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Middle Aptian Biostratigraphy and Ammonoids of the Northern Caucasus and Transcaspia

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Abstract—The Middle Aptian deposits of the central and eastern regions of the Northern Caucasus and Transcaspia (Turkmenistan) are described and discussed, including the history of their studies, lithology, and characterization of ammonite zones in each region. Ammonites of the superfamilies Parahoplitoidea and Douvilleiceratoidea, which form the basis for the Middle Aptian stratigraphic framework, are discussed and their origin and taxonomic composition are briefly considered. Forty species of 12 genera and 5 families are described. The historical stratotype section of the Gargasian stage of the French Lower Cretaceous scale is discussed, including the history of its recognition and subsequent study, and its present state. The authors' concept of the tripartite subdivision of the Aptian Stage in the Russian Scale is substantiated. The Middle Aptian deposits are described in detail, and the range and zonal subdivision of the Middle Aptian France, Great Britain, Germany, and other regions of the world are discussed. The correlation of the Middle Aptian in the Boreal and Tethyan realms is given.

Keywords: Northern Caucasus, Dagestan, Turkmenistan, Middle Aptian, Gargasian, ammonites, correlation

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CONTENTS

1. INTRODUCTION

In the second half of the last century, geological studies of the former Soviet Union developed very intensely, with many geological expeditions and surveys researching sedimentary formations especially in the regions with oil and gas deposits. These regions included the Northern Caucasus and Central Asia. Oil and gas in these regions were connected with, among others, the Lower Cretaceous deposits, the stratigraphy and fossils of which were studied by the present authors. I.A. Mikhailova comprehensively studied the Aptian stratigraphy and its ammonoids in the Northern Caucasus and Dagestan. From the middle of the last century, T.N. Bogdanova studied the Aptian beds of Transcaspia (Mangyshlak and Turkmenistan). In 1999, 2004, and 2005, we jointly generalized works on the Lower Aptian stratigraphy and ammonoids of the Northern Caucasus, Transcaspia, and Volga Region near Ulyanovsk and correlation with the synchronous beds of Western Europe.

As noted by many authors who studied the Lower Cretaceous of the northern slope of the Great Caucasus, the Upper Aptian beds (until 1971, the Aptian Stage was subdivided into two substages) contain abundant faunal remains, the assemblages with certainty indicate their Late Aptian age. For example, V.V. Drushchits wrote "... Of all Lower Cretaceous substages, the Upper Aptian contains the most diverse fossils, the study of which confirms the possibility of recognition of faunal zones, substantiated by V.P. Rengarten ..." (Drushchits, 1960a, p. 195). The same can be said of the Upper (and later Middle) Aptian of the Transcaspia. No large problems exist in the biostratigraphic subdivision of this portion of the Lower Cretaceous section of both regions and their correlations. This explains the absence of more recent large generalized stratigraphic and paleontological publications on this interval of the Lower Cretaceous sections.

This paper aims at characterizing the deposits, bed-by-bed descriptions of sections, and monographic description of the exceptionally diverse Middle Aptian ammonoid fauna, substantiation of zonal subdivision and correlation of the Middle Aptian beds of the northern Caucasus, Transcaspia, and major regions of their distribution in Western Europe, North and South America, Africa, and some other regions of the globe.

This paper was based on the present authors' observations and studies and materials from our colleagues, stratigraphers and paleontologists, who conducted joint field work in the Caucasus and Central Asia.

For the Turkmenistan sections, we used materials of E.Ya. Yakhnin, who studied the Aptian and Albian deposits in the following regions: Tuarkyr, Kuba Dagh, Great Balkhan, and Lesser Balkhan, Kopet Dagh; S.Z. Tovbina, who monographically studied the ammonite family Parahoplitidae from sections across Transcaspia; and S.V. Lobacheva, who studied brachiopods and echinoids from these regions. Vast paleontological material was assembled by mapping geologists working in this area, including V.F. Ludwig, A.A. Kudelin, L.D. Yatchenko, V.N. Krymus, and others. A unique collection of Aptian and Albian ammonites of Turkmenistan was donated to I.A. Mikhailova by M.I. Sokolov. This collection was supplemented by the Middle Aptian ammonite collection from this region assembled by V.A. Korotkov. Valuable data on the Middle Aptian of the Caucasus contained published and unpublished materials (geological reports) by M.P. Kudryavtsev, V.V. Drushchits, I.M. Krisyuk, and G.A. Tkachuk.

The monograph consists of two parts, stratigraphic and paleontological.

The stratigraphic part is preceded by a review of the modern state of the stratotype section of the Aptian Gargasian Substage. For a long time, stratotypes of three parts of the Aptian (Bedoulian, Gargasian, and Clansayesian horizons), which were introduced in the stratigraphic scale of the Cretaceous of France in the 19th century, were not studied. The Bedoulian–Gargasian boundary in the historical stratotypes was drawn at the base of the *Dufrenoyia* beds. Therefore, attempts to synonymize the Lower and Middle Aptian with the Bedoulian and Gargasian horizons were always debatable. After French stratigraphers studied the Bedoulian stratotype in the stratotype region at the end of the 20th century (*Le stratotype historique...*, (1998) 2000), its upper boundary was raised to the top of the beds with *Dufrenoyia*, and zonal ranges of the Aptian horizons compared became equal. However, at present, after the revision of the Gargasian Horizon, French stratigraphers and paleontologists who conducted this revision returned to the original definition of the Bedoulian and Gargasian horizons by placing their boundary at the base of the *Dufrenoyia* beds. In addition, the same group of stratigraphers proposed to subdivide the Aptian Stage into two substages, considering its upper substage to include two horizons, Gargasian and Clansayesian, using these names as regional biostratigraphic units. In 2010 in Dijon (France), stratigraphers and paleontologists of the Kilian Group accepted the bifid subdivision of the Aptian for the Mediterranean region (Report on the 4th..., 2011), however, the Lower-Upper Aptian boundary was retained at the top of the beds with *Dufrenoyia*. When writing a chapter on the historical stratotype of the Gargasian (and the correlation of the beds in the last chapter of the monograph), the present authors mainly focused on the appearance and temporal changes in the ammonite zonation in the Gargasian sections and substantiation of zonal boundaries in connection with differently interpreted substage boundaries. Moullade, Granier, and Tronchetti (2011) revised existing works on the subdivision of the Lower Cretaceous interval between the modern Barremian and Albian, and concluded that the range of the Aptian Stage should be restricted to the Gargasian Horizon, according to the rule of priority. This was the

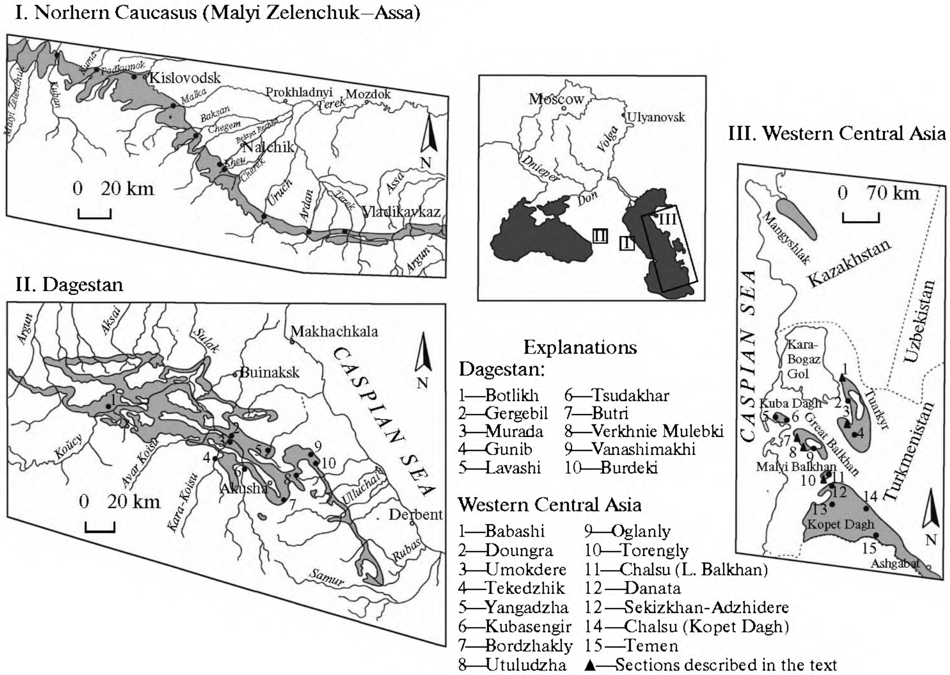


Fig. 1. Sites of the major sections.

interpretation of d'Orbigny, who established this stage in the 19th century. These authors proposed to consider the deposits between the Barremian and Aptian, i.e., the Bedoulian Horizon, as a separate Bedoulian Stage. In their opinion, the Bedoulian–Aptian boundary should be placed at the base of the beds with *Dufrenoyia*; and the Clansayesian Horizon should be placed in the Albian. Before being put into practice, these proposals should be considered by the International Stratigraphic Cretaceous Subcommission and the Kilian group. Therefore, in this paper, we accept the trifid subdivision of the Aptian Stage (*Postanovlenie*..., 1981). We also consider that it is not practical to use French regional names for the subdivision of the Aptian stage for our section.

The Middle Aptian stratigraphy of the northern slope of the Main Caucasus Range is given in the two large parts: central and southeastern, called Dagestan in the monograph (Fig. 1). The stratigraphic descriptions of the regions of the Caucasus are given in abbreviated form because a description of the Middle Aptian, as of part of the Cretaceous system, was several times given in the published works (see the "History of Studies"). In describing beds of the central region and Dagestan, the authors used sections published in two monographs by Mordvilko (1960. 1962). These works contain long lists of bivalves, which are not repeated here because this paper focuses on ammonites.

The stratigraphy of Transcaspia (except Mangyshlak) is given in greater detail, because the results of virtually half a century's study of the Aptian and Albian are briefly published in very few summaries.

In the paleontological part of this paper we describe 42 species of ammonites, belonging to 10 genera, 4 families, and 2 suborders with characterization of taxa of all ranks. The largest part of the collection described is housed in the museum of the Borissiak Paleontological Institute of the Russian Academy of Sciences, Moscow (PIN), under collection no. 5265. The authors, while describing and identifying the ammonites, studied many collections housed in F.N. Chernyshev TsNIGR Museum (St. Petersburg, All-Russia Research Geological Institute (VSEGEI) and the Earth Science Museum of Moscow State University (MZ MGU). The most representative paleontological collections of Middle Aptian ammonites of the regions studied are housed in the TsNIGR Museum: I.F. Sinzow (nos. 11064, 11066, 11068), M.M. Wassiliewskyi (no. 11320), I.I. Nikshich (no. 630), V.P. Renngarten (no. 334), N.P. Luppov (nos. 5180. 6136), A.E. Glazunova (nos. 6426, 8196), I.G. Sazonova (no. 11805), S.Z. Tovbina (nos. 10686, 11087, 11909), T.N. Bogdanova and M.V. Kakabadze (no. 11276), T.N. Bogdanova and I.A. Mikhailova (no. 11288). Unfortunately, one of the most important collections, by I.F. Sinzow, has important gaps; some specimens are missing from it (see "Paleontology"), most likely as a result of repeated transportation and movements of this collection from Leningrad to Moscow and back, until it was finally housed in the TsNIGR Museum in the 1960s.

In the Earth Science Museum of Moscow State University, we studied collections by V.V. Drushchits (no. 5), I.A. Mikhailova (nos. 96, 99), V.V. Drushchits, I.A. Mikhailova and V.M. Nerodenko (no. 79), and I.A. Sakharova (no. 85). We also used data on the ammonite collections from the museums of Tübingen (Germany), Geological Institute of the Academy of Sciences of Georgia (Tbilisi), Central Geological Museum of Turkmenistan, Ashgabat (TsGM).

2. HISTORICAL STRATOTYPE OF THE GARGASIAN SUBSTAGE AND ITS SUBDIVISION

The Aptian Stage is currently subdivided into three substages in most regions of Europe and Central Asia. French stratigraphers traditionally referred to the middle substage as "Gargasien" or "Gargasian" (Fig. 2). In the latest publications on the Gargasian beds (Atrops and Dutour, 2005; Dutour, 2005), the French authors rejected the subdivision into three stages in favor of two stages, but in the Upper Aptian they recognize the Gargasian and Cansenian parts interpreting them as regional biostrata.

The first description of the Aptian beds near Gargas (Vaucluse, southeastern France) was published by Leenhardt (1883, pp. 98–99). In this section, the author recognized seven beds, of which beds from 3 to 6 he assigned to the Aptian Stage (Table 1).

The name "Gargasien" was proposed in 1887 by Kilian (1887, pp. 50, 53–54), who studied Mesozoic sections in the Montagne de Lure (Lower Alps) for the portion of the Aptian Stage above the Rhodanien (currently Rhodanian, Lower Aptian) and below the Gault beds. Since Kilian indicated the Early Aptian ammonite species from the lower horizon (a) *"Ammonites (Acanthoceras) Martini*[1] et *Cornueli, A. (Hoplites) consobrinus, Toxoceras Royeri..."* (p. 53), this horizon most likely represented the basal bed of the Gargasian with redeposited Lower Aptian (Rhodanian according to Kilian) species. The second horizon (b) contained species that were thought at that time to be characteristic of the Gargasian: *"Ammonites (Phylloceras) Guettardi, Nisus, Am. (Hoplites) Dufrenoyi, gargasensis, A. (Desmoceras) Emerici,* etc." (p. 53), and the third (uppermost) horizon contained the belemnite *Belemnites semicanaliculatus.*

A year later, the name "Gargasian" was accepted by Toucas (1888), who studied sections in the valley of the Rhône. He correlated his sections with the Aptian section composed by Leenhardt (1883) in the vicinity of Gargas and proposed the name "Bedoulien" (currently Bedoulian) for the lower unit recognized by Leenhardt (A^1) and used Kilian's name "Gargasien" (currently Gargasian) for units A^2 and A^3.

Kilian (1896), in a report on stratigraphy in the vicinity of Sisteron, recognized two types of Aptian

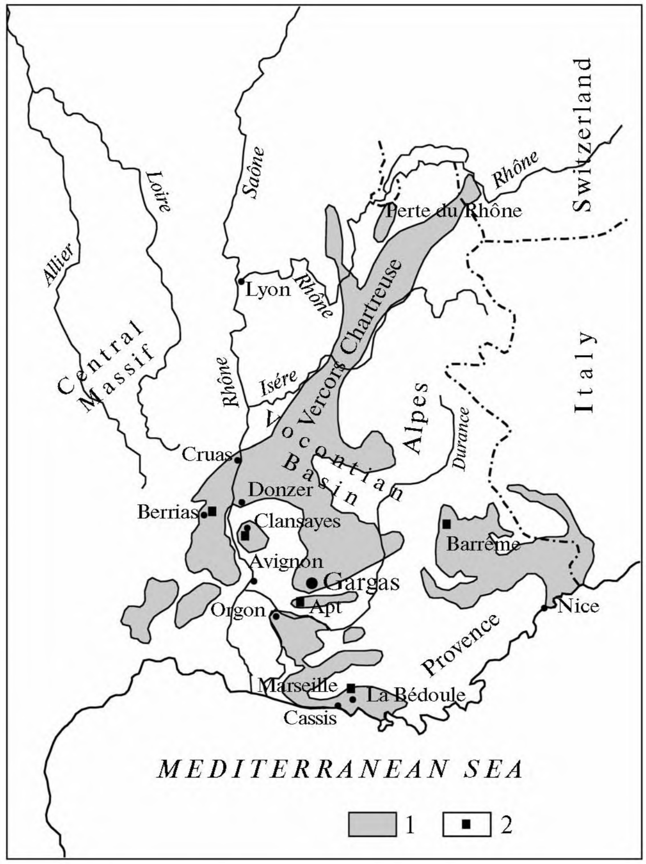


Fig. 2. Lower Cretaceous deposits (1) and location of the stratotype (2) Southeastern France.

successions, western (occidental) and eastern (oriental) (Kilian, 1896, p. 769, table XIV). The western type Kilian also called Provençal and oriental—Alpian (alpin). The western type located near Apt and Carniol (Kilian, 1896, table XIV) is characterized according to Kilian by predominance of the ammonite genera *Hoplites, Oppelia, Sonneratia,* and *Acanthoceras,* whereas the eastern type (vicinity of Castellane and Barrême) shows absence or extreme rarity of *Hoplites* and *Oppelia* and abundance of *Lytoceras, Phylloceras,* and *Desmoceras* (Fig. 3).

Jacob (1904, 1905, 1907) subdivided the marl Gargasian facies into two parts: Lower Gargasian and Upper Gargasian. The Lower Gargasian includes its IIa Subzone with *Oppelia nisus* d'Orb. and *Hoplites furcatus* J. de C. Sow. (=*Dufrenoyi*); the Upper Gargasian corresponded to the IIb Subzone with *Douvilleiceras subnodosocostatum* Sinz., *D. buxtorfi* Jacob, and *Belemnites semicanaliculatus* Blainville. The Lower Subzone was characterized based on the sections from the Drôme Province, an area with widespread eastern Gargasian facies. The upper zone was characterized based on a section in Switzerland (Luitre Zug).

In the later works, Kilian (1907–1913) and Kilian and Reboul (1915) summarized all the data on the

[1] The spelling of the names *Acanthoplites* or *Acanthohoplites* of the species *nisum* or *nisus* from the capital letter, presence or absence of the authors' names following the taxonomic names, is given as in the text cited.

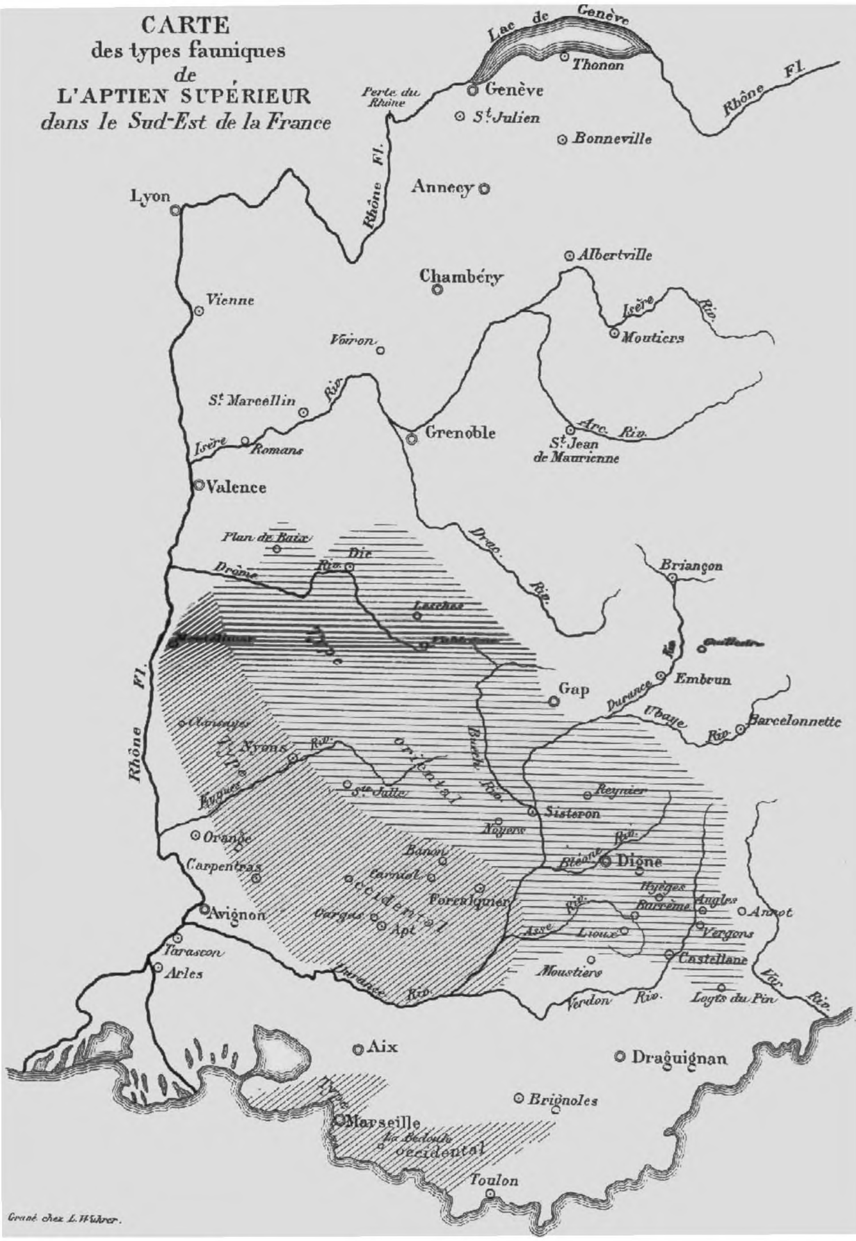


Fig. 3. The distribution of the faunal types of the Upper Aptian sections in southeastern France (Kilian, 1896); western and eastern types are dashed.

Aptian Stage (see Table 1a) and gave a detailed scheme of correlation of views of different authors (Leengardt, Lorie, Lambert, Jacob, and his own) on the subdivision of the Gargasian beds in various regions of France (Kilian, 1907–1913, table to p. 287; Kilian and Reboul, 1915, pp. 155–210). Kilian (1915) subdivided the Aptian into three substages, of which the Gargasian was the middle, and Clansayesian was the upper. He also discussed in detail the stratigraphic and geographic distribution of almost all ammonite species found in various Gargasian facies (Kilian, 1907–1913, pp. 304–310). This summary resulted in the scheme of the zonal subdivision of the Gargasian, accepted for the Mediterranean Province, which includes southern and central Europe (ibid., pp. 376–377). Kilian correlated the stratigraphic scheme of the Gargasian in the Mediterranean Province with the northern German scheme, where the Gargasian also included two zones, but with different names. No data on Gargasian deposits in England and Russia existed at that time.

After that, the study of the stratigraphy of the Gargasian in the stratotype region was not resumed for a long time. Therefore, Moullade (1965) in his report on the Gargasian Substage to the International Symposium on the Lower Cretaceous in Lyon in 1963 containing data on the history of studies of the stratotype, did not propose a zonal subdivision of these beds. However, in the same volume, the report of the results of the Lyon symposium contained a conclusion on the Aptian Stage (Anonymous, 1965), according to which the Aptian Stage was subdivided into two substages and several ammonite zones. The Upper Aptian contained the Gargasian and Clansayesian. The Gargasian Substage was subdivided into two zones, *Aconeceras nisus* (lower) and *Epicheloniceras subnodosocostatum* (upper).

