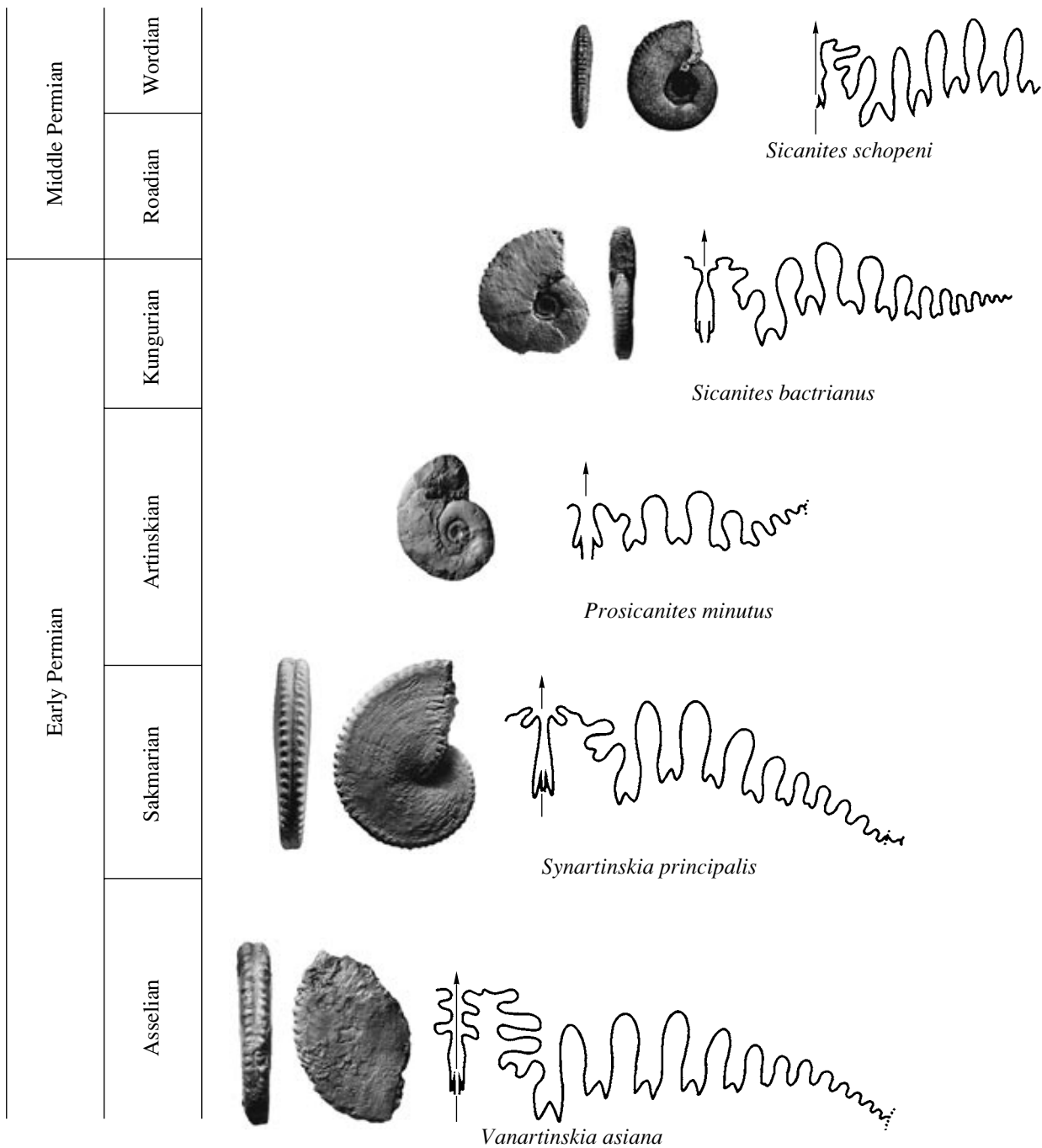


Fig. 12. Phylogenetic lineage *Vanartinskia* → *Synartinskia* → *Prosicanytes* → *Sicanites*.

Genus *Aktubinskia* Ruzhencev, 1947

Only the type species *A. notabilis* Ruzhencev, 1947 from the Artinskian (Aktastinian) of the Urals.

Genus *Parasicanytes* Leonova, 1985

(1) Type species *P. meridionalis* Leonova, 1985 from the Kungurian of the Pamirs (Kochusu Formation);

(2) *P. apertus* Leonova, 1992 from the Artinskian of the Pamirs (Chelamcha Formation);

(3) *?P. belcheri* (Nassichuk, 1970) from the Roadian of the Canadian Arctic (Assistance Formation); and

(4) *?P.* sp. described by Zhou, 1988 as *Aktubinskia* sp. from the Artinskian–Kungurian stages of southern China.

Phylogeny. Apparently, Sicanitinae also evolved from Uddenitinae. The main phylogenetic lineage includes *Vanartinskia* → *Synartinskia* → *Prosicanytes* → *Sicanites*, representing a regressive deviate series (Fig. 12). The genera *Aktubinskia* and *Parasi-*