At approximately the same time, Thomel (1964) published a small note on the zonal subdivision of the Aptian Stage in the Lower Alps. As known from publications on the Gargasian of France, the Aptian Stage is represented by various facies containing different ammonite assemblages, the so-called western and eastern types. In the Lower Alps, the eastern facies of the substage are widespread. According to Kilian, they are characterized by argillaceous sediments with smooth ammonite shells dominating over ornamented species (Thomel, 1964, p. 4308). Thomel subdivided the Gargasian into the lower and upper parts (Table 1). In the lower part, he recognized the *Protetragonites obliquestrangulatum* and *Diadochoceras pretiosum* zones (on the generic affinity of the species *pretiosum,* see below) and, in the upper part, the *Argonauticeras depereti* and *Melchiorites melchioris* zones. In Thomel's opinion, the lower zone is the best represented in the Blieux and Baume localities. From here, the authors listed the following ammonite species: *Protetragonites obliquestrangulatum* (Kil.), *Macroscaphites striatisulcatus* (d'Orb.), *Melchiorites emerici* (Rasp.) var. *strigosa* (Fallot). The section in the Robines ravine also contains "éléments caractéristiques du Gargasien inferieur d' Apt et de Carniol ..." (p. 4309), including *Aconeceras nisus* (d'Orb.), *A. aptiana* (Sar.), *Diadochoceras pretiosum* (d'Orb.), *Dufrenoyia dufrenoyi* (d'Orb.), *Colombiceras crassicostatum* (d'Orb.), *C. subpeltoceroides* (Sinz.), *Cheloniceras cornuelianum* (d'Orb.). Apart from that, Thomel listed many smooth ammonites of the families Phylloceratidae, Tetragonitidae, and Desmoceratidae. The Upper Gargasian contains a fauna which in Thomel's opinion "correspond au principal horizon fossilifère des "marnes aptiennes", bien développé à Hyeges, Barrême, Tartonne, Angles, Vergons, etc." ... (p. 4309): *Argonauticeras depereti* (Kil.), *Gabbioceras lamberti* (Brst.), *Melchiorites melchioris* (Tietze), *M. melchioris* var. *alpina* (Fallot), *Hypacanthoplites* nov. sp. cf. *malgachensis* Brst. Thomel considered these species to be geochronologically restricted, i.e., confined to a particular zone. Apart from these species, there were found many taxa not restricted to the Upper Gargasian. For instance, the presence of *C. buxtorfi* in the Clansayesian *Diadochoceras nodosocostatum–Cheloniceras buxtorfi* Zone, was unexpected, as this species is characteristic of the lower Gargasian Zone recognized based on the predominance in it of the members of the family Douvilleiceratidae. Thomel concluded in his note that "the ammonoid-based subdivision of the eastern Gargasian facies is better achieved than of the eastern facies" (p. 4310).

About two decades later, Moullade (1980) and Rawson (1983) in reviews of the state of the knowledge and subdivision of the Cretaceous stages and substages accepted for the Aptian Stage a bifid subdivision, and for the Gargasian, a zonal subdivision of this horizon proposed by an anonymous author in the materials from the Lyon colloquium.

Up to the 1990s, natural outcrops of the historical stratotypes of the Aptian substages remained virtually unstudied. Their regular study began from the Lower Aptian or Bedoulian (Roquefort-La Bédoule, Bouches-du-Rhône, southeastern France) [Le stratotype..., (1998) 2000]. This research included the base of the Gargasian. Conte (1994) noted that many, mainly European, stratigraphers consider that the ranges of the Lower and Middle Aptian in different regions do not coincide with the ranges of the Bedoulian and Gargasian in France owing to the inconsistent stratigraphic position of the *Dufrenoyia furcata* Zone. Conte also analyzed the distribution of ammonites in the Comte quarry in the area of the Bedoulian stratotype (Conte, 1994, text-fig. 1) and established that *Dufrenoyia* are found together with the representatives of the genus *Tropaeum* and below the beds where the ammonite species *Aconeceras nisus,* numerous *Gargasiceras,* and also *Epicheloniceras, Colombiceras,* and others are found. On this basis, he raised the Bedoulian–Gargasian boundary by recognizing in the boundary beds of these two substages the *Dufrenoyia* spp. and *Tropaeum bowerbanki* (Bedoulian) and *Epicheloniceras* spp. and *Aconeceras nisus* (Gargasian) zones.

In a small note, Ropolo and Moullade (2002) published in the material of the colloquium dedicated to the 200th anniversary of the birth of Alcide d'Orbigny, briefly described the history of studies of the Gargasian and focused mainly on the problems related to the modern state of the natural section of the historical stratotype, lower and upper boundaries of the substage and its zonal subdivision. The authors of the note concluded that, for the detailed study of the Aptian beds in the stratotype locality in the vicinity of Apt and Gargas and in other sections in southeastern France, corresponding to the sections of different facies and development of zonal subdivision, in Marseille in 2001 formed the "Gargasian Working Group," which included geologists and paleontologists studying various faunal groups (Ropolo and Moullade, 2002).

This group includes almost all the same authors who revised the stratotypes of the Bedoulian Substage [Le stratotype..., (1998) 2000].

French workers established that the sections in the vicinity of the Aptian (slopes of the hill near Gargas), which were studied from the 19th century and considered as the stratotype of the Gargasian Substage, were destroyed by modern urbanization (Moullade and

Table 1. History of stratigraphy of the Gargasian in the stratotype

Leenhardt, 1883		Kilian, 1887		Toucas, 1888		Jacob, 1904, 1905, 1907		Kilian, 1907–1913		Breistroffer, 1947			Thomel, 1964		
Gaultian	7. Arenaceous marl with sand-stone beds	Lower Gaultian	Traces of erosion of Aptian deposits	Gaultian	Sand and clay with abundant fauna of Gaultian and hori-zons of phosphorite nodules	Albian	III. Zone with *Douvilleiceras bigoureti Seunes* and *D. nodoso-costatum* d'Orb.	Gaultian	1. Zone *Parahop-lites nolani* Seun. (so-called *Mille-tianus* Beds) and *Douvilleiceras nodosocostatum* d'Orb. sp., *D. bigoureti* Seun. sp.	Aptian	Upper Aptian = Clansayesien	Acanthhoplitien = zone with *Diado-choceras nodoso-costatum* and *Acanthohoplites bigoureti*	Aptian	Clansayesian	*Diadochoceras nodosocostatum* and *Cheloniceras buxtorfi* Zone
Upper subdivision of the Aptian marl, 65 m A^3	6. Dark or yellow arenaceous marl *Belemnites semi-canaliculatus* 5. Dark arena-ceous marl *B. semicanaliculatus*	Gargasian (Gargasien)	(c) arenaceous marl with *Bel. semicanaliculatus*	Upper Aptian (or Gargasian)	1. Sand and clay with *Belemnites semicanaliculatus*	Aptian – Gargasian (Gargasien)	IIb. Subzone with *Douvilleiceras subnodosocos-tatum* Sinz., *D. buxtorfi* Jacob — Upper Gargasian, Luitre Zug locality	Upper Aptian–Gargasien	2b. Zone *Douville-iceras subnodoso-costatum* Sinz. and *D. buxtorfi* Jacob		Middle Aptian = Gargasien	Tropaeumien and Parahoplitien		Upper Gargasian	*Argonauticeras depereti* and *Mel-chiorites melchioris* Zone
"Typical Aptian marl", 5 m A^2	4. Ash-gray gray and less com-monly argilla-ceous marl: *Ammonites duf-renoyi*, *Plicatula radiola*		(b) Marl with *Am. dufrenoyi*, *nisus*, *guettardi*, *martini*, *Plicatula radiola* etc. (a) Limestone with *Am. Martini*, *A. Dufrenoyi*, *Pli-catula radiola*, *Pecten Cottaldi*		2. Calcareous marl with *Discoidea dec-orata*, *Echinospata-gus collegnoi*, *Belemnites semi-canaliculatus* 3. Marl with *Belem-nites semicanalicu-latus*, *Ammonites nisus*, *A. martini*, *Plicatula placunea*, *P. radiola*		IIa. Subzone *Oppelia nisus* d'Orb., *Hoplites furcatus* Sow. (=*Dufrenoyi* d'Orb.)—Lower Gargasian, east-ern facies		2a. Zone *Hoplites furcatus* Sow. and *Oppelia nisus* d'Orb. *Phylloceras guettardi* Rasp.					Lower Gargasian	*Protetragonites obliquestrangulatum* and *Diadochoceras pretiosum* Zone
Lower Aptian, 10–15 m A^1	3. Similar marl with beds of blue marly limestone 2. Yellow, ash-gray or blue argillaceous marl	Rhodanien	Cherty limestone with *Am. Conso-brinus*, *Ancylo-ceras matheroni*, *Ammonites recti-costatus*, *Am. Matheroni*, *Plica-tula placunea*, *Ostrea aquila*	Lower Aptian (or Bedoulian)	4. Limestone marl and marl with *Belemnites semi-canaliculatus*, large ammonites, *Ammonites conso-brinus A. Cornueli*, *A. Matheroni*, *Nautilus plicatus*, *Ancyloceras matheroni*, *Oatrea aquila*, *Echinospat-agus collegnoi*	Aptian–Bedoulian (Bédoulien)	I. Zone *Parahop-lites deshayesi* Leym. and *Ancy-loceras matheroni*	Lower Aptian = Bédoulien (Voconcien)	I. Zone *Parahop-lites deshayesi* Leym., *Ancylo-ceras Matheroni* d'Orb.			Lower Aptian = Bédoulien		Lower Aptian = Bedoulian	Zone *Pseudohaplo-ceras matheroni*
	1. Urgonian lime-stone with corals and Requiniae														

Table 1. (Contd.)

Anonymous, 1965; Moullade et al., 1980; Rawson. 1983			Conte, 1985, 1994		Dauphin, 2002		Atrops et Dutour, 2005; Dutour, 2005			
Upper Aptian	Clansayesian	*Diadochoceras nodosocostatum* Zone	Upper Aptian	*Hypacanthoplites jacobi* Zone	Upper Aptian	*Nolani* Zone	Upper Aptian	*A. nolani* Zone		
									D. nodosocostatum subZone	
	Gargasian	*Epicheloniceras subnodosocostarum* Zone	Middle Aptian	*Parahoplites nutfieldiensis* Zone		Barren interval		*P. melchioris* Zone		
				Epicheloniceras subnodosocostatum Zone		*Tobleri* Zone		*E. martini* Zone	*E. buxtorfi* Subzone	*S. caucasica* Horizon
										E. depressus Horizon
									E. gracile Subzone	
		Aconeceras nisus Zone		*Epicheloniceras* spp. and *Aconeceras nisus* Zone		*Crassicostatum* Zone			*E. debile* Subzone	*E. raspaili* Horizon
			Lower Aptian	*Dufrenoyia* spp. and *Tropaeum bowerbanki* Zone	Lower Aptian	*Furcata* Zone		*Dufrenoyia furcata* Zone	*D. dufrenoyi* Subzone	*D. dufrenoyi* Horizon
										D. praedufrenoyi Horizon
									D. furcata Subzone	
Lower Aptian	Bédoulien	*Deshayesites deshayesi* Zone		*Deshayesites grandis* Zone		*D. deshayesi* Zone	Lower Aptian	*D. deshayesi* Zone	*D. grandis* Subzone	

Tronchetti, 2004). It was decided to transfer the place of the study of the Gargasian deposits to the northeast of Gargas Hill (4–5 km), in the vicinity of the La Tuiliére village, which is assigned to the Commune de Saint-Saturnin lès Apt (Dutour, 2005, vol. 2, p. 223). By 2005 several natural Gargasian outcrops around this village were studied (Atrops and Dutour, 2005), which were correlated with one another and with the generalized, continuous, although "synthetic" section of the new stratotype of the Gargasian Substage. Primarily, it should be noted that the base of the Gargasian was reinstated by Atrops and Dutour at the base of the *Dufrenoyia furcata* Zone thereby increasing the range of the substage and, hence, reinstating the incongruence of the ranges of the French Bedoulian and Gargasian to the Lower and Middle Aptian of other regions mentioned by Conte.

A large monograph by Dutour (2005) was devoted to the Gargasian biostratigraphy in its new stratotype and revision of ammonites. Based on the study of many ammonite species (over 50) and their distribution in the section, a new biostratigraphic subdivision into zones, subzone, and horizons was proposed. The Aptian Stage was subdivided into two parts, with the Gargasian and Clansayesian united into the Upper Substage. Fifteen outcrops studied around the village of La Tuiliére constituted the section of the new Gargasian, only including the *Dufrenoyia furcata* Zone and lower part of the *Epicheloniceras martini* Zone (*Raspaili* Zone, *Debile* Horizon) (Atrops and Dutour, 2005). The complete section of the Upper Aptian was characterized by Dutour (2005). For this, the geography of the outcrops studied was expanded to the entire Vocontian basin. This complete section was composed of outcrops in Le Pègue (*Deshayesi* Zone), Serre Chaitieu (*Furcata* and *Martini* Zones), Baudinard (from the upper part of the *Martini* Zone to the *Nolani* Zone). No *Parahoplites* has been found in the *Melchioris* Zone. Thus, the succession of the new Gargasian stratotype not only does not contain *Parahoplites,* but also does not contain this part of the section, whereas only one specimen of *Parahoplites melchioris* was recorded in the Vocontian Basin (Baudinard section) by Dauphin (2002, p. 138, pl. 4, fig. 16).

Dutour (2005, p. 220, text-fig. 15) gave the taxonomic list and stratigraphic ranges of 53 ammonite species (Table 2). Of these, there are 11 species of phylloceratins, 13 lytocerathins, 13 ammonitins (including haploceratаceans and desmocerataceans), and 16 species of ancyloceratins. The last taxa are the basis of the zonal scheme of the Gargasian Substage. The lower *Dufrenoyia furcata* Zone includes two subzones, *furcata* and *dufrenoyi,* and the latter is subdivided into two horizons: *praedufrenoyi* and *dufrenoyi.* According to Atrops and Dutour (2005), the biostratigraphic subdivision of this part of the section is based on the phylogenetic development of the genus *Dufrenoyia: furcata* → *praedufrenoyi* → *dufrenoyi.*

It is unexpected to see in the same table 15, the occurrence of the species *Diadochoceras (Vergunniceras) pretiosus* in the *debile* and *gracile* subzones of the *martini* Zone. The genus *Diadochoceras* is typical of the Clansayesian deposits and is not found in the earlier beds.

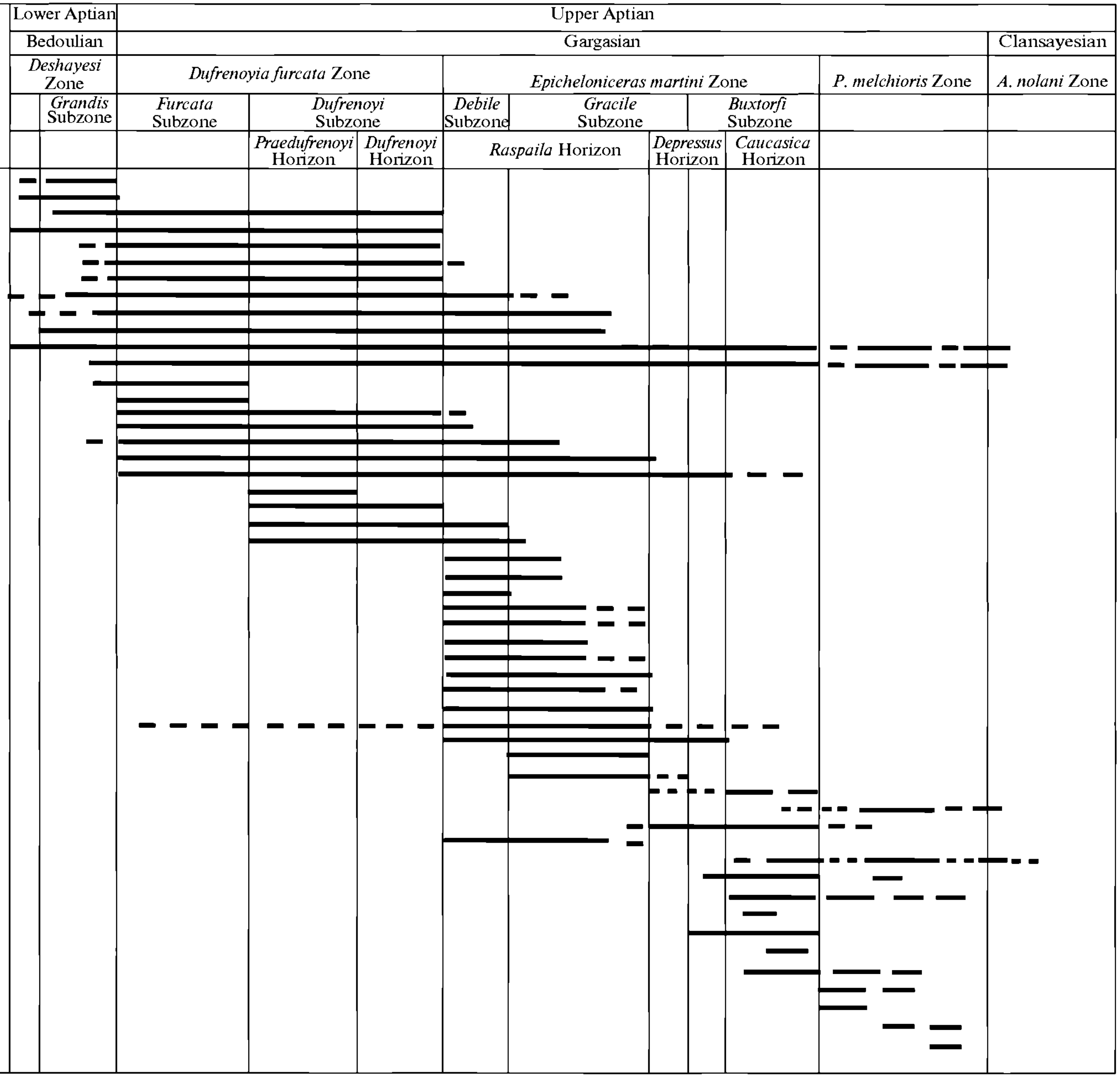
The upper boundary of the *martini* Zone is drawn most likely based on the disappearance of *Epicheloniceras.* As mentioned above, *Parahoplites* has not been found in the interval of the section assigned to the *melchioris* Zone. This interval contains only a few lytoceratin and desmoceratin species. Dutour (2005, p. 276) draws the upper boundary of the *melchioris* Zone below the beds with the earliest *Nolaniceras* in association with *Diadochoceras,* although none of the figures showing the distribution of the species (Dutour, 2005, text-figs. 24, 26, 28, 30. 32, 34, 36, 38, 40) mention representatives of these genera.

According to Dutour (2005, p. 282), the presence in the Gargas assemblage of the Vocontian ammonites of the genera *Epicheloniceras, Deshayesites,* and *Dufrenoyia* allows the correlation of the French sections with the Middle Aptian beds of the Boreal Realm and the introduction into the biostratigraphic schemes of the Gargasian of France, the English index species which were used in his schemes by Casey (1961b): *Dufrenoyia praedufrenoyi, Epicheloniceras debile, E. gracile,* and others. In our view, presence of the above ammonite genera shows positive correlation of the French sections not only with the English sections, but also with the sections in the same Mediterranean (or Tethyan) Paleozoogeographic Realm (see below).

3. HISTORY OF STUDIES OF THE MIDDLE APTIAN OF THE NORTHERN CAUCASUS AND TRANSCASPIA

The Cretaceous deposits of the Northern Caucasus and Transcaspia (Turkmenistan) have for a long time attracted the attention of geologists primarily because of their good exposure, fossil fauna diversity, and overall accessibility of the sections. In the northern Caucasus by the middle of the 19th century, Cretaceous sections of the central and southeastern zones of this region (Dagestan) were intensely studied. In Transcaspia, at the end of the 19th and beginning of the 20th century, data on the stratigraphy of this region were obtained primarily from observations during mapping trips across the territory (Tuarkyr) or visiting the separate sections (Kopet Dagh). These random observations provided data on the presence of the Lower Cretaceous, in particular, Aptian deposits, composing the ranges of the extreme west and south of this region.

Table 2. Stratigraphic distribution of ammonite species in the Gargasian in the historical stratotype (after Dutour, 2005, p. 220, text-fig. 15)



	Ammonite species
1	*Deshayesites grandis* Spath
2	*Sinzowia nisoides*. Saras.
3	*Salfeldiella* (S.) *opegana* Sayn
4	*Pseudohaploceras liptoviensis* Zeuschn.
5	*Cheloniceras cornuelianum* d'Orb.
6	*Cheloniceras* gr. *meyendorffi* d'Orb.
7	*Cheloniceras seminodosum* Sinz.
8	*Melchiorites strigosa* Fall.
9	*Pseudohaploceras angladei* Sayn
10	*Salfeldiella* (*Gyrophyllites*) *paquieri* Sayn
11	*Phyllopachyceras baborense* Coq.
12	*Zuercherella zuercheri* Jac. et Tobl.
13	*Eogaudryceras* (*Eotetragonites*) *blieuxiensis* Breistr.
14	*Dufrenoyia furcata* J. de C. Sow.
15	*Gargasiceras gargasense* d'Orb.
16	*Aconeceras nisus* d'Orb.
17	*Eogaudriceras numidum* Coq.
18	*Protetragonites strangulatum* d'Orb.
19	*Colombiceras crassicostatum* d'Orb.
20	*Dufrenoyia praedufrenoyi* Casey
21	*Eogaudryceras* (*Eotetragonites*) *ambiguus* Breistr.
22	*Dufrenoyia dufrenoyi* d'Orb.
23	*Phylloceras* (*Hypophylloceras*) *morelanum* d'Orb.
24	*Epicheloniceras martini* d'Orb.
25	*Epicheloniceras debile* Casey
26	*Epicheloniceras eotipicum* Casey
27	*Uhligella jacobi* Burckh.
28	*Aconeceras* nov. sp. 1
29	*Gabbioceras lamberti* Breistr.
30	*Protetragonites* cf. *oblique-strangulatum* Kil.
31	*Phylloceras* (*Hypophylloceras*) *cypris* Fall. et Termier
32	*Diadochoceras* (*Verguniceras*) *pretiosum* d'Orb.
33	*Eogaudryceras* (*Eotetragonites*) *raspaili* Breistr.
34	*Phylloceras* (*Hypophylloceras*) *aptiense* Fallot
35	*Salfeldiella* (*S.*) *guettardi* Rasp.
36	*Epicheloniceras tschernyschewi* Sinz.
37	*Epicheloniceras gracile* Casey
38	*Epicheloniceras nickchitchi* nov. sp.
39	*Melchiorites alpina* Fall.
40	*Eogaudryceras* (*Eotetragonites*) *depressus* Rasp.
41	*Salfeldiella* (*Gyrophillites*) *lateumbilicatum* Perv.
42	*Jauberticeras caloti* sp. nov.
43	*Phylloceras* (*Goretophylloceras*) *fortunei* Honn.-Bast.
44	*Eogaudryceras* (*Eotetragonites*) *duvali* d'Orb.
45	*Epicheloniceras buxtorfi* Jac. et Tobl.
46	"*Sinzovia*" *aptiana* Saras.
47	*Phylloceras* (*Hypophylloceras*) *moriezense* Fallot
48	*Salfeldiella* (*S.*) *caucasica* Sayn
49	*Jauberticeras jauberti* d'Orb.
50	*Melchiorites emerici* Rasp.
51	*Valdedorsella akuschaensis* Anth.
52	*Pseudohaploceras falcistriatum* Anth.

3.1. Northern Caucasus

The Lower Cretaceous deposits of the northern slope of the Main Caucasus Range along its length from northwest to southeast extremities are facially strongly different. Belousov (1937a) recognized for them five facial types, of which four belong to the northern slope: (1) typical sandy–clayey, from the Laba River to the Gunib River; (2) coarse-brecciated rocks, watershed of the Belaya and Laba rivers; (3) flysch type occurring mainly on the southern slope, but on the northwestern range, intermediate passing onto the northern slope; and (4) facies of southern Dagestan. The Lower Cretaceous section of these facial types is different in thickness and amount of the fossil fauna, and the region with a particular facies is considered as a region with a particular geological history (Egoian, 1959a, p. 14). Historically, the stratigraphy of the Lower Cretaceous in the Northern-Caucasian region was conducted in three areas: northwestern Caucasus, central area of the northern slope, and in the southeast, which is often referred to as Dagestan. The boundary of the region "Northwestern Caucasus" with the central area is accepted by many workers, along the Pshekha River (Belousov, 1937b). Mordvilko (1956) drew the boundary between the central and southeastern areas approximately along the Chanty-Argun River. Mordvilko (1956, p. 37) considered the territory to the east of the Belaya River (which is geographically very close to the border between the northwestern and central areas of Belousov) to Shakhdag Mountain in the southeast of Dagestan as the area of accumulation of sediments of the Northern Caucasus Foredeep. However, the subdivision of this tectonically uniform territory into two parts, Central and Dagestan, was based on a difference in facies, in the faunal assemblages and, accordingly, on the stratigraphy of the sections. The Dagestan portion of the "...Northern Caucasus Foredeep combined stages of the development of the Northern-Caucasus and Transcaspian regions" (Mordvilko, 1956, p. 38).

3.1.1. Central Regions of the Northern Slope of the Main Caucasus Range

The studies of the central part of the northern slope began earlier than in other regions, because the terrigenous sediments in this region contain many fossils, which allowed dating of the host rocks. The Aptian portion of the Lower Cretaceous section is most consistent along the strike and absent only in the region of the Laba River and southern Dagestan (Renngarten, 1959).

Mordvilko (1960) in the first part of her monograph, considered the region of Kislovodsk most accessible and, therefore, more attractive for the early scholars of Cretaceous beds. Abich (1858), who was one of the first to study the Kislovodsk section, recognized several stratigraphic subdivisions (Table 3). These subdivisions corresponded to the deposits between the natural ledges or terraces, which form the entire Cretaceous section near Kislovodsk. The so-called "Unterer Gault" between the first and second ledge was assigned to the Aptian, most likely Middle and Upper Aptian (in modern understanding). Of these deposits, Abich listed the following ammonites: *A. milletianus, A. crassicostatus, A. nodosocostatus, A. velledae,* and also *A. deshayesi* and *A. fissicostatus* characteristic of the Lower Aptian. The large paleontological monograph by Eichwald (1868), unfortunately does not contain a description of a single middle Aptian species from the Kislovodsk region. Several sections in the Kislovodsk Region were described by Batsevich, Sorokin, and Simonovich (1876), who also characterized fossils from these sections. Among the Aptian ammonites they listed *Acanthohoplites trautscholdi,* which is found in the Clansayesian beds.

At the very end of the 19th century, geological observations in the central part of the northern slope of the Caucasus Range (in the valleys of the Urukh, Ardon, Malka, Kichmalka, and other rivers) were conducted by Karakash (1896). In several valleys near Kislovodsk, he described the presence of dark or loosely-cemented glauconite sandstones (p. 26) with cephalopods characteristic of the Aptian Stage. These included *Acanthoceras* cf. *crassicostatum, A. martini,* and the belemnite *Belemnites semicanaliculatus,* which come from the Middle Aptian. However, in the conclusion, Karakash wrote that he assigned the entire sandstone series to the Lower Albian. The red sandstone beds with *Toxoceras emerici* d'Orb. Karakash (1896, p. 27) erroneously assigned to the Aptian. A year later, Karakash (1897) characterized the Aptian beds from the basin of the Assa and Kambileevka rivers to the Kislovodsk area. He considered that these deposits are the best developed in this area. He listed many diverse fossils, including ammonites. The general ammonites list includes Early Aptian (*Hoplites deshayesi, Acanthoceras cornueli*) and the Albian (Clansayesian) species (*Acanthoceras nodosocostatum*). Only the species *A. martini* and *A. crassicostatum* can to some extent indicate the presence of the Middle Aptian. It is interesting that Karakash concluded about the type of the Aptian fauna that the deposits were of the southern Mediterranean type, which suggests that the comparison of the deposits of this age in Caucasus should be made with the synchronous beds of Western Europe of the same facial type, i.e., deposits of southern France and Switzerland (Karakash, 1897, p. 177). The fossil faunas described by Sinzow (1906, 1913) are direct evidence of the presence of Middle Aptian deposits in this area. The first fauna was based on the collection housed in the museum of the Petersburg Academy of Sciences and Petersburg University. These collections contained ammonites from three regions of Russia, including central areas of the northern Caucasus: *Douvilleiceras subnodosocostatum, D. subnodosocostatum* var. *pusilla, D. tschernyschewi,* and *D. martini.* The first three forms

Table 3. History of studies and stratigraphy of the Middle Aptian in the central part of the northern Caucasus

<table>
<tr><th colspan="2" rowspan="2">Abich, 1858
Kislovodsk</th><th colspan="2" rowspan="2">Renngarten, 1931
Mountainous Ingushetia</th><th colspan="2">Mordvilko, 1937, 1939
Kislovodsk District</th><th colspan="2">Renngarten, 1946, Nalchik</th><th colspan="2">Renngarten, 1951
Great Caucasus</th><th colspan="3">Mordvilko, 1960
Northern Caucasus and Ciscaucasia</th><th>Drushchits, 1960a; Drushchits and Mikhailova, 1960; 1966 Northern Caucasus and Ciscaucasia</th><th colspan="2">Drushchits, Mikhailova and Tkachuk, 1985, 1986, Central regions of the northern slope of the Caucasus</th></tr>
<tr><th colspan="2">zone</th><th colspan="2">zone</th><th colspan="2">zone</th><th colspan="3">zone</th><th>zone</th><th colspan="2">zone</th></tr>
<tr><td rowspan="9">Unterer Gault</td><td rowspan="9">Ammonites milletianus, A. crassicostatus, A. nodosocostatus, A. velledae, A. deshayesi, A. fissicostalus</td><td rowspan="2">Albian</td><td rowspan="2">Dark gray clays with septarians, Acanthoplites nolani Seun.</td><td rowspan="2">Lower Albian</td><td rowspan="2">With Acanthoplites nolani Seun.</td><td rowspan="2">Albian</td><td rowspan="2">Acanthohoplites nolani Seun.; up to 200 m</td><td rowspan="2">Lower Albian</td><td>Hyacanthoplites jacobi–H. tscharlokensis</td><td rowspan="2">Lower Albian</td><td colspan="2" rowspan="2">Hypacantlioplites nolani</td><td rowspan="2">Aacanthoplites nolani</td><td rowspan="2">Upper Aptian</td><td rowspan="2">Acanthohoplites nolani–Diadochoceras nodosocostatum</td></tr>
<tr><td>Hypacanthoplites nolani</td></tr>
<tr><td rowspan="3">Upper Aptian or Gargasian</td><td>5 formation: Ammonites sp. ind., Neohiboiites sp. ind.</td><td rowspan="3">Upper Aptian</td><td>With Acanthoplites aschiltaensis Anth. and A. tobleri Jacob</td><td rowspan="4">Upper Aptian</td><td rowspan="2">Parahoplites mtlchioris</td><td rowspan="3">Upper Aptian</td><td>Acanthohoplites aschiltaensis–A. evolutus</td><td rowspan="3">Upper Aptian</td><td rowspan="2">Colombiceras tobleri–C. subtobleri</td><td>Acanthohoplites aschiltaensis</td><td>Zonation indistinct</td><td rowspan="3">Middle Aptian</td><td rowspan="2">Parahoplites melchioris</td></tr>
<tr><td>4 formation: Phylloceras guettaedi – var. Gelmiensis, Latidorzella akuschensis, Acanthoplites subpaltoceroides</td><td>With Parahoplites melchioris Anth. and P. multicostatus Sinz.</td><td>Parahoplites melchioris–P. subcampichei</td><td>Parahoplites melchioris</td><td>Parahoplites melchioris</td></tr>
<tr><td>3 formation: Latidorseila cf. Akuschensis, Douvileiceras martini var. Caucasica</td><td>With Cheloniceras tschernyschewi Sinz., Ch. martini d'Orb. var. caucasica Anth. ?</td><td>Acanthoplites gargasense</td><td>Colombiceras gargasensis–C. crassicostatum</td><td colspan="2">Cheloniceras tschernyschewi, Ch. subnodosocostatum</td><td>Cheloniceras subnodosocostatum</td><td>Colombiceras crassicostatum–Epicheloniceras subnodosocostatu</td></tr>
<tr><td rowspan="4">Lower Aptian or Bedoulian</td><td rowspan="2">2 formation: Douvilieiceras comueli, D. Seminodosum, D. Tschernyschewi var. Lalicasla, Deschayesites lalilobalus et al.</td><td rowspan="4">Lower Aptian</td><td rowspan="2">With Deshayesites weissi Neum. et Uhl., D. dechyi Papp</td><td>Dufrenoia furcata</td><td rowspan="4">Lower Aptian</td><td>Dufrenoya subfurcata–D. furcata</td><td rowspan="4">Lower Aptian</td><td colspan="2">Dufrenoyia furcata, D. sinzowi, D. subfurcata</td><td>Dufrenoya furcata</td><td rowspan="4">Lower Aptian</td><td>Dufrenoya furcata</td></tr>
<tr><td rowspan="3">Lower Aptian</td><td>Deshayesites dechyi</td><td>Deshayesites dechyi–D. weissi</td><td colspan="2">Deshayesites deshayesi, D. weissi, D. dechyi</td><td>Deshayesites deshayesi</td><td>Deshayesites dechyi</td></tr>
<tr><td rowspan="2">1 formation: Oppelia traulscholdi, Douvilleiceras comueli var. pygmea, Matheronites ridzewskyi, Deshayesites weissi, D. dechyi, Crioceras (Acrioceras) furcatum et al.</td><td rowspan="2">With Tropaeum hillsi Sow. and other evolute ammonites</td><td rowspan="2">Saynella termieri</td><td rowspan="2">Matheronites ridzewskyi–Tropaeum hillsi–Imerites densecostatus</td><td colspan="2" rowspan="2">Tropaeum hillsi, Matheronites ridzewskyi, Acrioceras furcatum</td><td rowspan="2">Matheronites ridzewskyi</td><td>Deshayesites weissi–Procheloniceras albrechtiaustriae</td></tr>
<tr><td>Turkmeniceras turkmenicum</td></tr>
</table>

came from the section in the vicinity of Kislovodsk, whereas the fourth was found in the basin of the Ardon River. Sinzow (1913) published results of the study of the Caucasian collections of P.V. Vittenburg and V.N. Robinson. The Middle Aptian ammonite species come from localities on the Vonyuchka River, tributary to the Balaya River. The paper contains descriptions of the ammonites *Lytoceras belliseptatum, Parahoplites multicostatus,* and *Acanthohoplites tobleri.* Neither paper contains stratigraphic analysis.

At the end of the first decade of the 20th century, V.P. Renngarten began his studies in the central part of the Northern Caucasus. He studied the Cretaceous section on the Nalchik and Shalushka rivers, in which he recognized series of yellowish and gray loosely cemented sandstones with compact calcareous kidney-shaped concretions (Renngarten, 1910, p. 77), from which he identified *Acanthohoplites tobleri, Phylloceras guettardi,* and *Desmoceras zuercheri.* Although all the above taxa are Gargasian (or Middle Aptian), in the modern understanding, Renngarten dated this series as Late Aptian and Clansayesian (undivided).

The studies of Nikshich (1915) were interesting and important for the understanding of the stratigraphic significance of ammonite assemblages. He monographically studied the diverse collection of the genus *Douvilleiceras* collected in various sites of the Central Caucasus by K.I. Bogdanovich (Vonyuchka River), Renngarten (vicinity of Nalchik and the Assa River), A.N. Ogilvi (vicinity of Kislovodsk), and others; the main task of these studies was the recognition of the phylogenetic links between species based on the study of each specimen (Nikshich, 1915, p. 3). All species described in the paper were separated into two phylogenetic groups and, for each species, its precise stratigraphic range within the Aptian was indicated. A younger ammonite group is represented by *Douvilleiceras tschernyschewi, D. subnodosocostatum , D. buxtorfi* , and *D. Martini* var. *orientalis.* Nikshich did not indicate the precise age of each group within the Aptian, but it is certain that the above group characterized the Upper Aptian (as then understood) and its lower zone (as presently understood). In the same paper, Nikshich answered a question which had been discussed for a long time in the western literature and which had been posed previously by Sinzow: what is the difference between *D. Cornueli* d'Orb. and *D. Martini* d'Orb.? Nikshich showed that the initial whorls of the shells of both species up to diameter of 5–6 mm are almost the same and, later, the shells grew in different directions, which is why they were referred to different phylogenetic groups. Nikshich stated that "if there is genetic connection between *D. Cornueli* d'Orb. and *D. martini* d'Orb., it is a very distant connection." (Nikshich, 1915, p. 4).

Renngarten (1926) published the first monograph with a description of the fauna of the Assa–Kambileyevka region. It did not contain a stratigraphic description, since Renngarten worked with the fauna from the section composed by Karakash in 1897. The table of species (pp. 114–117) contains four taxa found in the so-called Upper Aptian: *Phylloceras Guettardi* var. *gelmiensis, Latidorsella akuschensis, Douvilleiceras Martini* var. *caucasica* and *Acanthoplites subpeltoceroides.* The stratigraphic review of this region was published by Renngarten in 1931, although, as written by the author himself, it was prepared as early as 1917. In 1931, Renngarten, when writing the stratigraphic description, took into account all existing data on the Mesozoic of the Caucasus. The Aptian deposits in the watershed of the Assa and Kambileyevka were subdivided into five beds (or formations), of which 3, 4, and 5 formations contained only local forms of cephalopods, virtually unknown in Western Europe. However, all of these belong to groups, which emerged only in the Late Aptian. At the same time, the absence of the forms restricted to the Clansayesian "allows correlations of our formations with the G a r g a s i a n (spaced orthography by Renngarten) substage of the Aptian. Further subdivision into zones is not possible based on our material" (Renngarten, 1931, p. 66). Thus, by the 1920s, Renngarten began using in stratigraphy the terms "Gargasian" and "Clansayesian." For these three formations, Renngarten listed the same taxa that he mentioned in his 1926 paper. He also discussed the stratigraphic ranges of these species in other regions of the Caucasus and in Western Europe. He wrote about *Acanthoplites subpeltoceroides* that the author of the species (Sinzow), when describing this species from the Mangyshlak collections, erroneously dated this horizon with this taxon as Clansayesian. In Renngarten's opinion, this horizon should be Late Aptian (if it is considered that the Clansayesian was then assigned to the Albian). A large part of his 1931 paper is dedicated to tracing the Aptian beds along the entire northern slope of the Caucasus. Renngarten noted some deepening of the marine basin in the Aptian compared to the Barremian. He also noted that the shallowest basin was in the western region of the central Caucasus (vicinity of Kislovodsk) (Renngarten, 1931, p. 72).

In preparation to the 17th International Geological Congress, Mordvilko published a description of a section exposed near Kislovodsk (1937, 1939). She referred it to as the "classic section of the Lower Cretaceous of the Northern Caucasus" (Mordvilko, 1937, p. 55). The stratigraphic log (Mordvilko, 1937, test-fig. 3; 1939, text-fig. 2) contains a 164-m series of glauconitic greenish gray Upper Aptian sandstone (Gargasian Substage), in which Mordvilko recognized two horizons. The lower horizon, more strongly calcareous and with impoverished glauconite (V horizon of Renngarten,[2] which corresponds to the Beds U–L

[2] Renngarten's description of the Kislovodsk section was not published, but Mordvilko in her papers and the 1960 monograph cited his horizons.

of Mordvilko in the 1937 paper, L–V_1 in her 1939 work), containing *Crioceras pawlovi* Wassil., *Douvilleiceras martini* d'Orb., *D. subnodosocostatum* Sinz., *Oppelia trautscholdi* Sinz., *Parahoplites melchioris* Anth., and a rich bivalve assemblage. The upper horizon of the Gargasian Substage (VI horizon of Renngarten or beds of K_1–G of Mordvilko) contains the ammonites *Acanthoplites tobleri* Jacob, *A. aschiltaensis* Anth., *Parahoplites maximus* Sinz., and *Oppelia trautscholdi* Sinz. In the paper of 1939, all of the Upper Aptian or the Gargasian Substage was subdivided into the zone with *Cheloniceras tschernyschewi* Sinz., *Cheloniceras martini* d'Orb. var. *caucasica* Anth. (horizon V, Beds O–V, thickness 45–63 m), zone with *Parahoplites melchioris* Anth., and *Parahoplites multicostatus* Sinz. (horizon V, Beds L–O, thickness 18–23 m) and zone with *Acanthoplites aschiltaensis* Anth. and *Acanthoplites tobleri* Jacob (horizon VI, Beds G–K, thickness 97 m) (Mordvilko, 1939, p. 131).

Krymholz (1939) published a large study on belemnites, listing five belemnite species for the Upper Aptian, *Mesohibolites moderatus* Schwetz., *M. longus* Schwetz., *Neohibolites semicanaliculatus* Bl., *N. wollemanni* Stolley, and *N. strombecki* Mull. Of these *N. semicanaliculatus* is a characteristic taxon of the Gargasian stratotype.

Gerasimov (1940), in a review of the geology of the area between the Malka River in the east and the Kuma Rivers in the west, repeated Mordvilko's data on the Aptian stage of the Kislovodsk section without mentioning her zones.

Somewhat surprisingly Renngarten (1946) included different data on the Aptian Stage in the chapter "Cretaceous System" in the volume "Prirodnye resursy Kabardinskoi ASSR" (Natural Resources of the Kabardian ASSR), without taking into account previous detailed stratigraphic and paleontological studies. Text-figure 10 in that work shows the Upper Aptian, including two lithological series 140 m thick, of which in the text (p. 113) it is said that they are subdivided into three zones: *Dufrenoyia furcata* d'Orb., *Acanthoplites gargasensis* d'Orb., and *Parahoplites melchioris* Anth. The inclusion of the *D. furcata* Zone in the Upper Aptian was conducted by Renngarten similar to that in the Gargasian stratotype in southeastern France, where the Beds with *Dufrenoyia* until the end of the 20th century were placed in the Gargasian. This zone is in the same place in the sections described by Renngarten in the review on the Lower Cretaceous of the northern Caucasus (Renngarten, 1947).

This was the end of the "accumulative" stage in Cretaceous research in the northern Caucasus, including the Upper Aptian, when each subsequent paper added something new on the fauna of these deposits and, since that time, attempts at zonal subdivision and substantiation of this subdivision began.

The first study of this kind was a paper by Renngarten (1951), which proposed substantiation of the faunal (ammonite) zone recognized in the Cretaceous. The region with the best prospects for zonal subdivision of the Caucasus, according to Renngarten was the Kislovodsk and Nalchik regions. In the Upper Aptian beds of this region, there were recognized three ammonite zones: (4) (counting after three zones of the Lower Aptian) *Colombiceras gargasense* d'Orb. and *C. crassicostatum* d'Orb., (5) *Parahoplites melchioris* Anth. and *P. subcampichei* Sinz., (6) *Acanthoplites aschiltaensis* Anth. and *A. evolutus* Sinz. For each zone, the author gave extensive ammonite lists. The substantiation of the zonal subdivision is based on the discussion of the stratigraphic position of ammonites and its comparison with that in the stratotype of the Gargasian. The author concluded that the "Stratigraphic substages of the local significance of the southeastern France are not easily applicable to the Caucasus" (1951, p. 56). On this basis, Zone 3, *Dufrenoyia subfurcata* Kasan. and *D. furcata* Sow., in contrast to the French scheme, was included in the Lower Aptian. In this Renngarten's scheme, the sixth zone of the Upper Aptian recognized in the 1930s is preserved and substantiated as a separate unit. This zone shows the first appearance of *Acanthohoplites, A. aschiltaensis,* and *A. evolutus* associated with the Upper Aptian *Parahoplites,* and lacking Clansayesian species in this part of the section. It should be said that the recognition in the Upper Aptian of a stratigraphic unit above the *Parahoplites* zone not only in the central part of the northern slope of the Caucasus, but also in the northwest of the Caucasus (Luppov, 1952), was instrumental in the later subdivision of the Upper Aptian beds in Turkmenistan (Luppov et al., 1960; Bogdanova et al., 1963). Until now, a separate *Acanthohoplites prodromus* Zone is recognized here between the *Parahoplites melchioris* and *Acanthohoplites nolani* zones. This zone was transferred according to the previous division from the Upper Aptian to the Albian, or in modern terminology, from the Middle Aptian (Gargasian) to the Upper (Clansayesian).

The data on the subdivision of the Cretaceous beds of the Caucasus and their correlation with the standard sections of Western Europe were represented by Renngarten (1959) on the 20th session of the International Geological Congress. In that publication, the characterization of the Upper Aptian is the same as that in his 1951 paper.

All previous studies culminated in the "scheme of stratigraphy of the Lower Cretaceous of the Northern Caucasus and Ciscaucasia," proposed at the stratigraphic meeting on the Russian Platform (Mordvilko, 1956). In that scheme, the Upper Aptian Substage was composed of three zones proposed by Renngarten. For the lower zone, Mordvilko used the name *Cheloniceras tschernyschewi* instead of *Colombiceras gargasense* (after Renngarten), as the latter species is found in the Caucasus sporadically, whereas *C. tschernyschewi* is found abundantly. The *Parahoplites melchioris* and *Acanthoplites aschiltaensis* are described below in the section on the southeastern Caucasus (=Dagestan). In a large monograph on the northern Caucasus, Mordvilko (1960) also used a tripartite division of the Upper Aptian. In a paper on heterodont bivalves, Mordvilko (1979) gave a table of zonal subdivision of the Lower Cretaceous based on ammonites (Table 1, p. 11), in which from bottom to top six zonal species were listed for the Middle Aptian or Gargasian, which apparently reflected the possible subdivision of this part of the scheme into five "subdivisions" (species *Epicheloniceras tschernyschewi* and *E. subnodosocostatum* in the same "subdivision"):

Aptian Stage	Upper Substage	Gargasian Substage	
			*Acanthohoplites aschiltaensis**, *A. uhligi*, *A. evolutus*
			*Colombiceras tobleri**, *C. subtobleri**, *C. subpeltoceroides*, *C. planidorsatum*
			*Parahoplites melchioris**, *P. maximus*, *P. multispinatus*, *P. campichei*
			*Epicheloniceras tschernyschewi**, *E. subnodosocostatum**, *E. martini occidentale*, *E. martini caucasicum*
			*Colombiceras gargasense**

The author of the scheme marks zonal species by (*).

From the end of the 1950s, a group of stratigraphers and paleontologists began working in the central regions of the northern Caucasus (V.V. Drushchits, M.P. Kudryavtsev, I.A. Mikhailova, I.M. Krisyuk, G.A. Tkachuk, and others). Drushchits (1960a, p. 195) noted, "...of all Lower Cretaceous substages, the Upper Aptian was the richest in fossils...." Rengarten's zonal subdivision, and the stage and zonal boundaries were refined and updated. In the papers of these authors, the upper Gargasian *Acanthohoplites aschiltaensis* Zone was removed (Drushchits, 1960a, 1960b; Drushchits and Mikhailova, 1960; 1966) (see also below in the "Dagestan" section). Around that time began the studies of the phylogenetic relationships of Aptian ammonites (Drushchits and Mikhailova, 1979; Mikhailova, 1983): Deshayesitidae, Parahoplitidae, and Douvilleiceratidae. The distribution of these families and relationships between them and within them allow substantiation of the Aptian zones and boundaries between the stages, substages, and zones (Drushchits and Mikhailova, 1979, p. 52). The lower boundary at that time already of the Middle Aptian or Gargasian was placed based on the disappearance of the family Deshayesitidae and on the replacement of the genus of *Cheloniceras* by *Epicheloniceras*. The boundary between the zones within the Middle Aptian coincides with the appearance of the genus *Parahoplites* and evolution of the genera within the family Douvilleiceratidae. The genera *Parahoplites* and *Colombiceras* completely disappear above the boundary of the Middle and Upper Aptian and are replaced by the new genera *Diadochoceras* and *Eodouvilleiceras* typical of the Clansayesian. Beginning from the Middle Aptian, parahoplitids become the dominated family, the lower zone of the substage was referred to as *Colombiceras crassicostatum–Epicheloniceras subnodosocostatum*, where the first species was a member of the family Parahoplitidae (Drushchits and Mikhailova, 1979, p. 56).

Thus, the Middle Aptian or Gargasian in the central part of the northern slope of the Caucasus is composed of two ammonite zones, *Colombiceras crassicostatum– Epicheloniceras subnodosocostatum* and *Parahoplites melchioris*. This subdivision of this substage was used in the large Cretaceous reviews (*Nizhnii mel ...*, 1985; *Stratigrafiya SSSR ...*, 1986).

3.1.2. Southeastern Caucasus (Dagestan)

The study of the Lower Cretaceous, including the Aptian beds of Dagestan began in the middle of the 19th century. Abich (1851) was one of the first authors to recognize the Aptian beds in this region. In this paper, Abich described a section near the village of Akusha. Three upper beds of this section most likely belonged to the Aptian. In 1862, he recognized in the Cretaceous beds three stages, the middle of which included the "green sandstone" and gault (Abich, 1862). This middle stage, according to Abich, is represented by a "thick series of loose marly sandstone with concretions" (Abich, pp. 7, 11, text-fig. I, II), containing *Ammonites milletianus* d'Orb., *A. fissicostatus* d'Orb., and *Ancyloceras matheronianum* d'Orb." (Abich, 1899) (Table 4).

Barbot de Marni (1895) recognized two series in the Lower Cretaceous of Dagestan, upper of which he called the gault. In his interpretation, gault included Aptian and Albian beds, from which he mentioned one Aptian taxon, *Hoplites deshayesi*. Importantly, in this paper Barbot de Marni indicated regions where the gault deposits are most completely developed, Lavashi and Hodzhal-Makha districts (at present, in the latter region, the Albian deposits are assigned to the Hodzhal-Makha Formation (Snezhko, 2008). The first descriptions of the Middle Aptian fauna are given by Anthula (1899). Anthula mainly described the collections by G. Abich from a section near the village of Akusha, the subdivision of which into three parts

Table 4. History of studies and stratigraphy of the Middle Aptian of the southwestern Caucasus (Dagestan)

Abich, 1862, 1899	Anthula, 1899		Renngarten, 1927; Drobyshev, 1931b		Renngarten, 1951		Mordvilko, 1956		Drushchits, 1960a	Mordvilko, 1962		Drushchits, Mikhailova and Tkachuk, 1985, 1986	
Upper stage: modern Middle and Upper Albian	Gaultian	Clay and sandstone with *Aucella coquandi*, *Panopea acutisulcata*	Albian	Dark shaly clay	Albian	*Hypacantlioplites jacobi–H. tscharlokensis* Zone	Albian	*Hypacanthoplites jacobi* Zone	*Hypacanthoplites jacobi* Zone	*Hypacanthoplites jacobi* Coll.–*H. tscharlokensis* Glasun. Zone		Upper Aptian (Clansayesian)	*Hypacantlioplites jacobi* Zone
						Hypacanthoplites nolani Zone		*Hypacanthoplites nolani* Zone	*Acanthohoplites nolani* Zone	*Acanthoplites nolani* Seun. Zone			*Acanthohoplites nolani–Diadochoceras nodosocostum* Zone
Middle Stage: Gaultian and green sandstone–thick Formation of loose marly sandstone with concretions" modern Aptian and Lower Albian *Ammonites milletianus* d'Orb., *A. fissicostatus* d'Orb., *Ancyloceras Matheronianum* d'Orb.	Aptian	1. Gray arenaceous marl *Anomia laevigata* 2. Dark gray clay *Perna Mulleti*, *Thetis major* 3. Marl with calcareous concretions with *Phylloceras Velledae*, *Lytoceras Duvalii*, *Hoplites Deshayesi*	Aptian	Horizon 6: Argillaceous sandstone with beds of more compact marly sandstone with *Acanthoplites tobleri* Jacob Horizons 4 and 5: Gray sandstone with large spheroidal concretions with *Douvilleiceras Tschernyschewi* Sinz.	Upper Aptian	*Acanthohoplites aschiltaensis–A. evolutus* Zone	Upper Aptian	*Acanthohoplites aschiltaensis* Zone	*Parahoplites melchioris* Zone	Colombiceras tobleri Jacob, C. Subtobleri Kas. zone	*Acanthoplites aschiltaensis* Anth., *A. uhligi* Anth.	Middle Aptian (Gargasian)	*Parahoplites melchioris* Zone
						Parahoplites melchioris–P. subcampichei Zone		*Parahoplites melchioris* Zone			*Parahoplites melchioris* Anth.		
						Colombiceras gargasense–C. crassicostatum Zone		*Cheloniceras tschemyschewi* Zone	*Epicheloniceras subnodosocosatum* Sinz. Zone	*Cheloniceras tschernyschewi* Sinz., *Ch. subnodosocostatum* Sinz. Zone			*Colombiceras crassicostatum–Epicheloniceras subnodosocostatum* Zone
				Horizons 2 and 3: *Lytoceras belliseptatum* Anth., *Crioceras* (*Ancyloceras* cf. *Bowerbanki* Sow., large *Deshayesites*	Lower Aptian	*Dufrenoya subfurcata–D. furcata* Zone	Lower Aptian	*Dufrenoya dufrenovi* Zone	*Dufrenoya furcata* Zone	*Dufrenoya furcata* Sow., *D. subfurcata* Kas. Zone		Lower Aptian (Bedoulian)	*Dufrenoya furcata* Zone
								Deshayesites dechyi Zone	*Deshayesites dechyi*, *D. weissi* Zone	*Deshayesites weissi* Neum. et Uhl., *D. dechyi* Papp Zone			*Deshayesites deshayesi* Zone
													Deshayesites weissi–Procheloniceras albrechtiaustriae Zone
								Acrioceras furcatum Zone	*Matheronites ridzewskyi* Karak., *Acrioceras furcatum* Orb. Zone	*Matheronites ridzewskyi* Karak., *Acrioceras furcatum* Orb. Zone			*Turkmeniceras turkmenicum–Matheronites ridzewskyi* Zone
Lower Stage, Neocomian	Barremian (Urgonian)	Gray marl with *Crioceras Orbignyi*, *Crioceras ramososeptatum*	Barremian	Sandy-marly formation of the Barremian *Exogyra* cf. *latissima*, *Trigonia subdaedalea* et al.	Barremian	*Heteroceras astieri* d'Orb., *H. leenhardti* Kil., *Imerites giraudi* Kil.	Barremian	*Heteroceras* sp.		Ammonite-based zones not recognized		Barremian	*Colchidites securiformis* Zone

Anthula also cited from Abich (1851). However, in the concluding table in p. 150, the Aptian Stage was subdivided by Anthula into three parts based on his own data of 1896. In the table in p. 134, Anthula listed 24 ammonite species, described by him from Akusha. The described species of "parahoplitids" were subdivided into two groups. Later, species of these groups were assigned either to *Parahoplites: P. melchioris* Anth., *P. sjöegreni* Anth., or to *Acanthohoplites: A. trautscholdi* Sim., Bač. Sor., *A. uhligi* Anth., *A. aschiltaensis* Anth., *A. bigoureti* Seun., *A. bigoti* Seun., *A. bergeroni* Seun., *A. abichi* Anth., and others. Anthula considered the Aptian Stage of the Caucasus the richest fossiliferous horizon in the Lower Cretaceous and the assemblage of the ammonite fauna to belong to the Tethyan (or Alpian) type.

Anthula's data on the ammonite assemblages from the Middle Aptian deposits of Dagestan were supplemented by a monograph by Kazansky (1914). Kazansky described a diverse assemblage of Aptian species belonging to the genera *"Crioceras"* (nine species), *Douvilleiceras* (ten species), *Parahoplites* (four species), and *Acanthohoplites* (20 species, of which six are new) from the localities of Akusha, Lavashi, Gergebil, Tsudakhar, Hodzhal-Makha, Kaka-Makha, Shakh Dagh, and others. The Gargasian species include *"Crioceras" (?) caucasicum* sp. nov., *"C."* aff. *ramososeptatum* Anth., *"Douvilleiceras" martini* d'Orb., *"D." stuckenbergi* sp. nov., *"D." tschernyschewi* Sinz., *"D." pusillum* sp. nov., *"D". intermedium* sp. nov., *"D." subnodosocostatum* Sinz., *Parahoplites melchioris* Anth., *P. campichei* Sinz., and *P. sjogreni* Anth. Interestingly, in descriptions of many species of *Acanthohoplites,* Kazansky indicates their possible Aptian age. In other words, although many paleontologists of that time assigned deposits in Western Europe and Russia containing these species to the Albian (Clansayesian horizon), Kazansky considered them to be Aptian.

Renngarten began working in Dagestan from the first decade of the 20th century. His observations in the Kaitago-Tabasaran and Darga regions (Renngarten, 1927) were accompanied by descriptions of sections in virtually the same sites where G. Abich, D. Anthula, and P.A. Kazansky made their collections. In the section near the village of Akusha (approximately 3 km south of the village), Renngarten recognized 18 beds (in the interval of Barremian–Upper Cretaceous). Deposits from the second to the tenth bed he assigned to the Upper (Middle in the modern understanding) Aptian. This part of the section is represented mostly by marly sandstones with beds of coquina and layers of large sandy–calcareous concretions. These deposits contained fragments of large shells of *Douvilleiceras, Parahoplites melchioris,* many bivalves and gastropods. These beds are overlain by lithologically similar deposits with *Acanthohoplites* characteristic of the Clansayesian horizon. Aptian beds with *Parahoplites melchioris* were also recorded by Renngarten in the Tsudakhar section. In the concluding stratigraphic chapter, Renngarten recognized a sandy–marly formation in the middle of the Lower Cretaceous section, which embraced deposits from the Upper Barremian to the Cenomanian, in which the Upper (=Middle) Aptian corresponded to the «marly sandstones with lenses and concretions of sandy limestones and a phosphorite bed with *Parahoplites melchioris* Anth., *Exogyra latissimi* Lam. etc". (Renngarten, 1927, p. 51).

Drobyshev (1929, 1931a, 1931b) worked in Dagestan at approximately the same time. When describing sections, Drobyshev referred mainly to the scheme by Renngarten (1927) and, only in the first paper, he described a section of the Khadum region, in which he recognized a 78-m series of sand with large concretions, containing *Douvilleiceras tschernyschewi* followed by a six-meter bed with *Acanthoplites tobleri.* He assigned this bed to the Upper Aptian (Drobyshev, 1929, p. 27).

In 1951, Renngarten published the first zonal scheme of the stratigraphic subdivision of the Lower Cretaceous in the Great Caucasus. In this scheme, three ammonite zones corresponded to the previous Upper Aptian (from bottom to top): *Colombiceras gargasense* d'Orb. and *C. crassicostatum* d'Orb., *Parahoplites melchioris* Anth. and *P. subcampichei* Sinz., *Acanthoplites aschiltaensis* Anth. and *A. evolutus* Sinz. In explanations to this scheme, there was no mention of Dagestan. However, when characterizing the Upper Aptian, Renngarten referred to the studies of Abich and Kazansky, who studied this fauna from the Dagestan sections.

Slightly later, Mordvilko (1956, pp. 45, 46) published a partly emended work (mainly emended in the names of the zones), covering the Lower Cretaceous of the Groznyi Region, Dagestan, and Trans-Kuma Plain. Upper Aptian also corresponded to three zones, *Cheloniceras tschernyschewi, Parahoplites melchioris,* and *Acanthoplites aschiltaensis,* each containing numerous ammonite species, slightly fewer belemnites, and bivalves. Ammonite lists included species identified by Anthula, Kazansky, and Renngarten. Mordvilko considered *Cheloniceras tschernyschewi* as a better zonal species than *Colombiceras gargasense,* because the latter occurs both in the Lower (!) and Upper Aptian, whereas *C. tschernyschewi* is restricted to the Lower Zone of the Upper Aptian. In addition, *C. tschernyschewi,* like its accompanying species *C. subnodosocostatum,* has a wide geographical distribution. Mordvilko considered the recognition of the *Parahoplites melchioris* Zone as a "specific feature of the Caucasian scheme" due to the restricted distribution of this species in other regions. Mordvilko wrote that the recognition of a third zone is not always convenient (p. 54), because the lower part of this zone contains *Parahoplites,* and the species *Acanthoplites aschiltaensis,* continues in the overlying *A. nolani* Zone. For the same reason, Drushchits removed this zone from the stratigraphic scheme of the Upper Aptian of the Dagestan sections (Drushchits, 1960b).

In his opinion, the inconvenience of this zone is evident from the composition of the ammonite fauna. In addition, at the top of the *P. melchioris* Zone, almost in all sections of Dagestan, there is a layer of phosphoritic conglomerate containing a mixed fauna of the Upper Aptian and Lower Albian (then Clansayesian). Thus, "there is no space for *A. aschiltaensis*" (Drushchits, 1960b, p. 32). However, in the later papers of Renngarten (1961) and Mordvilko (1962), all three Upper Aptian zones were still present.

Renngarten (1961) summarized all existing data on the Lower Cretaceous of Dagestan and gave descriptions of eight standard sections with identifications of many fossil groups considering this summary useful for scientific and applied purposes. The standard section of the Upper Aptian was chosen in the succession of beds along the Khokh-Bort River in the vicinity of the village of Hodzhal-Makha. *Tetragonites heterosulcatus* Anth., *Puzosia saltaense* Anth., *Parahoplites sjogreni* Anth., and *Colombiceras subtobleri* Kas., previously established in Dagestan were listed as characteristic species.

Mordvilko's (1962) Dagestan monograph focused on the cyclicity of sedimentation and correlation mainly based on bivalves and ammonite scales developed by Renngarten. Mordvilko, in contrast to Drushchits, considered that the Upper Aptian beds overlie the Lower Aptian conformably, whereas at that time Drushchits noted the presence of phosphoritic horizons in some sections of Dagestan. These phosphoritic horizons were studied by paleontologists from various institutions. Kakabadze et al. (1978b) in a small note on the Lower Aptian of Central Dagestan gave a somewhat generalized section of the Lower and Middle Aptian in the vicinity of the villages of Nizhnie Chugli, Levashi, Khodzhal-Makha, Tsudakhar, Akusha, and Mekegi. These authors established that a conglomerate bed lies at the base of the *Epicheloniceras subnodosocostatum–Colombiceras crassicostatum* Zone referred to as the "loaded horizon," containing various Lower and Middle Aptian fossils (p. 123, text-fig. 1).

Large summaries (*Nizhnii mel ...,* 1985; *Stratigrafiya SSSR ...,* 1986) give brief information on the Middle Aptian beds of Dagestan, known from earlier studied on his region (see above). The Middle Aptian contained two zones, lower *Colombiceras crassicostatum–Epicheloniceras subnodosocostatum* and upper *Parahoplites melchioris* zones.

3.2. Transcaspia (Turkmenistan)

Cretaceous deposits are widespread in Turkmenistan, but over a larger area, they are buried beneath a thick cover of a younger sedimentary series and are only opened in boreholes. They are exposed in the south of the country in the Kopet Dagh Range System, extending from northwest to southeast along the Iranian border. To the northwest from the Kopet Dagh Range and its northwestern fringes, the Kyurendag Range, they play an essential role in the geological structure of the Lesser Balkhan and Great Balkhan and, in the west of the Kuba Dagh Range, and at the foothills of the Tuarkyr. Cretaceous sections in the listed mountainous regions are very different in composition, thickness, and partly in fossils.

In contrast to other intervals of the section, the Middle Aptian beds over the entire area are marine and do not contain large gaps in sedimentation and are characterized by rich ammonite assemblages.

3.2.1. Kopet Dagh

The first evidence on the presence of the Lower Cretaceous, including the Aptian beds, in the Kopet Dagh are given in a paper by K. Bogdanovich. However, apart from the Lower Aptian species *"Hoplites"* cf. *deshayesi*, no Aptian fossils are mentioned. In 1913, Natsky (1914, 1915a) studied in detail the deposits in the Kyurendag Range. In the core of the Danata Syncline, he recognized several faunal horizons, of which three upper horizons he assigned to the Middle and Upper Aptian. In the Lower part of the Aptian series, Natsky recorded *Acanthoplites tobleri*, *Parahoplites melchioris, P. multicostatus*, *P. maximus*, and *Aucellina* sp. and *"Hoplites" furcatus*, which is not characteristic of the beds with the above listed ammonites. According to Natsky, overlying dark clay with concretions contained *Acanthoplites uhligi* and *A.* ex gr. *nolani.* Beds 12 and 13 of the sections with *Acanthohoplites* Natsky correlated with the Clansayesian of France and, following E. Haug, assigned it to the Aptian based on closer relationships of ammonites of the Clansayesian horizon with the underlying Aptian fauna than with the Albian (Table 5).

Andrusov (1914) worked in the Kopet Dagh at approximately the same time. Natsky and Andrusov worked synchronously and often used for comparison stratigraphic schemes composed by one of them. For instance, Andrusov, studying the stratigraphy of the Cretaceous beds from Kyzyl-Arvat to Kara-Kala, based his subdivisions on the data from Natsky (1913, 1914) from Kyurendag. Also, Natsky (1915b), when describing a section near the Sekiz-Khan spring, compared it with the section near Kamyshly studied by Andrusov. In the Sekiz-Khan section, Natsky recognized three horizons: (1) loose gray sandstone, alternating with limestones containing large *Exogyra* (in modern understanding, this is the *Dufrenoyia furcata* Zone); (2) thick bluish clay with septarian nodules containing *Parahoplites*, *Acanthohoplites*, and *Aucellines;* these clays Natsky considered to be Middle Aptian; (3) sandstone with concretions containing *Acanthoplites milletianus* followed by the Albian beds with *Leymeriella tardefurcata*.

Numerous collections of the Lower Cretaceous ammonites of Kopet Dagh, assembled by Natsky were monographically studied by Glazunova (1953). Based on these studies was a scheme of the Aptian stratigra-

Table 5. History of studies and stratigraphy of the Middle Aptian of the Kopet Dagh Range

Natsky, 1914, 1915a		Glazunova, 1953			Luppov et al., 1960		Luppov, 1965		Marchenko et al., 1972		Resheniya..., 1977			Tovbina et al., 1985; Luppov et al., 1986	
Upper Aptian	Beds with *Aucellina caucasica*	Lower Albian	Acanthohoplites Zone	Subzone jacobi	Lower Albian	*Hypacanthoplites jacobi* Zone	Lower Albian (Clansayesian)	*Hypacanthoplites jacobi* Zone	Lower Albian	*Hypacanthoplites jacobi* Zone	Upper Aptian	Clansayesian beds	*Hypacanthoplites jacobi* Zone	Upper Aptian	*Hypacanthoplites jacobi* Zone
	Beds with *Acanthoplites uhligi* and *A.* ex gr. *nolani*			Subzone nolani		*Acanthohoplites nolani* Zone		*Acanthohoplites nolani* Zone		*Acanthohoplites nolani* Zone			*Acanthohoplites nolani* Zone		*Acanthohoplites nolani* Zone
					Upper Aptian	Beds with *Acanthohoplites* ex gr. *uhligi*, *Diadohoceras*	Upper Aptian (Gargasian)	*Acanthohoplites* sp. n. Zone (beds with *Acanthohoplites* ex gr. uhligi and *Diadohoceras*)		*Acanthohoplites prodromus* Zone			*Acanthohoplites prodromus* Zone		*Acanthohoplites prodromus* Zone
Middle Aptian	Beds with *Parahoplites* aff. *multicostatus*, *P. grossouvrei*	Upper Aptian	Parahoplites Zone	Subzone melchioris		*Parahoplites melchioris* Zone		*Parahoplites melchioris* Zone	Upper Aptian	*Parahoplites melchioris* Zone		Gargasian beds	*Parahoplites melchioris* Zone	Middle Aptian	*Parahoplites melchioris* Zone
Lower Aptian	Beds with *Peina*, *Exogyra* sp., *Pecten* sp., *Trigonia* sp., *Astarte* cf. *gigantea* Desh.	Lower Aptian	Oyster Zone	Subzone Ostrea		*Epicheloniceras subnodosocostatum* Zone		*Epicheloniceras subnodosocostatum* Zone		*Epicheloniceras subnodosocostatum* Zone			*Epicheloniceras subnodosocostatum* Zone		*Epicheloniceras subnodosocostatum* Zone
	Beds with *Alectrionia* sp., *Exogyra* sp.		Deshayesites Zone	Subzone weissi	Lower Aptian	Beds with *Dufrenoya furcata*	Lower Aptian (Bedoulian)	*Dufrenoya furcata* Zone	Lower Aptian	*Dufrenoya furcata* Zone	Lower Aptian		*Dufrenoya furcata* Zone	Lower Aptian	*Dufrenoya furcata* zone
						Beds with *Deshayesites deshayesi*		*Deshayesites deshayesi* Zone		*Deshayesites deshayesi* Zone			*Deshayesites deshayesi* Zone		*Deshayesites deshayesi* zone

phy of this area. The Aptian contained two substages. In the Lower Aptian, the *Deshayesites* Zone is overlain by the "oyster" zone, which in modern understanding should correspond to the lower part of the Middle Aptian *subnodosocostatum* Zone. The Upper Aptian corresponded to the *Parahoplites* Zone with a single *Melchioris* Zone. The interval of the Aptian with *Acanthohoplites* was recognized as the *Acanthohoplites* Zone in the Lower Albian with two subzones, *nolani* and *jacobi*.

M.I. Sokolov worked in the 1950s in western Turkmenistan (unpublished work of 1958). In southern Turkmenistan, he studied only the Kyurendag Range, where in the Upper Aptian beds, he recognized the same ammonite zones, as in the Lesser Balkhan: *Cheloniceras subnodosocostatum*, *Parahoplites melchioris*, and *Acanthoplites aschiltaensis*.

In 1956, geologists from the Central Asian expedition of All-Russia Research Geological Institute (VSEGEI) (1956–1964) began comprehensive research on the Lower Cretaceous of Turkmenistan. Sections studied at that time included all the above regions of western and southern Turkmenistan: Kopet Dagh, Tuarkyr, Great and Lesser Balkhans, and in Kuba Dagh. The first detailed ammonite scheme of the Aptian and Clansayesian beds of Kopet Dagh was published in 1960 (Luppov et al., 1960). Beds with *Acanthohoplites* and *Diadochoceras*, which at that time were correlated with the Caucasus *Acanthohoplites aschiltaensis* Zone were recognized above the *P. melchioris* Zone.

The first results of studies in Turkmenistan were given in the paper by Luppov (1965), in which the Aptian Stage was accepted as two substages, Bedoulian and Gargasian. The Clansayesian horizon was at the same time the lower part of the Lower Albian. The Upper Aptian included three zones: *Epicheloniceras subnodosocostatum*, *Parahoplites melchioris*, and *Acanthohoplites* sp. nov. Zone (Beds with *Acanthohoplites* ex gr. *uhligi* and *Diadochoceras* of the schemes of 1960). After Tovbina's (1968) works, who studied ammonites of the Upper Aptian and Lower Albian (Clansayesian) of all Turkmenistan, the Upper Aptian *Acanthohoplites* sp. nov. Zone received the name *Acanthohoplites prodromus* (Marchenko et al., 1972).

To develop a unified stratigraphic scheme of the Lower Cretaceous of Turkmenistan in 1966 an excursion was held to all sections of the Lower Cretaceous. Results of this excursion and stratigraphic meeting held in Samarkand in 1971 were published in "Resheniya" (1977). By this time, the ranges of the Aptian and Albian Stages were changed in connection with the transfer of the Clansayesian horizon in the Aptian Stage (*Postanovleniya* ... 1973). However, the subdivision of the Aptian into three substages had not yet been accepted. Therefore, the Upper Aptian included five zones: *E. subnodosocostatum*, *P. melchioris*, *A. prodromus*, *A. nolani*, and *H. jacobi*.

The subdivision of the Aptian into three parts was accepted in 1979 (*Postanovleniya* ..., 1981) and published in a paper about the Aptian beds of Kopet Dagh (Tovbina et al., 1985), which described several most complete sections of the Aptian beds with detailed lists of four fossil groups, including ammonites, bivalves, brachiopods, and echinoids. This scheme was included in the summary of stratigraphy of the Cretaceous System (Luppov et al., 1986). The Middle Aptian included the *Epicheloniceras subnodosocostatum* and *Parahoplites melchioris* zones.

3.2.2. Lesser Balkhan

Originally, the Aptian beds in the Lesser Balkhan Range were recorded by Natsky (1916), which is subdivided into three parts: lower, gray loose sandstone with *Deshayesites consobrinus* and *D. weissi;* middle, argillaceous bluish marl; and upper, thickly bedded sandstone (Table 6). In modern understanding, the marl belongs to the Lower Aptian *D. weissi* Zone, whereas the thickly bedded sandstone belongs to the Middle Aptian *Epicheloniceras subnodosocostatum* Zone. The beds of this zone, according to Natsky, are overlain by the Cenomanian with a large stratigraphic unconformity.

Over 40 years later, Sokolov (1958) recognized in the sections of Lesser Balkhan and Kyurendag, two zones in the Upper Aptian: *Cheloniceras subnodosocostatum* with *Colombiceras tobleri* and *C. crassicostatum* and *Parahoplites melchioris* zones. He also noted that the *Dufrenoyia sinzovi* Zone recognized in Tuarkyr, is most likely missing in the sections of Lesser Balkhan : "... because fragments of very large undeterminable ammonites were found above the beds with *D. deshayesi*" (Sokolov, 1958, p. 10). In the current understanding, the "large ammonite fragments" belong to the genus *"Ammonitoceras"* and are found in the *Epicheloniceras subnodosocostatum* Zone.

At the beginning of the 1960s, a conclusion was made in the course of geological mapping works (Yatchenko, 1962) above the erosion of the *Dufrenoyia furcata* Zone (=*D. sinzovi* Zone after M.I. Sokolov), and two zones were recognized in the Upper Aptian, *Epicheloniceras subnodosocostatum* and *Parahoplites melchioris*. Above the *P. melchioris* Zone, Yatchenko showed an erosion surface, where he assigned the overlying beds to the Lower Albian.

Volume 22 of *Geologiya SSSR* (Marchenko et al., 1972) took into account works of stratigraphers of VSEGEI from the second half of the 1960s in the Upper Aptian of Lesser Balkhan two zones were recognized, *E. subnodosocostatum* and *P. melchioris*. The erosion of the *Deshayesites deshayesi* Zone rather than the *Dufrenoyia furcata* Zone in the Lower Aptian, and the erosion between the *P. melchioris* Zone and undivided beds of the *Acanthohoplites nolani* and *Hypacanthoplites jacobi* Zones were recorded. In the Unified Scheme of the Lower Cretaceous of Turkmenistan

Table 6. History of studies and stratigraphy of the Middle Aptian of the Lesser Balkhan Range

	Natsky, 1916		Sokolov, 1958			Yatchenko, 1962		Marchenko et al., 1972		Resheniya..., 1977		Luppov et al., 1986
Middle and upper Aptian	Beds 4. Sandstone with *Aucellina caucasica* and *Acanthoplites* sp.	In Portsaiman gorge, under beds with *Leymeriella*, *Parahoplites multicostatus* is recorded	Lower Albian	?		Lower Albian	*Hypacanthoplite jacobi* Zone	Lower Albian	*Hypacanthoplite jacobi* and *Acanthohoplites nolani* Zones	Upper Aptian	*Hypacanthoplite jacobi* Zone	Upper Aptian	*Hypacanthoplite jacobi* Zone
				Acanthohoplites ex gr. *nolani*			*Acanthohoplites nolani* Zone				*Acanthohoplites nolani* Zone		*Acanthohoplites nolani* Zone
	Beds 3. Sandstone with *Acanthoplites aschiltaensis*		Upper Aptian	*Parahoplites melchioris* Zone	*Acanthohoplites aschiltaensis*		Beds with *Diadochoceras* and *Acanthohoplites* ex gr. *uhligi*						
	Beds 3. *Crioceras* sp., *Acanthoplites* sp.					Upper Aptian	*Parahoplites melchioris* Zone	Upper Aptian	*Parahoplites melchioris* Zone		*Parahoplites melchioris* Zone	Middle Aptian	*Parahoplites melchioris* Zone
				Cheloniceras subnodosocostatum Zone			*Cheloniceras subnodosocostatum* Zone		*Epicheloniceras subnodosocostatum* Zone		*Epicheloniceras subnodosocostatum* Zone		*Epicheloniceras subnodosocostatum* Zone
Lower Aptian	Gray loose sandstone *Deshayesites consobrinus*, *D. weissi*		Lower Aptian	not recognized		Lower Aptian	Beds with *Dufrenoya* (washed)	Lower Aptian	*Dufrenoya furcata* Zone	Lower Aptian	*Dufrenoya furcata* Zone	Lower Aptian	*Dufrenoya furcata* Zone
				Deshayesites deshayesi Zone			Beds with *Deshayesites deshayesi*						

(*Resheniya*, 1977), both *E. subnodosocostatum* and *P. melchioris* zones were accepted for Lesser Balkhan; these zones were then placed in the lower Upper Aptian, whereas in the review of the Cretaceous stratigraphy (*Stratigrafiya SSSR*..., 1986), these zones constituted the Middle Aptian Substage.

3.2.3. Great Balkhan and Kuba Dagh

Wassiliewskyi (1926) was the first to record Aptian beds in the Great Balkhan Range. He studied sections of the northern slope of the range and noted presence in these sections of series of sandy–clayey rocks with sandstone interbeds in the Lower Aptian (or Bedoulian) and, from the higher beds, he identified the Gargasian ammonite assemblage: *Ammonitoceras pavlowi*, *Acanthoplites tobleri*, *Parahoplites melchioris*, and *Douvilleiceras martini* (Table 7). This researcher was the first after V.P. Semenov and A.D. Natsky to use French names of the substages for parts of the Aptian in the Great Balkhan sections.

Considerably later, Luppov (1949) recognized in the Kuba Dagh Range near Krasnovodsk (presently Turkmenbashi) two substages of Aptian, Lower and Upper, without using the French terminology. He placed Clansayesian in the Albian. Luppov assigned sandstone with concretions (ca. 100 m thick), from which he identified *Ammonitoceras pavlowi*, *Parahoplites melchioris*, *P. multicostatus*, and *Tetragonites duvalianus*, to the Upper Aptian.

An attempt at stratigraphic subdivision of the Lower Cretaceous and the Aptian, in particular, of the Great Balkhan by Aliev and Purliev (1965) seems to have been unproductive. Their stratigraphic subdivision is at substage level, which is less detailed than the schemes previously proposed for this region. The stratigraphic position of some species (and even genera) is clearly incorrectly recorded. For instance, the incorrect records included the Early Albian ammonite *Beudanticeras dupinianum* in the Upper Aptian beds and Late Aptian (or as currently interpreted, Middle Aptian) species *Parahoplites maximus* in the Lower Aptian deposits. This caused T.N. Bogdanova and E.Ya. Yakhnin, who studied the sections of Great Balkhan a few years earlier (1960–1963), to publish the zonal scheme of the Aptian and Albian stages, which was as detailed as the Tuarkyr scheme (Bogdanova and Yakhnin, 1967). In Volume 22 of *Geologiya SSSR* (Bogdanova et al., 1972b), the Aptian Stage of Great Balkhan and Kuba Dagh included two substages. The upper substage included three ammonite zones. In contrast to the scheme of Bogdanova and Yakhnin (1963), the lower subdivision of the Lower Albian was referred to as the beds with *Acanthohoplites nolani*, rather than the zone.

In the summary of the stratigraphy of the Cretaceous System (Luppov et al., 1986), the Aptian Stage of Great Balkhan and Kuba Dagh included three substages, of which two zones are present in the Middle Aptian.

3.2.4. Tuarkyr

At the end of the 19th century, this area was visited by Andrusov (1889) and Semenov (1899). They made the short traverses of the Tuarkyr ancticlinal folds and noted the presence of Cretaceous beds on its wings. Luppov (1931) was the first to record here the presence of the Aptian; he recognized above the bed with Lower Aptian *Deshayesites* and *Dufrenoyia* a series of dark clay and correlated it with the septarian clay of Mangyshlak. Later, in an unpublished work of 1936, he characterized the Upper Aptian beds with *Parahoplites melchioris*, *Hypacanthoplites nolani*, and *H. jacobi* zones in the Lower Albian (Table 8).

Sokolov (1958) observed that ammonite zones cannot be recognized in Tuarkyr. This especially concerns the section of Tekedzhik, in which Sokolov did not find characteristic fossils. However, in this section he recognized the *Dufrenoyia sinzovi* Zone, represented by phosphoritic conglomerates and a series of black clays at the base of the Upper Aptian. In the region of the Babashi wells, Sokolov observed analogous series of clay, and in the sideritic and arenaceous concretions, a large amount of ammonites, representatives of the *Cheloniceras subnodosocostatum* Zone recognized in the Lesser Balkhan: *Cheloniceras subnodosocostatum*, *Colombiceras tobleri*, and others. The upper part of the clay series, assigned to the Upper Aptian, contains abundant *Parahoplites melchioris* and others characteristic of the *Parahoplites melchioris* Zone. In the uppermost horizons of this series, Sokolov recorded the presence of *Acanthoplites aschiltaensis*. Sokolov considered that the beds, including the Aptian, of Tuarkyr are assigned to the platform type, in contrast to the geosyncline Lesser Balkhan and Kyuren-Dag. In addition, he considered that the area of Tuarkyr is transitional to the Mangyshlak type of deposits.

A detailed study of the Aptian and Albian beds of Tuarkyr was conducted only at the end of the 1950s. As a result of these works, the presence of the *Epicheloniceras subnodosocostatum* and *Parahoplites melchioris* zones was substantiated in the lower part of then the Upper Aptian (Bogdanova et al., 1963). The third (uppermost) stratigraphic subdivision of the Upper Aptian (the Clansayesian was referred to the Albian) in this work contained the "Beds with *Acanthohoplites* ex gr. *uhligi* and *Diadochoceras*." The ammonite assemblage of these beds contained many *Acanthohoplites* species, including *Acanthohoplites* sp. nov. ex gr. *uhligi*, *A. abichi*, *A. bigoti*, *A.* cf. *planidorsatus*, *A. aschiltaensis*, and representatives of the genus *Diadochoceras*, and was distinguished from the assemblage of the *Parahoplites melchioris* Zone. At the same time, as was mentioned by the above paleontologists, this assemblage did not contain the key Lower Albian species of

Table 7. History of studies and stratigraphy of the Middle Aptian of the Great Balkhan Range and Kuba Dagh Range

Wassiliewsky, 1926			Luppov, 1949		Aliev and Purliev, 1965		Bogdanova and Yakhnin, 1967		Bogdanova et al., 1976b		Luppov et al., 1986	
Sandstone and marl: *Lytoceras*, *Tetragonites duvali*		Albian	Albian	Gray-green sandstone and clay with *Phylloceras* (*Salfeldiella*) ex gr. *guettardi* Rasp., *Acanthoplites nolani* Seun. var. *crassa* Sinz., *A. lorioli* Sinz., *A. bergeroni Seun.*	Lower Albian	Yellowish gray finely and small-grained sandstone *Aucellina* ex gr. *caucasica* Buch, *A. nassibiana* Sok.	Lower Albian	*Acanthohoplites nolani* Zone	Lower Albian	Beds with *Acanthohoplites nolani*	Upper Aptian	*Acanthohoplites nolani* Zone
Sandy-clayey rocks of Formation 4 (succession of ammonoid occurrences)	*Acanthoplites tobleri*	Upper Aptian (Gargasian)	Upper Aptian	Yellow-green sandstone, with large spherical concretions *Tetragonites* cf. *duvalianus* d'Orb., *Parahoplites multicostatus* Sinz., *P. melchioris* Anth., *Ammonitoceras pavlowi* Wass.	Upper Aptian	Yellowish, less commonly greenish gray finely and small-grained, often argillaceous sandstone with thin layers of compact calcareous sandstone with spherical calcareous concretions *Parahoplites melchioris*, *P. melchioris* var. *transitans*, *Beudanticeras dupinianum*, *Colombiceras tobleri*, *C. tobleri* var. *discoidalis*, *C. subcampischei* et al.	Upper Aptian	*Aacanthohoplites prodromus* Zone	Upper Aptian	*Aacanthohoplites prodromus* Zone		*Aacanthohoplites prodromus* Zone
	Parahoplites melchioris							*Parahoplites melchioris* Zone		*Parahoplites melchioris* Zone	Middle Aptian	*Parahoplites melchioris* Zone
	Ammonitoceras pavlovi, *Douvilleiceras martini*							*Epicheloniceras subnodosocostatum* Zone		*Epicheloniceras subnodosocostatum* Zone		*Epicheloniceras subnodosocostatum* Zone
	Deshayesites weissi, *D. consobrinoides*	Lower Aptian (Bedoulian)	Lower Aptian	Deshayesites weissi Neum. et Uhl., *D.* ex gr. *deshayesi* Leym., *Neohibolites ewaldi* Stromb., *Mesohibolites* cf. *elegans* Stromb	Lower Aptian	Gray and greenish gray sandstone with layers of arenaceous clay with *Deshayesites weissi*, *D.* aff. *volgensis*, *D. bodei*, *Parahoplites maximus*	Lower Aptian	*Dufrenoya furcata* Zone	Lower Aptian	*Dufrenoya furcata* Zone	Lower Aptian	*Dufrenoya furcata* Zone
								Deshayesites deshayesi Zone		*Deshayesites deshayesi* Zone		*Deshayesites deshayesi* Zone

Table 8. History of studies and stratigraphy of the Middle Aptian of Tuarkyr

<table>
<tr><th colspan="2">Luppov, 1935</th><th colspan="2">Bogdanova et al., 1963</th><th>Bogdanova et al., 1972a</th><th>Substage</th><th>Luppov et al., 1986</th></tr>
<tr><td colspan="2" rowspan="2">IV. Lower Albian
a. Zone
Hypacanthoplites nolani,
H. jacobi</td><td rowspan="2">Lower Albian</td><td rowspan="2">Beds with Acanthohoplites nolani and Hypacanthoplites</td><td rowspan="2">Beds with Acanthohoplites nolani and Hypacanthoplites</td><td rowspan="3">Upper Aptian</td><td>Beds with Hypacanthoplites</td></tr>
<tr><td>Acanthohoplites nolani Zone</td></tr>
<tr><td colspan="2" rowspan="3">III. Upper Aptian
2. Parahoplites melchioris Anth.
1. Desmoceras cf. akuschaensis Anth.</td><td rowspan="3">Upper Aptian</td><td>Beds with Acanthohoplites ex gr. uhligi and Diadochoceras</td><td>Acanthohoplites prodromus Zone</td><td>Acanthohoplites prodromus Zone</td></tr>
<tr><td>Parahoplites melchioris Zone</td><td>Parahoplites melchioris Zone</td><td rowspan="2">Middle Aptian</td><td>Parahoplites melchioris Zone</td></tr>
<tr><td>Epicheloniceras subnodosocostatum Zone</td><td>Epicheloniceras subnodosocostatum Zone</td><td>Epicheloniceras subnodosocostatum Zone</td></tr>
<tr><td colspan="2">II. Upper part of the lower Aptian or lower part of the Upper Aptian
2. Cheloniceras n. sp.(?) ex gr. martini d'Orb.
1. Dufrenoya sinzowi nov. sp.</td><td rowspan="3">Lower Aptian</td><td rowspan="2">Dufrenoya furcata Zone</td><td rowspan="2">Dufrenoya furcata Zone</td><td rowspan="3">Lower Aptian</td><td rowspan="2">Dufrenoya furcata Zone</td></tr>
<tr><td rowspan="2">I. Lower Aptian</td><td>b) Upper horizon
3. Cheloniceras cf. crassum Spath
2. Dufrenoya cf. truncata Spath
1. Dufrenoya aff. dufrenoyi d'Orb.</td></tr>
<tr><td></td><td>Deshayesites deshayesi Zone</td><td>Deshayesites deshayesi Zone</td><td>Deshayesites deshayesi Zone</td></tr>
</table>

the *Acanthohoplites nolani* Zone. The above beds completely corresponded to the upper beds of the Aptian in Kopet Dagh (Luppov et al., 1960) and correlated with the *Acanthohoplites aschiltaensis* Zone (or Subzone) then recognized in the northern Caucasus. Later, Tovbina (1968) studied the ammonite assemblage of the beds with *Acanthohoplites* ex gr. *uhligi* and *Diadochoceras* and established that it is distinguished from both the assemblage of the *Acanthohoplites nolani* Zone and the *Parahoplites melchioris* Zone and described characteristic ammonites and recognized the *Acanthohoplites prodromus* Zone. At that time, this zone was included in the Upper Aptian Substage.

In characterizing the Lower Cretaceous of Tuarkyr in 22 volume of *Geologiya SSSR* (Bogdanova et al., 1972a), the Aptian Stage of this region was subdivided into two substages, the upper of which was composed of three zones. The Upper Aptian of Tuarkyr, also with three zones, was included in the Cretaceous System (Luppov et al., 1986).

At the end of the 1990s, the Italian stratigrapher and paleontologist F. Cecca visited several sections of the Tuarkyr Anticline (region of the village of Geokdere). He studied several sections in the interval of the Lower Aptian and adjacent beds. In the ammonite assemblage from the beds assigned to the *Epicheloniceras subnodosocostatum* Zone, Cecca identified *Epicheloniceras buxtorfi* along with *Epicheloniceras subnodosocostatum* and *E. tschernyschewi* and on this basis considered that the *Epicheloniceras subnodosocostatum* Zone of Tuarkyr can be correlated only with the upper (third) *Epicheloniceras buxtorfi* Subzone of the *Epicheloniceras martinioides* Zone of England (Casey et al., 1998), rather than the entire latest zone, as it had been done by the preceding workers (Cecca et al., 1999).

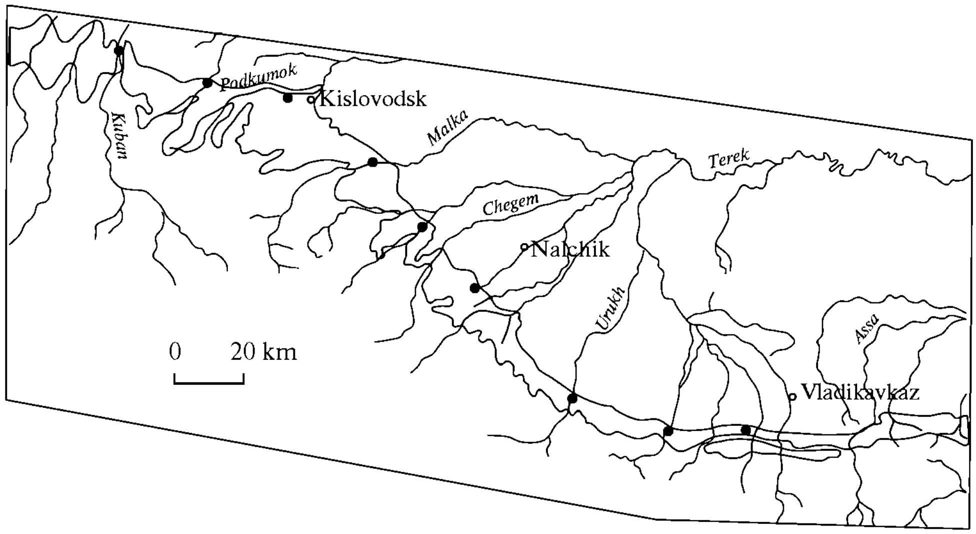


Fig. 4. Cretaceous outcrops and main studied sections in the central part of the northern Caucasus.

4. MIDDLE APTIAN STRATIGRAPHY

4.1. Northern Caucasus

The Lower Cretaceous beds are widespread in the Mesozoic complexes of the Russian part of the Caucasus. Their exposures extend from the southeast to northwest from southern Dagestan to the northwestern Caucasus Range. The so-called monoclinal of the northern slope –(central regions of the Caucasus and Dagestan) is mainly represented by terrigenous facies. In the northwestern termination of the Caucasus Range, the Lower Cretaceous is mainly composed of the flysch beds of the northern and southern slopes. The border between the two facial regions of the Caucasus, in opinion of many workers, extends approximately along the Pshekha River. The Lower Cretaceous beds in the two zones differ in lithology, the completeness of sections, and in the abundance and taxonomic composition of the Early Cretaceous fauna. This was most strikingly observed in the Aptian in the middle (Gargasian) and late (Clansayesian) stages.

4.1.1. Central Zone of the Northern Caucasus

This territory extends from the Pshekha River in the west to the Argun River in the east (Fig. 4). The Middle Aptian beds are widespread and represented by marine siliciclastic beds, mainly siltstones and sandstones with concretions of various composition and size, often forming consistent rows. The Middle Aptian beds overlie various horizons of the Jurassic and Lower Cretaceous horizons.

The classic standard section of this area is the Kislovodsk section, which was studied and described by Mordvilko (1937, 1939) in preparation to the 17th International Geological Congress. Later, it was described by Drushchits and Mikhailova (1966, p. 150). The thickness of the Middle Aptian in the above authors is virtually the same, in Mordvilko about 165 m, in Drushchits and Mikhailova, about 150 m.

Below we give descriptions of a section in the vicinity of Kislovodsk, and higher horizons are well traced on the left bank of the Podkumok River, near Kol'tso Mountain according to Drushchits and Mikhailova (Fig. 5).

Lower Aptian. *Dufrenoyia furcata–Dufrenoyia subfurcata* Zone (provisionally).

Bed 1. Dark gray, argillaceous siltstone..5 m thick.

Middle Aptian. *Colombiceras crassicostatum–Epicheloniceras subnodosocostatum* Zone.

Bed 2. Gray with dark gray and brown ferruginous stains, quartz–micaceous siltstone, containing horizons of spherical calcareous concretions. The ammonites *Colombiceras subtobleri* Kas., *C. caucasica* Lupp., *Epicheloniceras subnodosocostatum* Sinz. the bivalves *Gervillaria extenuata* Eichw. and *Thetironia minor* J. de C. Sow., and gastropods are present. The bed is..23 m thick.

Bed 3. Brownish gray, arenaceous, quartz–micaceous siltstone; at the base, with a horizon of calcareous siltstone. The ammonites *Colombiceras tobleri* Jac. et Tobl., the bivalves *Gervillaria extenuata* Eichw., *Pterotrigonia aliformis* Park., and *Thetironia minor* J. de C. Sow. have been found. The bed is..........14 m thick.

Bed 4. Greenish gray, arenaceous, quartz–glauconitic siltstone; at the base, with a horizon of compact calcareous concretions with the ammonites *Epicheloniceras subnodosocostatum* Sinz., *Colombiceras crassicostatum* Lupp. and the bivalves *Pterotrigonia aliformis* Park., *P. piriformis* Mordv., *Thetironia minor* J. de C. Sow. The bed is...................................14 m thick.

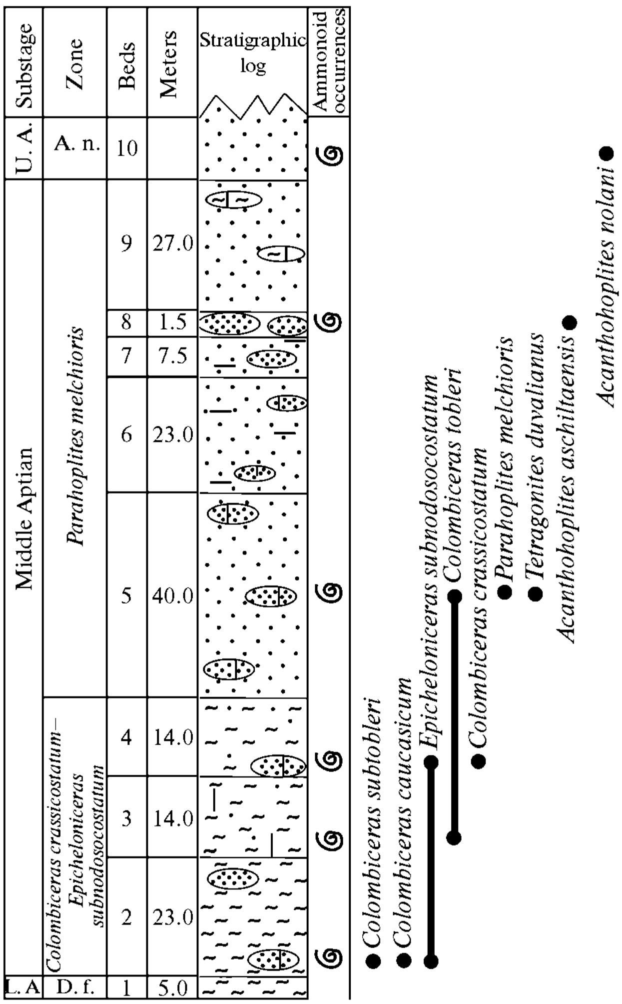


Fig. 5. Section near Kislovodsk (Drushchits and Mikhailova, 1966, p. 150).

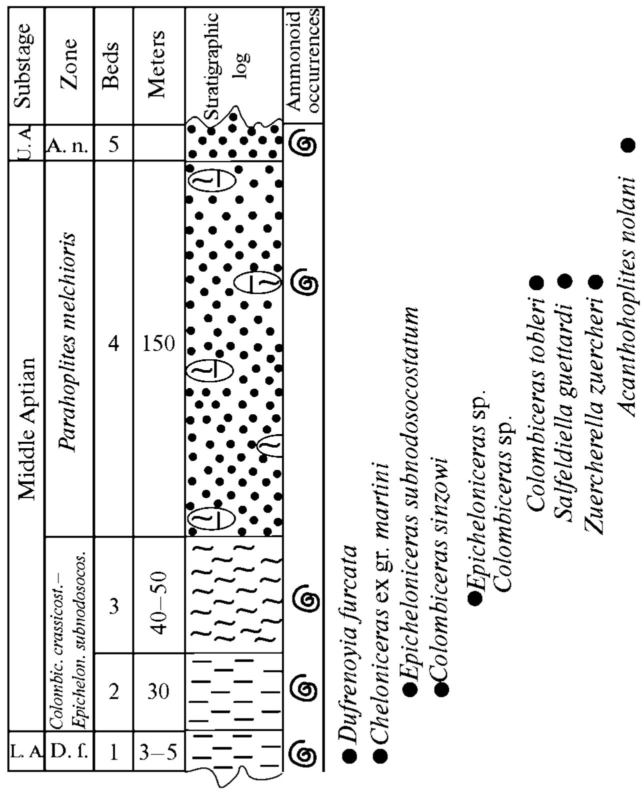


Fig. 6. Section on the Belaya Rechka River (Drushchits and Mikhailova, 1966, p. 149).

Parahoplites melchioris Zone

Bed 5. Brownish gray with greenish hue, quartz–glauconitic sandstone, containing several horizons of calcareous concretions, with the ammonites *Colombiceras tobleri* Jac. et Tobl., *Parahoplites melchioris* Anth., *Tetragonites duvalianus* d'Orb., the bivalves *Idonearca localis* Mordv., *Pterotrigonia aliformis* Park., *P. piriformis* Mordv., *Linotrigonia spinosa* Park., and *Venilicardia triangulata* Mordv. The bed is..40 m thick.

Bed 6. Sandstone ranging from light gray to dark gray, argillaceous, quartz–glauconitic, unbedded, containing horizons of calcareous concretions. The bed is...23 m thick.

Bed 7. Brownish green, argillaceous, quartz–glauconitic, micaceous sandstone; at the base, with a horizon of calcareous concretions..................7.5 m thick.

Bed 8. Horizon of very large loaflike concretions up to 3 m in the largest dimension. The ammonite *Acanthohoplites aschiltaensis* Anth. and bivalve *Pterotrigonia aliformis* Park. occur. The bed is................1.5 m thick.

Bed 9. Brownish yellow, quartz–glauconitic, micaceous, indistinctly bedded sandstone; at the top, with a horizon of large concretions of calcareous siltstone...27 m thick.

Upper Aptian. *Acanthohoplites nolani* Zone.

Bed 10. Brownish yellow sandstone with the ammonites *Acanthohoplites nolani* Seun., *A. abichi* Anth.

The total thickness of the Middle Aptian beds in the section studied is 151 m; the *C. crassicostatum–E. subnodosocostatum* Zone is 51 m thick and the *P. melchioris* Zone is 100 m thick.

To the east of Kislovodsk, the thickness of the Middle Aptian increases from 130 m on the Baksan River to approximately 200 m in the sections of Nalchik, along the Kheu, Belaya Rechka, and Urukh rivers. Further east, on the Ardon River, it sharply decreases to 50 m.

The section on the Belaya River (south of Nalchik) is the reference section for this region. It was described by Drushchits and Mikhailova (1966, p. 149). Below this section is redescribed with no modifications (Fig. 6).

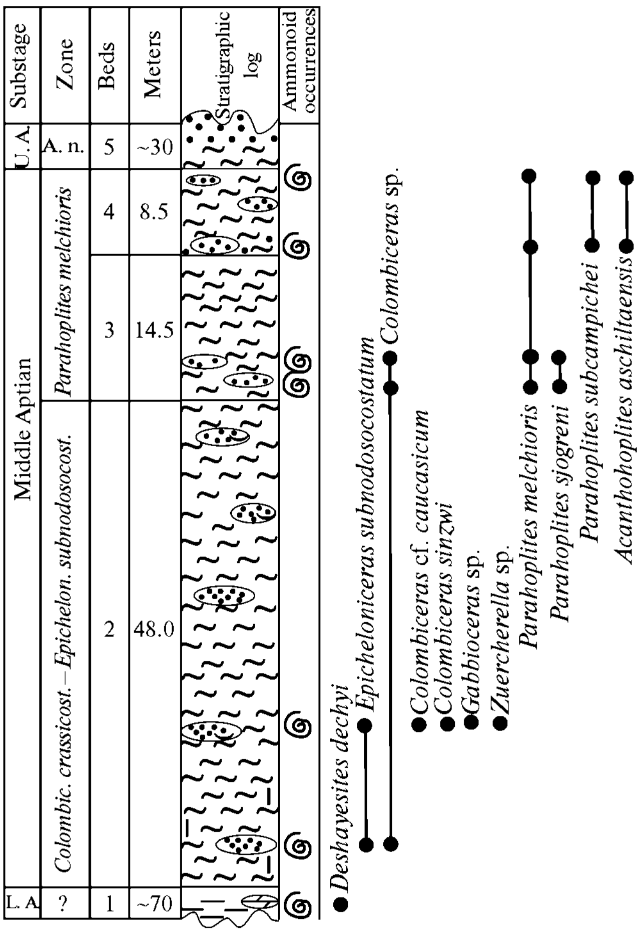


Fig. 7. Section on the Kuma River (Drushchits and Mikhailova, 1966, p. 74).

Lower Aptian. *Dufrenoyia furcata—Dufrenoyia subfurcata* Zone.

Bed 1. Black compact, unbedded, micaceous clay, with the ammonites *Dufrenoyia furcata* J. de C. Sow. and *Cheloniceras* ex gr. *martini* Jac..........3– 5 m thick.

Middle Aptian. *Colombiceras crassicostatum—Epicheloniceras subnodosocostatum* Zone.

Bed 2. Dark gray, when wet black, micaceous, unbedded clay, with the ammonites *Colombiceras sinzowi* Kas., *Epicheloniceras subnodosocostatum* Sinz., *Neohibolites ewaldi* Stromb., and the gastropods *Cirsoceritium subspinosum* Desh. *Solarium* sp...30 m thick.

Bed 3. From gray to dark gray, quartz—micaceous siltstone, with the ammonites *Colombiceras* sp. and *Epicheloniceras* sp..............................40—50 m thick.

Parahoplites melchioris Zone.

Bed 4. From brownish yellow to yellow and grayish yellow, quartz, homogenous Sandstone, with horizons of concretions of calcareous siltstone. Rare ammonites *Colombiceras tobleri* Jac. et Tobl., *Salfeldiella guettardi* Rasp., Zuercherella zuercheri Jac. et Tobl. occur. The bed is..150 m thick.

Upper Aptian. *Acanthohoplites nolani* Zone.

Bed 5. Fine-grained sandstone with *Acanthohoplites nolani* Seun.

The total thickness of the Middle Aptian beds is about 230 m, including the *C. crassicostatum—E. subnodosocostatum* Zone (70–80 m) and *P. melchioris* Zone (150 m).

To the west of the Baksan River to Kislovodsk, the thickness of the Middle Aptian ranges from 150 to 100 m, sharply decreasing in the Kuban River Basin down to 30–40 m. The least thickness is observed in the sections of the Bolshaya Laba and Khodz rivers (about 15 m), where the Middle Aptian beds are recognized provisionally.

Sections on the Kuma and Kuban rivers are faunistically most representative.

The section in the Kuma River Basin is given after Drushchits and Mikhailova (1966, pp. 74, 76) (Fig. 7).

Lower Aptian. *Dufrenoyia furcata—Dufrenoyia subfurcata* Zone.

Bed 1. From greenish gray to brownish gray, thinly bedded, calcareous clay, containing discoid concretions of light gray and yellowish brown marl. Concretions contained the ammonite *Deshayesites dechyi* Papp, and clay, ferruginous ammonites and the oyster *Aetostreon* sp. The total thickness of poorly exposed clay is ca. 70 m.

Middle Aptian. *Colombiceras crassicostatum—Epicheloniceras subnodosocostatum* Zone.

Bed 2. Gray, quartz—micaceous siltstone; at the base containing plates of calcareous siltstone, overfilled by shells of the trigoniids *Pterotrigonia aliformis* Park., less commonly, the ammonites *Epicheloniceras subnodosocostatum* Sinz. and *Colombiceras* sp. The siltstone contains several horizons of large concretions containing the ammonites *Colombiceras* cf. *caucasicum* Lupp., *C. sinzowi* Kas., *Epicheloniceras subnodosocostatum* Sinz., *Gabbioceras* sp., *Zuercherella* sp., the bivalves *Quadratotrigonia nodosa* J. de C. Sow., *Pterotrigonia piriformis* Mordv., *P. aliformis* Park., *Thetironia minor* J. De C. Sow., *Dosinimeria parva* J. De C. Sow., and poorly preserved gastropods. The bed is...48 m thick.

Parahoplites melchioris Zone.

Bed 3. Yellowish gray, quartz—glauconitic, micaceous siltstone, containing two horizons of concretions (at the base and in 2 m from the base), with the ammonites *Parahoplites melchioris* Anth., *P. sjogreni* Anth., *Colombiceras* sp. and the bivalves *Pterotrigonia scabricola* Lyc., *P. aliformis* Park., and *Quadratotrigonia nodosa* J. de C. Sow..........................14.5 m thick.

Bed 4. Yellowish gray, quartz—glauconitic, micaceous, unbedded, homogenous siltstone; in the upper part, arenaceous, containing at the base and at the top horizons of concretions and in the series also small concretions, with the ammonites *Parahoplites melchioris* Anth., *P. sub-campichei* Sinz., *Acanthohoplites aschiltaensis* Anth., *Tetragonites duvalianus* d'Orb., the bivalves *Thetironia caucasica* Eichw., *Astarte obovata*

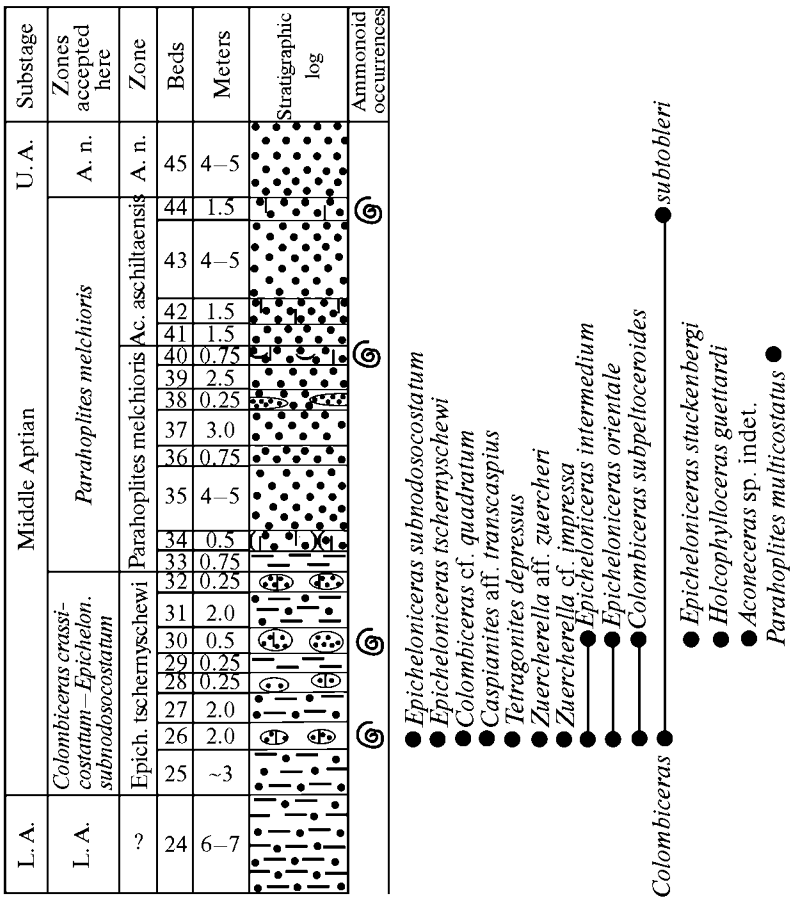


Fig. 8. Section on the Kuban River (after Mordvilko, 1960, pp. 62, 63).

J. Sow., *Pterotrigonia scabricola* Lyc., *P. aliformis* Park., and *Linotrigonia spinosa* Park. The bed is...8.5 m thick.

Upper Aptian. *Acanthohoplites nolani* Zone.

Bed 5. Siltstone passing into yellowish gray, quartz–micaceous sandstone, unbedded. In the middle part, it contains two beds of compact calcareous sandstone; the lower bed contains the ammonites *Acanthohoplites* ex gr. *bigoureti* Seun., and the bivalves *Quadratitrigonia nodosa* J. de C. Sow., *Pterotrigonia aliformis* Park., and *Thetironia caucasica* Eichw. The bed is...30 m thick.

The section on the Kuban River was described by Mordvilko (1960, pp. 62, 63)[3]. (Fig. 8). That paper says that the Middle Aptian beds ... "show continuous 2-km-long exposures on the right bank of the river (from the bridge near the village of Ust'-Dzhegutinskaya) upstream to a wide third meander of the river" (Mordvilko, 1960, p. 62).

Lower Aptian. *Dufrenoyia furcata–Dufrenoyia sinzowi* Zone.

Bed 24. Gray, strongly arenaceous, very loosely cemented clay, with the belemnites *Neohibolites* cf. *ewaldi* Stromb. and numerous *Aetostreon latissimum* Lam..6–7 m thick.

Upper Aptian. *Epicheloniceras tschernyschewi* Zone

Bed 25. Arenaceous clay...............2.5–3.0 m thick.

Bed 26. A bed of small calcareous concretions with abundant fossils: *Colombiceras subpeltoceroides* Sinz., *C. subtobleri* Kas., *C.* cf. *quadratum* Kas., *Epicheloniceras orientale* Jac., *E. tschernyschewi* Sinz., *E. intermedium* Kas., *E. subnodosocostatum* Sinz., *Caspianites* aff. *transcaspius* Sinz., *Zuercherella* aff. *zuercheri* Jac., *Z.* cf. *impressa* d'Orb., *Tetragonites depereti* Kil. and numerous bivalves. The bed is 0.15–0.20 m thick.

Bed 27. Dark gray arenaceous clay...........2 m thick.

Bed 28. A bed of small calcareous concretions with impoverished bivalve fauna....................0.25 m thick.

Bed 29. Dark gray clay.......................0.25 m thick.

[3] Bed numbers, subdivision into substages and zones, the names of zones in section descriptions in papers by Morfvilko (1960, 1962) are given according to this author. In Figs. 8, 10, and 12 to the right of the substage scale, there is the modern division of the substage scale into the zones, and generic and specific names of ammonites studied by the present authors and described in this paper, also given in the modern understanding.

Bed 30. A horizon of small very compact calcareous concretions (up to 15–20 cm in diameter), with the ammonites *Colombiceras subpeltoceroides* Sinz., *Epicheloniceras stuckenbergi* Kas., *E. orientale* Jac., *E.* cf. *intermedium* Kas., *Phylloceras* cf. *guettardi* Rasp., *Aconeceras* sp. indet. and many bivalves....0.50 m thick.

Bed 31. Blackish gray, arenaceous clay......2 m thick.

Bed 32. Concretions of dark gray argillaceous and calcareous sandstone with bivalves..........0.25 m thick.

Parahoplites melchioris Zone

Bed 33. Grayish brown clay................0.75 m thick.

Bed 34. Gray compact calcareous sandstone, with numerous bivalve shells.........................0.50 m thick.

Bed 35. Loose glauconitic sandstone.....................4–5 m thick.

Bed 36. Compact nodular coquina with bivalves; 0.75 m thick.

Bed 37. Loose glauconitic sandstone.......3 m thick.

Bed 38. Gray compact lenslike sandstone..............0.25 m thick.

Bed 39. Loose glauconitic sandstone with no fossils..2.5 m thick.

Bed 40. Light gray calcareous sandstone with the ammonite *Parahoplites multicostatus* Sinz. and bivalves..0.75 m thick.

Acanthoplites aschiltaensis Zone

Bed 41. Loose fine-grained, glauconitic sandstone.....1.5 m thick.

Bed 42. Compact, calcareous sandstone with numerous bivalves..............................1–1.5 m thick.

Bed 43. Loose glauconitic sandstone.....................4–5 m thick.

Bed 44. Grayish green calcareous, compact glauconitic sandstone with the ammonite *Colombiceras subtobleri* Kas. and numerous bivalves............1.5 m thick.

Lower Albian. *Acanthoplites nolani* Zone

Bed 45. Yellowish green loose, glauconitic sandstone..4–5 m thick.

Thus, two ammonite zones, *Colombiceras crassicostatum–Epicheloniceras subnodosocostatum* and *Parahoplites melchioris* are recognized in the Middle Aptian of the central region of the northern Caucasus (Drushchits and Mikhailova, 1979).

Colombiceras crassicostatum–Epicheloniceras subnodosocostatum Zone

The beds assigned to this zone, as shown in the sections figured, can be traced virtually along the entire central region of the northern slope of the Caucasus Range, from the Fiagdon River in the east, to the Khokodz River in the west. To the east of Kislovodsk, the thickness as mentioned above, increases suddenly and considerably. They are represented in the lower part by clay, becoming siltstone upward in the section. However, in the easternmost sections on the Fiagdon and Ardon rivers, this part of the section is composed by siltstone ca. 20 m thick with rare ammonites *Epicheloniceras buxtorfi* Jac., *Colombiceras subpeltoceroides* Sinz., and *Salfeldiella guettardi* Rasp. The boundary with the underlying Lower Aptian beds is not substantiated paleontologically.

To the west of the Baksan River, the thickness of this zone decreases and, in the interval to the Kuma River, it is 150–70 m thick. In the Baksan, Kislovodsk, and Kuma sections, the zone is represented by siltstone with horizons of large and small concretions.

To the west, the beds of the lower zone become more coarse-grained. In the Kuban sections, the zone is mainly represented by sandstone and, further west, by clay. The thickness of the zone decreased in the same direction. Drushchits and Mikhailova considered that the Middle Aptian on the Bolshaya Laba River can include only 15 m of clay series. However, Mordvilko (1960) recognized here the Middle Aptian beds 10–15 m thick but believed that the lower zone was absent.

To the west of the Shedok River, rocks of the Middle Aptian, overlying the Upper Jurassic beds only represented by the upper zones, while the lower zone is usually eroded. However, in the westernmost section of the central region of the Northern Caucasus, in the section on the Khokodz River, the lower zone is represented by its upper part with the ammonites *Colombiceras crassicostatum* d'Orb., *Epicheloniceras* aff. *meyendorfi* d'Orb., *Salfeldiella guettardi* Rasp., *Tetragonites crudus* Drushits.

In total a representative ammonite material is collected in the central regions of the northern Caucasus (Table 9), composed mainly of cheloniceratid species (genus *Epicheloniceras*) and parahoplitids (genus *Colombiceras*). The most characteristic group of species is represented by *Epicheloniceras*. It includes eight species, of which *E. tschernyschewi* and *E. subnodosocostatum* should be considered as index species, as both these are the index species of the lower zone of the Middle Aptian in many regions of Europe and Asia. *E. intermedium* and *E. stuckenbergi* were recognized by Kazansky on the material from the Dagestan section, whereas *E. caucasicum* was described by Anthula from this region and, finally, two species, *E. orientale* and *E. buxtorfi*, occur in Western Europe. Species of *Colombiceras* are widespread in the sections of this region, of which the species *crassicostatum*, which is mentioned in the chapter on the history of studies, is taken for the first index of the zone. In the middle of the 20th century, Luppov (1952) considered that this European species not found anywhere outside the northwestern Caucasus. However, it is now known from the central region of the Caucasus, Georgia, and Turkmenistan. The distribution of the representatives of the genus *Colombiceras* is not restricted by the zone under consideration, as *Epicheloniceras*, whereas they are found in the higher beds. Apart from the ammonite group listed above, two tetragonitid species are found in this zone, *Tetragonites depereti* Kil. and the local

Table 9. Distribition of ammonites in the Middle Aptian of the central part of the northern Caucasus

No.	Ammonite species	Lower Aptian Zone *Dufrenoya furcata*	Middle Aptian: *Colombiceras crassicostatum–Epicheloniceras subnodosocostatum* Zone	Middle Aptian: *Parahoplites melchioris* Zone	Upper Aptian
1	*Dufrenoyia furcata* J. de C. Sow.	—			
2	*Dufrenoyia subfurcata* Kas.	—			
3	*D. lurensis* Kil.	—			
4	*Cheloniceras seminodosum* Sinz.	—			
5	*Cheloniceras meyendorfi* d'Orb.	—			
6	*Cheloniceras gottchei* Kil.	—			
7	*Tetragonites depereti* Kil.		—		
8	*T. crudus* Drushits		—		
9	*Epicheloniceras subnodosocostatum* Sinz.		—		
10	*E. tschernyschewi* Sinz.		—		
11	*E. intermedium* Kas.		—		
12	*E. stuckenbergi* Kas.		—		
13	*E. orientale* Jac.		—		
14	*E. caucasicum* Anth.		—		
15	*E. buxtorfi* Jac.		—		
16	*Colombiceras crassicostatum* d'Orb.		—		
17	*C. subpeltoceroides* Sinz.		—		
18	*C. caucasicum* Lupp.		—		
19	*C. sinzowi* Kas.		—		
20	*C. korotkovi* sp. nov.		—		
21	*C. quadrarium* Kas.		—		
22	*Holcophylloceras guettardi* Rasp.		—	—	
23	*Aconeceras (Sinzowia) aptianum* Saras.		—	—	
24	*Aconeceras (A.) haugi* Saras.		—	—	
25	*A. (A.) nisus* d'Orb.		—	—	
26	*Zuercherella zuercheri* Jac.		—	—	
27	*Colombiceras tobleri* Jac.		—	—	
28	*C. discoidale* Sinz.		—	—	
29	*C. subtobleri* Kas.		—	—	
30	*C. bogdanovae* Tovb.		—	—	
31	*Hypophylloceras velledae* Mich.			—	
32	*Tetragonites duvalianus* Rasp.			—	
33	*T. heterosulkatus* Anth.			—	
34	*Ptychoceras puzosianum* Jac. et Tobl.			—	
35	*Acanthohoplites laticostatus* Sinz.			—	
36	*A. subrectangulatus* Sinz.			—	
37	*Parahoplites melchioris* Anth.			—	
38	*P. schmidti* Jac. et Tobl.			—	
39	*P. debilicostatus* I. Mich.			—	
40	*P. multicostatus* Sinz.			—	
41	*P. subcampischei* Sinz.			—	
42	*P. sjogreni* Anth.			—	
43	*P. maximus* Sinz.			—	
44	*Acanthohoplites aschiltaensis* Anth.			— (upper part)	—
45	*Eodouvilleiceras clansayense* Jac.				—

species *T. crudus* Drushits. The desmoceratid *Zuercherella zuercheri* Jac. is extremely rare.

***Parahoplites melchioris* Zone.** In contrast to underlying beds, this part of the section is mainly composed of brownish gray, brownish green quartz–glauconitic sandstone with large loaf-shaped and spherical concretions, usually containing various fossils. Sometimes, concretions are extended along the strike, forming lens-shaped layers with fossils. Beds with *P. melchioris* are recognized almost in all sections from the Fiagdon River in the east to the Khokodz River in the west. Only in the valley of Bolshaya Laba, Middle Aptian beds are in general recognized provisionally, lying between the brownish red gypsum-bearing Upper Jurassic clay and Upper Aptian siltstone with *Acanthohoplites nolani* Seun. The greatest thickness is observed in the eastern part of this region from the Urukh River to the Chegem River. In the section on the Belaya River and in the vicinity of Nalchik, this zone becomes 150–160 m thick (Fig. 6). To the east, along the Ardon and Fiagdon rivers, the thickness sharply decreases to ca. 30 m, and the sections are composed of siltstone with similar large concretions and infrequent ammonites. To the west of the Chegem River, the thickness of the zone gradually decreases, becoming ca. 100 m in the Kislovodsk section (Fig. 5), 99 m along the Kuma River,(Fig. 7), and 21.5 m along the Kuban River (Fig. 8). As mentioned above, in the region of the Bolshaya Laba and Khodz rivers a series of siltstone ca. 15 m thick is tentatively assigned to the Middle Aptian. From the section on the Khodz River, Mordvilko (1960, p. 78) recorded the ammonites *Parahoplites melchioris* Anth., *Colombiceras tobleri* Jac., *C. subpeltoceroides* Sinz. Mordvilko considered that these ammonites suggest the presence of both zones of the Middle Aptian. However, the two latter species are found in both zones, whereas the former, in addition, is the index species of the upper zone. To the west of the Khodz River, the Middle Aptian beds are mainly represented by variously thick sandstones, from 30 m on the Fars River to 160 m on the Khokodz River. They rest on different horizons of Jurassic and Lower Cretaceous beds and, based on the ammonites found in these horizons, *Parahoplites melchioris* Anth. and *Colombiceras subpeltoceroides* Sinz., are assigned to the upper zone.

The fossil assemblage from the *P. melchioris* Zone is shown in Table 9. A group of *Parahoplites* species which are not found in the underlying beds and virtually do not continue to the Clansayesian *Acanthohoplites nolani* Zone is indexing. Egoian (1989, p. 128) considered that rare *Parahoplites* and *Colombiceras* are found in the lowermost beds of the Upper Aptian. This zone shows the appearance of the genus *Acanthohoplites: A. laticostatus* Sinz., *A. subrectangulatus* Sinz., and *A. aschiltaensis* Anth. The last species is found in the upper part of the zone, which was previously recognized as a separate zone with this index species. Species of *Colombiceras* found in this zone occurred in the lower zone, because they were less significant for the indexing of the two zones than *Epicheloniceras* and *Parahoplites.* It can be considered indicative of the Middle Aptian in general. Infrequent phylloceratids and tetragonitids, *Eophylloceras velledae* and *Tetragonites duvalianus*, are found only in this zone, although in other regions they are not restricted to it.

4.1.2. Southeastern Caucasus (Dagestan) (Fig. 9)

The Middle Aptian beds of Dagestan, in contrast to the Middle Aptian central regions of the northern slope of the Caucasus Range, are represented by a greater diversity of rock types and considerable thickness. In the last decade, formations were recognized in the Lower Cretaceous beds of Dagestan (Snezhko et al., 2011). The Aptian beds correspond to the Gundarin Formation, which is subdivided into three series, lower and upper are essentially argillaceous, middle is essentially arenaceous. The Middle Aptian includes the lower and middle parts of the upper series.

In northern Dagestan, in the vicinity of the villages of Botlikh, Rushukha, Chirkaty, and Zubutl', the Middle Aptian is composed of gray loose sandstones, alternating with compact calcareous sandstones and soft marly siltstones. The sandstone and siltstone are sometimes cross-bedded. Mordvilko indicated the presence in the sections of dark fissured clay. According to Renngarten, siltstone and sandstone contain septarian and small spherical concretions, sometimes forming horizons along the strike.

The Akusha section is the most representative Aptian section in northern Dagestan. It was described by Renngarten (1927), Mordvilko (1962), and Mikhailova (Bogdanova and Mikhailova, 2006). For comparison we give here a description of the sections composed by both Mordvilko and Mikhailova.

Mordvilko's section was composed on both banks of the Darga River beginning near the garden in the northern vicinity of the village of Akusha (Mordvilko, 1962, pp. 73, 74) (Fig. 10):

Lower Aptian. *Dufrenoyia furcata–Dufrenoyia subfurcata* Zone

Bed 76. Grayish green, loose, calcareous sandstone, with abundant bivalves and infrequent ammonites, *Dufrenoyia dufrenoyi* d'Orb., *D. subfurcata* Kas...0.40 m thick.

Upper Aptian. *Cheloniceras tschernyschewi–Cheloniceras subnodosocostatum* Zone

Bed 77. Dark fissured arenaceous clay with mica..18 m thick.

Bed 78. A member of regularly alternating black fissured, sometimes laminated clays and brown, loose fine-grained, noncalcareous sandstones with small pyritic concretions..................................80 m thick.

Bed 79. The sandstones are loose fine-grained cross-bedded with long lenses of gray fine-grained

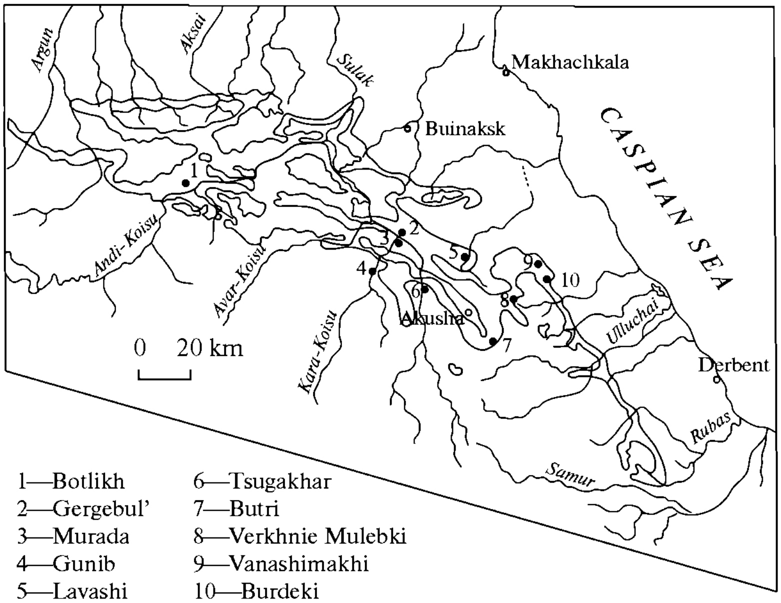


Fig. 9. Cretaceous outcrops and main studied sections in Dagestan.

sandstones and black laminated clay...80–100 m thick.

Bed 80. Sandstone similar to sandstones of Bed 79, loose, cross-bedded, with rows of spherical concretions..8 m thick.

Bed 81. Grayish brown fine-grained, loose, cross-bedded sandstone, with long thin lenses of thinly-bedded clay. There are several rows of large spherical concretions with abundant fossils. On the right bank of the Darga River, in the first gully downstream of the village, many bivalve remains were found, of which *Plicatula carteroni* d'Orb. was most abundant, which is why Mordvilko called these strata "Beds with *Plicatula.*" The ammonites include *Epicheloniceras tschernyschewi* Sinz., *E. subnodosocostatum* Sinz., *E. orientale* Jac., *E. waageni* Anth., *Cheloniceras seminodosum* Sinz., *Colombiceras sinzowi* Kas., *C. tobleri* Jac., *Desmoceras saltaense* Kas., *D. falcistriatum* Anth. On the left bank of the Darga River, somewhat upstream from the village, there were found *Epicheloniceras tschernyschewi* Sinz. and *Aconeceras* cf. *nisus* d'Orb. The bed is....................................10 m thick.

Parahoplites melchioris Zone

Bed 82. Brown, loose, cross-bedded, glauconitic sandstone with small pyritic concretions and arenaceous limestone and, in the upper part, a row of lens-shaped concretions of fine-grained arenaceous limestone with *Colombiceras subtobleri* Kas...10.4 m thick.

Bed 83. Loose, cross-bedded sandstone....7 m thick.

Bed 84. A row of concretions of arenaceous limestone with the ammonites *Parahoplites melchioris* Anth., *P. multicostatus* Sinz., *Colombiceras subtobleri* Kas..0.3 m thick.

Bed 85. Loose, cross-bedded sandstone, with very compact large spherical concretions with ammonite, which are difficult to get out, and with bivalves and gastropods...22 m thick.

Bed 86. Clayey and calcareous sandstone with phosphatized fossil bivalves, gastropod, and cephalopods: *Parahoplites melchioris* Anth., *P. maximus* Sinz., *Colombiceras* cf. *tobleri* Jac., *Acanthohoplites* cf. *planidorsatus* Kas., *Melchiorites emerici* Rasp., *Mesohibolites elegans* Schwetzov.............................0.4 m thick.

Bed 87. Black fissured, weakly arenaceous clay with mica. A row of concretions with the ammonites is near the bed base: *Parahoplites melchioris* Anth., *P.* cf. *campichei* Pict. et Ren.............................17 m thick.

Bed 88. Alternation of black and brown fissured weakly arenaceous clay with concretions of gray dense marl (10–20 cm long) and large septarians and, at the top, grayish brown weakly calcareous sandstone with globular concretions (up to 50 cm in diameter)..16 m thick.

Bed 89. A row of large concretions with *Parahoplites melchioris* Anth., *P. multicostatus* Sinz., and *Cymatoceras* sp.......................................1.5 m thick.

Bed 90. Brown, glauconitic sandstone with mica, forming wind niches. Ammonites: *Parahoplites melchioris* Anth., *P. multicostatus* Sinz...............8 m thick.

Acanthoplites aschiltaensis–Acanthoplites uhligi Zone

Bed 91. A row of large globular concretions of calcareous sandstone with bivalves..................2 m thick.

Bed 92. Brown, fine-grained, calcareous sandstone with *Acanthohoplites* sp..............................3 m thick.

Bed 93. Dark gray, arenaceous clay or siltstone with phosphoritic nodules and abundant fossils, including

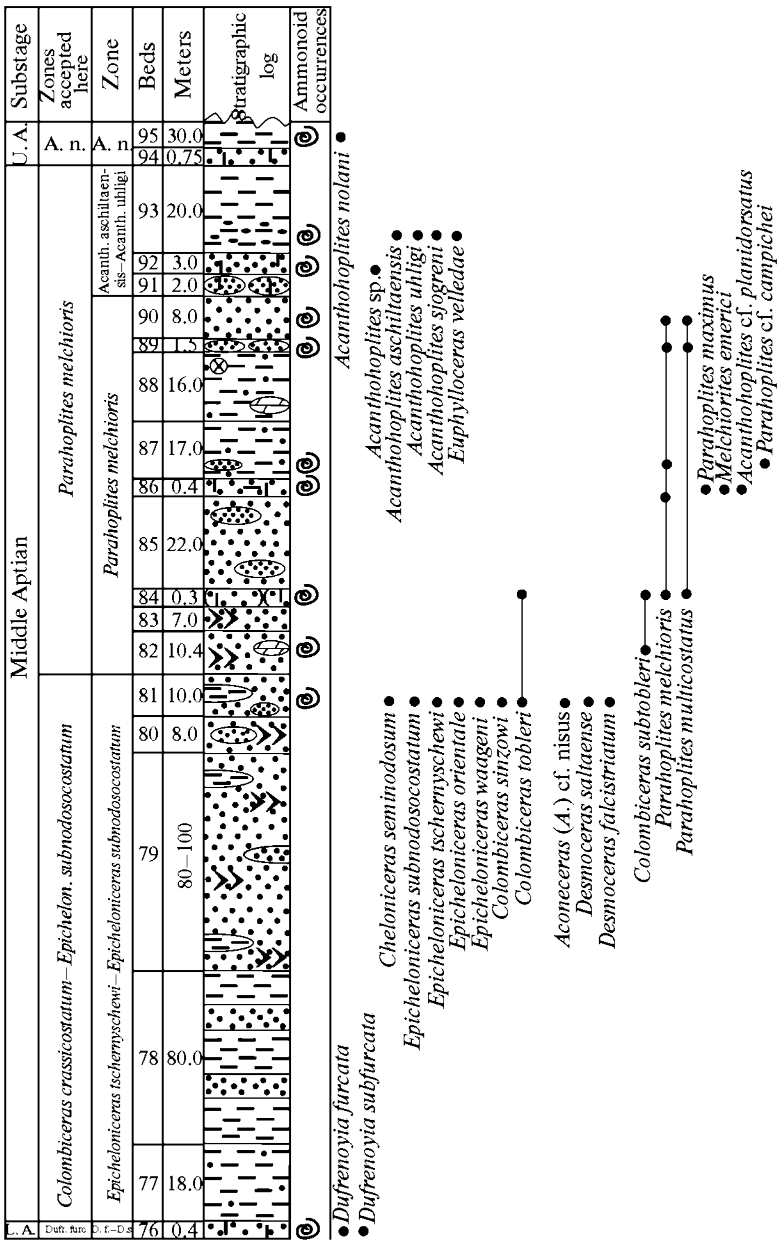


Fig. 10. Section on the Dargi River (village of Akusha) (after Mordvilko, 1962, p. 73, 74).

the ammonites *Acanthohoplites aschiltaensis* Anth., *A. uhligi* Anth., *Parahoplites sjogreni* Anth., *Euphylloceras velledae* Mich., *Aconeceras* sp., and *Cheloniceras* sp. ....20 m thick.

Lower Albian. *Acanthoplites nolani* Zone

Bed 94. Light gray, fine-grained, calcareous sandstone, with poikilitic texture of calcite cement with a silky luster...0.75 m thick.

Bed 95. Black fissured and laminated clay rich in pyrite, with pyritized shells of the ammonite *Acanthohoplites nolani* Seun. and thin-walled bivalves...30 m thick.

The *Epicheloniceras tschernyschewi* and *E. subnodosocostatum* (=*Colombiceras crassicostatum–Epicheloniceras subnodosocostatum*) zones, according to Mordvilko, constitute 196 m, and the *P. melchioris* + *A. aschiltaensis–A. uhligi* zones constitute 107. 6 m (modern *P. melchioris* Zone).

The description of the section composed by Mikhailova is based on the succession on the left and, then, the right bank of the Darga River near the villages of Kertug and Akusha (Fig. 11).

Lower Aptian. *Dufrenoyia furcata* Zone

Bed 1. Greenish gray argillaceous, micaceous, glauconitic siltstone with thin beds of silty clay, with infrequent ammonites *Dufrenoyia subfurcata* Kas........ ....10 m thick.

Middle Aptian. *Colombiceras crassicostatum–Epicheloniceras subnodosocostatum* Zone

Bed 2. Gray, when weathered yellowish gray, fine-grained siltstone, with interbeds of calcareous siltstone 0.05 to 0.15 m thick, 2–3 m over one another. Many concretions are present, most of them are small, 0.4 m in diameter, containing the ammonites *Epicheloniceras subnodosocostatum* Sinz., *E. buxtorfi* Jac., *E. tschernyschewi* Sinz., *E. stuckenbergi* Kas., *E. intermedium* Kas., *E. caucasicum* Anth., *Colombiceras sinzowi* Kas., *C. subtobleri* Kas. The lower 20 m are very poorly exposed. The bed is........................40 m thick.

Bed 3. Gray, argillaceous, laminated siltstone, in the middle part when weathered is lenslike–cross-bedded. Several horizons of concretions are found, containing the ammonites *Colombiceras* ex gr. *tobleri* Kas., *Zuercherella* sp. The bed is................20 m thick.

Bed 4. Argillaceous, loose siltstone with large concretions of calcareous siltstone..................25 m thick.

Parahoplites melchioris Zone

Bed 5. Phosphoritic horizon, containing phosphatized nodules with ammonites, bivalves and gastropods, belemnite rostra and phosphoritic nodules of irregular shape size not more than 2–3 cm, cemented by gray argillaceous and silty cement. Fossils show traces of transportation and are usually represented by shell and mold fragments. This level contains the ammonites *Parahoplites melchioris* Anth., *P. schmidti* Jac. et Tobl., *P. transitans* Sinz., *Acanthohoplites aschiltaensis* Anth., *A. rectangularis* Kas., A. laticostatus Sinz., *Euphylloceras velledae* Mich., the belemnites *Neohibolites wollemanni* Stoll., *N.* ex gr. *semicanaliculatus* Bl. The bed is...........0.10–0.15 m thick.

Bed 6. Dark gray, almost black, silty weakly micaceous clay, with two interbeds of calcareous siltstones and concretions, which contain the ammonites *Parahoplites melchioris* Anth., *P. schmidti* Jac. et Tobl., *P. subcampichei* Sinz., *Salfeldiella guettardi* Rasp., *Acanthohoplites laticostatus* Sinz. and others. Up the section, clay gradually becomes siltstone......17 m thick.

Bed 7. Gray, loose, argillaceous siltstone similar to that of Bed 4, with several horizons of concretions (at the levels 2.5, 19.5 and 22 m), which contain the ammonites *Parahoplites melchioris* Anth., *P. transitans* Sinz., *P. multicostatus* Sinz., and *Acanthohoplites aschiltaensis* Anth....................................24 m thick.

Upper Aptian. *Acanthohoplites nolani* Zone

Bed 8. Phosphoritic horizon composed of phosphatized molds of bivalve shells, belemnite rostra cemented by calcareous siltstone cement. Fragments of fossilized wood are present...........0.1–0.5 m thick.

The lower zone of the Middle Aptian in this section is 85 m thick and the upper zone is 41 m thick. This is about a third of the thickness indicated by Mordvilko, who considered that the Aptian beds in the Akusha region are considerably thicker than in other regions of

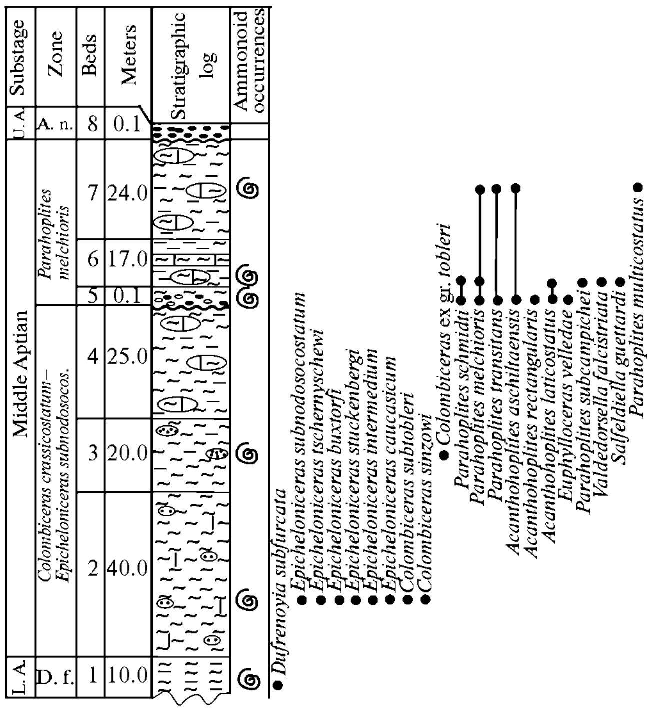


Fig. 11. Section on the Dargi River (villages of Kertug and Akusha).

Dagestan and explained it by consistent and quick subsidence of this area with compensated sedimentation. It should be said that large thickness indicated by Mordvilko, compatible with the thickness of the entire Gundarin Formation, estimated by mapping geologists as 500 m (Snezhko et al., 2011).

The *Colombiceras crassicostatum–Epicheloniceras subnodosocostatum* Zone, is not recognized in many sections of northern Dagestan. In the northernmost sections near the villages of Botlikh, Muni, and Rushukha, there is not paleontological data for subdivision of the Aptian beds into zones. These beds contain a few shells of *Parahoplites* and *Acanthohoplites*. Near the Chirkaty River, the lower part of the Middle Aptian section is provisionally assigned based on lithology to this zone (according to Mordvilko, it is ca. 144 m thick), whereas the upper part is 114 m thick and, based on numerous *Colombiceras* and *Acanthohoplites aschiltaensis*, is recognized in the upper zone. The presence of the lower zone in most northerly section of the lower zone near the village of Zubutl' is suggested, as only fragments of a large ammonite, presumably *Epicheloniceras tschernyschewi* Sinz. are found in beds assigned to this zone. The lower zone is best substantiated paleontologically in the central and southern regions of northern Dagestan (villages of Aimaki, Gunib, Murada, Gergebul', Tsudakhar, Lavashi, Akusha, Burdeki, Butri, and others). The thickness of the zone in this region ranges from 43 m (confluence of the rivers of the Avar Koisu and Karakoisu, according to Mordvilko) to 85 m in the Akusha

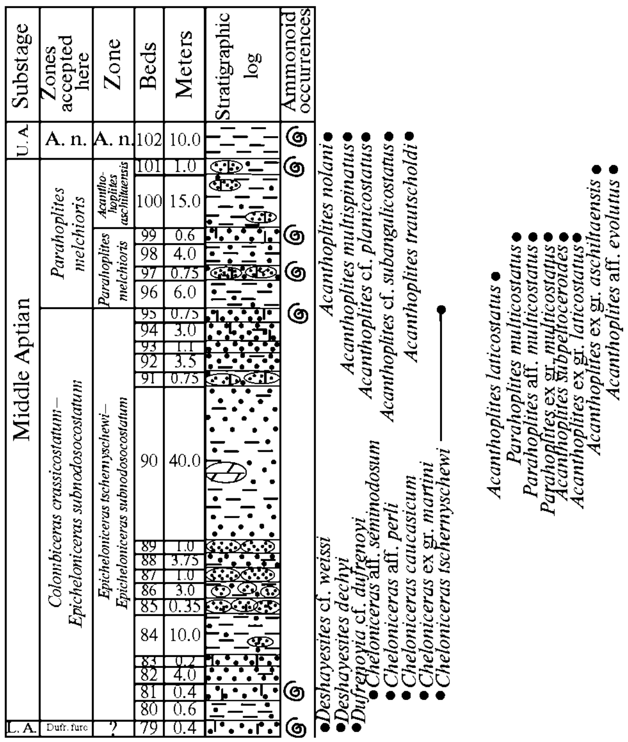


Fig. 12. Section on the Rubas-chai River (village of Khuchni) (after Mordvilko, 1962, p. 90–92).

section (according to Mikhailova). In general, this zone of northern Dagestan contains the following characteristic ammonite species: *Epicheloniceras subnodosocostatum* Sinz., *E. tschernyschewi* Sinz., *E. orientale* Jac., *E. pusillum* Kas., *E. intermedium* Kas., *E. stuckenbergi* Kas., *E. buxtorfi* Jac., *E. waageni* Anth., *Colombiceras crassicostatum* d'Orb., *C. sinzowi* Kas., *C. subtobleri* Kas., *C. discoidale* Sinz., *C.* aff. *quadratum* Kas., *Aconeceras (A.) nisus* d'Orb. and the nautiloid *Cymatoceras* ex gr. *neckeri* Pict. et Camp. (Table 10). This assemblage is almost identical to the assemblage of species found in this zone in the sections in the central regions of the Caucasus.

The *Parahoplites melchioris* Zone is paleontologically characterized in more sections than the lower zone. It is now recognized only near the villages of Botlikh and Rushukha, but the section here contains occasional *Parahoplites* and *Acanthohoplites*, i.e., ammonite genera characteristic of this portion of the Middle Aptian. Lithologically, the zone is represented by rocks almost the same as in the lower zone, i.e., clay, siltstones, loose marly and compact calcareous sandstones with globular concretions. Mordvilko noted that, in this part of the Aptian, cross-bedded sandstones play a less noticeable role. According to Mordvilko, the *P. melchioris* Zone is thickest in the region of the villages of Aimaki (ca. 164 m) and Akusha (107 m). In general, the zone contains the following typical species *Phyllopachyceras moreli* d'Orb., *Hypophylloceras velledae* Mich., *Tetragonites heterosulcatus* Anth., *T. duvalianus* Rasp., *Melchiorites emerici* Rasp., *Puzosia saltaensis* Kas., *Pseudoaustraliceras ramosum* Anth., *Colombiceras discoidale* Sinz., *C. tobleri* Jac., *C. planidorsatum* Kas., *C.* aff. *subpeltoceroides* Sinz., *Acanthohoplites laticostatus* Sinz., *A. aschiltaensis* Anth., *Parahoplites melchioris* Anth., *P. multicostatus* Sinz., *P. schmidti* Jac. et Tobl., *P. campichei* Pict. et Camp., *P. subcampichei* Sinz., *P. transitans* Sinz., *P. maximus* Sinz., *P. sjogreni* Anth., *P. grossouvrei* Jac., *P. artschmanensis* Glasun., *P. debilicostatus* I. Mich. (see Table 10). The ammonite assemblage of this zone is also very similar to that to the central Caucasus. The European species include phylloceratids, tetragonitids, and desmoceratids. Among *Acanthoholotes*, *Colombiceras*, and especially *Parahoplites*, most species are local or Transcaspian, in particular Mangyshlak species.

In southern Dagestan (south of the town of Madzhalis), there are several region of distribution of the Middle Aptian beds. Mordvilko (1962) noted that, despite the reduced thickness compared to the Akisha section, the section of the Upper Aptian along the Rubas-chai River, is the second complete Upper Aptian section in Dagestan, showing all three[4] zones of the Upper Aptian (Mordvilko, 1962, p. 157). This section is described below (Fig. 12). It was compiled along the Rubas-chai and its left tributary Khanag-chai in the vicinity of the village of Khuchni (Mordvilko, 1962, p. 90).

Lower Aptian. *Dufrenoyia furcata–Dufrenoyia subfurcata* Zone.

Bed 79. Sandstone compact, calcareous, with the ammonites *Paradeshayesites* cf. *weissi* Neum. et Uhl., *D. dechyi* Papp, *Dufrenoyia* cf. *dufrenoyi* d'Orb............. ....0.40 m thick.

Upper Aptian. *Cheloniceras tschernyschewi–Cheloniceras subnodosocostatum* Zone.

Bed 80. Gray arenaceous clay............0.60 m thick.

Bed 81. Sandstone compact, calcareous, glauconitic, with a rich cephalopod fauna: the ammonites *Epicheloniceras tschernyschewi* Sinz., *Ep.* aff. *perli* Spath, *Cheloniceras occidentale* Jac., *Ch.* aff. *seminodosum* Sinz., *Colombiceras* sp. and belemnites............ ....0.35–0.40 m thick.

Bed 82. Gray, unbedded, argillaceous sandstone.... ....4 m thick.

Bed 83. light gray, very compact, calcareous sandstone..0.2 m thick.

Bed 84. Gray, arenaceous clay, with very small (5–15 mm) concretions of calcareous sandstone.............. ....10 m thick.

Bed 85. A row of small calcareous concretions......... ....0.35 m thick.

[4] *Acanthohoplites aschiltaensis*, the third upper zone of the Middle (then Upper) Aptian, which was recognized at the time of Mordvilko's research.

Table 10. Distribution of ammonites in the Middle Aptian of southeastern Caucasus (Dagestan)

No.	Ammonite species	Lower Aptian	Middle Aptian		Upper Aptian
		Dufrenoyia furcata Zone	*Colombiceras crassicostatum*–*Epicheloniceras subnodosocostatum* Zone	*Parahoplites melchioris* Zone	*Acanthohoplites nolani* Zone
1	*Tropaeum bowerbancki* J. de C. Sow.	—			
2	*Cheloniceras seminodosum* Sinz.	—			
3	*Dufrenoyia furcata* J. de C. Sow.	—			
4	*D. dufrenoyi* d'Orb.	—			
5	*D. subfurcata* Kas.	—			
6	*Epicheloniceras* ex gr. *tschernyschewi* Sinz.	? —			
7	*E. waageni* Anth.	—			
8	*Pseudohaploceras matheroni* d'Orb.	—	—		
9	*Cymatoceras* ex gr. *neckeri* Pict. et Camp.	- -	- -	—	
10	*Aconeceras* (*A.*) *nisum* d'Orb.		—		
11	*Puzosia falcistriata* Anth.		—		
12	*Epicheloniceras subnodosocostatum* Sinz.		—		
13	*E. tschernyschewi* Sinz.		—		
14	*E. orientale* Jac.		—		
15	*E. pusillum* Kas.		—		
16	*E. intermedium* Kas.		—		
17	*E. stuckenbergi* Kas.		—		
18	*E. buxtorfi* Jac.		—		
19	*Colombiceras crassicostatum* d'Orb.		—		
20	*C. sinzowi* Kas.		—		
21	*C. subtobleri* Kas.		—		
22	*C.* aff. *quadrarium* Kas.		—		
23	*C. discoidale* Sinz.		—		
24	*Puzosia saltaensis* Kas.		—		
25	*Phyllopachyceras moreli* d'Orb.		—	—	
26	*Hypophylloceras velledae* Mich.			—	
27	*Tetragonites heterosulcatus* Anth.			—	
28	*T. duvalianus* Rasp.			—	
29	*Melchiorites emerici* Rasp.			—	
30	*Pseudoaustraliceras ramosum* Anth.			—	
31	*Colombiceras tobleri* Jac.			—	
32	*C. planidorsatum* Kas.			—	
33	*C.* aff. *subpeltoceroides* Sinz.			—	
34	*Acanthohoplites laticostatus* Sinz.			—	
35	*Parahoplites melchioris* Anth.			—	
36	*P. multicostatus* Sinz.			—	
37	*P. schmidti* Jac. et Tobl.			—	
38	*P. campichei* Pict. et Ren.			—	
39	*P. subcampichei* Sinz.			—	
40	*P. transitans* Sinz.			—	
41	*P. maximus* Sinz.			—	
42	*P. sjogreni* Anth.			—	
43	*P. grossouvrei* Jac.			—	
44	*P. artschmanensis* Glasun.			—	
45	*P. debilicostatus* I. Mich.			—	
46	*Acanthohoplites aschiltaensis* Anth.			—	—
47	*Eodouvilleiceras badkhysicum* Urman.				—
48	*E. clansayense* Jac.				—

Bed 86. Gray, argillaceous sandstone, with small concretions..3 m thick.

Bed 87. A row of large globular concretions (0.75–1 m)..1 m thick.

Bed 88. Gray, argillaceous, thinly bedded sandstone...3.75 m thick.

Bed 89. A series of large globular concretions.........
....1 m thick.

Bed 90. Argillaceous sandstone and arenaceous clay, with occasional small concretions of compact limestone. The bed is poor in fossils..........40 m thick.

Bed 91. A row of large globular concretions of dark gray calcareous sandstones with infrequent bivalves.......
....0.75 m thick.

Bed 92. Loose argillaceous sandstone....3.5 m thick.

Bed 93. Thinly laminated sandstone......1.1 m thick.

Bed 94. Compact calcareous sandstone, with inter beds of argillaceous sandstones with no fossils...........
....3 m thick.

Bed 95. Compact, calcareous sandstone with poikilitic texture of calcite cement. A large specimen of *Cheloniceras* sp. ex gr. *tschernyschewi* Sinz. was found at this level.

Parahoplites melchioris Zone

Bed 96. Gray, almost black near the water, arenaceous clay, with *Acanthohoplites* aff. *subpeltoceroides* Sinz...6 m thick.

Bed 97. Concretions of calcareous glauconitic sandstone coquina with bivalves and infrequent *Acanthohoplites laticostatus* Sinz....................0.75 m thick.

Bed 98. Gray weakly calcareous sandstone, with a very rich fauna of bivalves and ammonites: *Parahoplites multicostatus* Sinz., *P.* aff. *multicostatus* Sinz., *P.* sp. ex gr. *multicostatus* Sinz., *Colombiceras* aff. *subpeltoceroides* Sinz., *A.* sp. ex gr. *A. laticostatus* Sinz., large *Phylloceras* sp................................0.6 m thick.

Acanthohoplites aschiltaensis–A. uhligi Zone

Bed 100. Gray arenaceous clay with several rows of globular concretions of calcareous sandstones with infrequent bivalves..................................15 m thick.

Bed 101. Almost black arenaceous clay, with pyrite and several large concretions of compact calcareous sandstones with numerous bivalves; the ammonites *Acanthohoplites* cf. *aschiltaensis* Anth., *A.* aff. *evolutus* Sinz.; and the belemnite *Mesohibolites moderatus* Schum..1 m thick.

Lower Albian. *Acanthoplites nolani* Zone

Bed 102. Dark gray (near water black) fissured clay, with abundant pyritized shells of the small bivalve *Nuculana mariae* d'Orb., gastropods, and ammonites, including the characteristic zonal species *Acanthohoplites nolani* Seun., and also *A.* aff. *nolani* Seun., *A. multispinatus* Anth., *A.* cf. *planidorsatus* Kas., *A.* cf. *subangulicostatus* (Sinz.) Kas., *A. trautscholdi* Sim., Bač., Sor...10 m thick.

The lower zone is 71–72 m thick and two upper zones (in modern interpretation the *P. melchioris* Zone) are 28 m thick.

***C. crassicostatum–E. subnodosocostatum* Zone** is represented by black clay, argillaceous, often loose, sometimes cross-bedded sandstones, with lenses and concretions of compact calcareous sandstones. The concretions are small, usually with shells and large globular to 1–2 m in diameter. The ammonite assemblage is less diverse than that from the Central Caucasus.

***Parahoplites melchioris* Zone** is lithologically almost identical to the lower zone. The ammonite assemblage is somewhat different from that of the North Dagestan: does not contain smooth phyllocer-atids and tetragonitids, while representative of the genus *Colombiceras* are almost absent and the taxonomic compositions of *Parahoplites* and *Acanthohoplites* are strongly impoverished.

4.2. Transcaspia (Turkmenistan) (Fig. 13)

In Transcaspia (Kopet Dagh, Great and Lesser Balkhans, Kuba Dagh, Tuarkyr), the Aptian beds are represented by marine sediments with rich fossil assemblages. However, the lithology of deposits, thickness of all the stages and some of its parts, presence of large or small gaps in the succession, abundance, diversity and preservation of fossils differ in different regions.

The Middle Aptian has a diverse fossil assemblage, composed of ammonites (Table 11), bivalves, gastropods, brachiopods, echinoids, and representatives of many other groups. Coquinae with large bivalve shells are frequent. These coquinae and also rows of large calcareous–sandy concretions are frequent in the series of dark clays and siltstones. In contrast to the Lower Aptian, oolite–detrital limestones are usually absent. Fossils are usually found in coquinae and concretions. Ammonites are usually found in concretions.

4.2.1. Kopet Dagh

In Kopet Dagh, the Middle Aptian beds conformably overlie the Lower Aptian and are represented by siltstones, sandstones, and coquinae. The base of the Middle Aptian is drawn at the base of the member of bluish gray laminated marl, which is easily recognized in the sections and is traced over most regions of Kopet Dagh. This member shows the first appearance of the Middle Aptian ammonites of the genera *Epicheloniceras* and *Colombiceras.* The rarity of these ammonite occurrences and even greater rarity of occurrence of index ammonites in the underlying beds of the *Dufrenoyia furcata* Zone does not allow paleontological substantiation of this position of the boundary in most sections. However, the correlation of the data across the entire Kopet Dagh allows confident recognition of this boundary. In the westward direction, this member is enriched by silt material and, in the Danata and

Kazandzhik Kyurendag Mountains (western fringes of the Kopet Dagh Range), the Middle Aptian deposits begin with a siltstone bed.

For Kopet Dagh, we describe a section in the central part of the range, in the valley of the Adzhidere River. The section is described near the spring Sekiz-Khan, 20 km south of the Kyzylarvat (described by Tovbina et al. (1985), pp. 247–252) (Fig. 14).

Lower Aptian. *Dufrenoyia furcata* Zone.

Bed 1. Dark gray, compact calcareous–glauconitic, basally laminated, sandstone. At the top, there are rare bivalves, brachiopods, shell fragments of the genera *Dufrenoyia* and *Cheloniceras*. The bed is......30 m thick.

Bed 2. Calcareous arenaceous siltstone, gradually becoming silty glauconitic sandstone. At the top, thick coquina with oyster and *Trigonia* banks. Bivalves: *Gervillella* cf. *alaeformis* J. Sow., *Septifer lineatus* J. de C. Sow., *Pterotrigonia* ex gr. *aliformis* Park., *P.* aff. *vectiana* Lyp. and the brachiopods *Sellithyris sella* (J. de C. Sow.), *Platythyris comptonensis* Middl. The bed is...................................37 m thick.

Middle Aptian. *Epicheloniceras subnodoscostatum* Zone.

Bed 3. Dark to black, silty–calcareous argillites, upward in the section, becoming marly. In the westward direction, argillites are replaced by typical marls. The bed is..10.4 m thick.

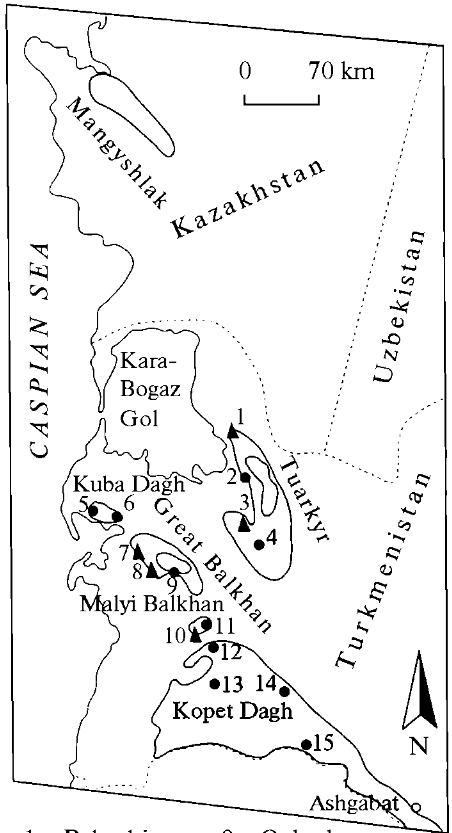
Bed 4. Dark gray, calcareous siltstone, gradually becoming massive glauconitic sandstone. At the top, oolitic detrital limestone with bryozoans, the bivalves *Gervillella* cf. *alaeformis* J. Sow., *Limatula tombeckiana* d'Orb., *Limaria (?) parallela* J. Sow., *Pseudolimea royeriana* d'Orb., *Modiolus* cf. *aequalis* J. Sow., *Septifer lineatus* J. de C. Sow., *Tellina woodsi* Mordv., *Psammobia* cf. *studeri* Pict. et Renev., the brachiopod *Sellithyris upwarensis* Walker, the ammonite *Epicheloniceras* sp. indet., and the echinoid *Toxaster* sp. indet. The bed is..... ....60.8 m thick.

Bed 5. Rhythmic alternation of calcareous–argillaceous siltstone and arenaceous calcareous siltstone. In the basal part of the bed, there are arenaceous nodules with oolites. The bed is..........................28.3 m thick.

Bed 6. Siltstone, gradually becoming upward the bed calcareous silty glauconitic sandstone. At the top of the coquina, dominating the brachiopod *Praelongithyris praelongiforma* Middl., occasional bivalves *Nuculana* sp. indet., Limidae gen et sp. indet., *Glossus* cf. *tabasarensis* Mordv., ammonites of the genera *Epicheloniceras* and *Colombiceras*. The bed is.......12.2 m thick.

Bed 7. Argillaceous–calcareous siltstone, gradually becoming calcareous siltstone and, upward in the section, becoming compact, glauconitic, indistinctly bedded, at the top, laminated sandstone. A layer of calcareous oolitic sandstone with indeterminable remains of bivalves and brachiopods lies five meters below the top. The bed is........................60.0 m thick.

Bed 8. A similar rhythm. Calcareous concretions 16 m below the top contain *Epicheloniceras caucasicum*



1—Babashi
2—Doungra
3—Umokdere
4—Tekedzhik
5—Yangadzha
6—Kubasengir
7—Bordzhakly
8—Utuludzha
9—Oglanly
10—Torengly
11—Chalsu (L. Balkhan)
12—Danata
12—Sekizkhan-Adzhidere
14—Chalsu (Kopet Dagh)
15—Temen
▲—Sections described in the text

Fig. 13. Cretaceous outcrops and main studied sections in Transcaspia.

Anth., *E. pusillum* Kasan., *E.* ex gr. *subnodosocostatum* Sinz., *Colombiceras caucasicum* Lupp., *C. subtobleri* Kas., *C.* aff. *sinzowi* Kas. The bed is............28.0 m thick.

Parahoplites melchioris Zone

Bed 9. Dark gray, loose, glauconitic sandstone, in the upper part of the bed, laminated; 9 m above the base, numerous ammonites *Parahoplites melchioris* Anth., *Pseudoaustraliceras pavlowi* Wassil., bivalves *Astarte obovata* J. Sow., *Dosiniopsis* ex gr. *parva* J. de C. Sow. are found. An oyster bed 1 m below the top contains numerous shells of *Aetostreon latissimum* Lam., and also *Arctica* cf. *sowerbyi* d'Orb., *Linotrigonia* sp. indet., indeterminable fragments of ammonites, belemnites, and brachiopods. The bed is...........................33.0 m thick.

Bed 10. Argillaceous siltstone, gradually becoming upward in the section more compact arenaceous–calcareous siltstone, replaced by sandstone with horizon of large concretions...............................33.0 m thick.

Table 11. Distribition of ammonites in the Middle Aptian Turkmenistan

No.	Ammonite species	Lower Aptian	Middle Aptian		Upper Aptian
		Dufrenoyia furcata Zone	*Epicheloniceras subnodosocostatum* Zone	*Parahoplites melchioris* Zone	*Acanthohoplites prodromus* Zone
1	*Deshayesites terminalis* Bogdanova	—			
2	*Dufrenoyia furcata* J. de C. sow.	—			
3	*Dufrenoyia dufrenoyi* d'Orb.	—			
4	*Dufrenoyia lurensis* Kil.	—			
5	*Dufrenoyia scalata* Casey	—			
6	*Dufrenoyia sinzovi* Lupp.	—			
7	*Dufrenoyia fursovae* Bogdanova	—			
8	*Burckhardtites palumbes* Humphrey	—			
9	*Burckhardtites gregoriensis* Humphrey	—			
10	*Toxoceratoides royerianus* d'Orb.	—			
11	*Aconeceras* (Sinzovia) *nisoides* Saras.	—			
12	*Cheloniceras seminodosum* Sinz.	—			
13	*Cheloniceras cornuelianum* d'Orb.	—			
14	*Colombiceras* ex gr. *crassicostatum* d'Orb.	—			
15	*Phyllopachyceras crassum* Drushits	—			
16	*Holcopnylloceras guettardi* Rasp.	—	—	—	—
17	*Jauberticeras latericarinatum* Anth.	—	—	—	
18	*Tetragonites depressus* Rasp.	—	—	—	
19	*Caspianites wassiliewskyi* Renng.		—	—	
20	*C.* aff. *wassiliewskyi* Renng.		—	—	
21	*Luppovia dostschanensis* Bogd., Kakab. et I. Mich.		—	—	
22	*L. adjiderensis* Bogd., Kakab. et I. Mich.		—	—	
23	*Epicheloniceras subnodosocostatum* Sinz.		—	—	
24	*E. tschernyschewi* Sinz.		—	—	
25	*E. caucasicum* Lupp.		—	—	
26	*E. pussilum* Kas.		—	—	
27	*E. buxtorfi* Jac.		—	—	
28	*E. stuckenbergi* Kas.		—	—	
29	*E. intermedium* Kas.		—	—	
30	*Colombiceras caucasicum* Lupp.		—	—	
31	*C. subtobleri* Kas.		—	—	
32	*C. subpeltoceroides* Sinz.		—	—	
33	*C.* aff. *sinzowi* Kas.		—	—	
34	*Aconeceras* (*Aconeceras*) *haugi* Saras.		—	—	—
35	*A.* (*A.*) *nisus* d'Orb.		—	—	—
36	*A.* (*Sinzovia*) *aptianum* Saras.		—	—	—
37	*Pseudoaustraliceras pavlowi* Wass.		—	—	—

Table 11. (Contd.)

No.	Ammonite species	Lower Aptian	Middle Aptian		Upper Aptian
		Dufrenoyia furcata Zone	*Epicheloniceras subnodosocostatum* Zone	*Parahoplites melchioris* Zone	*Acanthohoplites prodromus* Zone
38	*Colombiceras tobleri* Jac.		—	—	—
39	*Hypophylloceras velledae* Mich.		—	—	—
40	*H. aptiense* Sayn		—	—	—
41	*H. anthulai* Kas.		—	—	—
42	*Tetragonites heterosulcatus* Anth.			—	
43	*Zuerciierella zuercheri* Jac.			—	
44	*Parahoplites melchioris* Anth.			—	
45	*P. subcampichei* Sinz.			—	
46	*P. transitans* Sinz.			—	
47	*P. schmidti* Jac. et Tobl.			—	
48	*P. grossouvrei* Jac.			—	
49	*P. multicostatus* Sinz.			—	
50	*P. debilicostatus* I. Mich.			—	
51	*P. campichei* Pict. et Ren.			—	
52	*P. irregularis* Casey			—	
53	*P. sjogreni* Anth.			—	
54	*P. maximus* Sinz.			—	
55	*P. artschmanensis* Glasun.			—	
56	*P. luppovi* Tovb.			—	
57	*Protacanthoplites mirus* Tovb.			—	
58	*P. submirus* Tovb.			—	
59	*P. monilis* Tovb.			—	
60	*P.* aff. *monilis* Tovb.			—	
61	*P. multinodosus* Tovb.			—	
62	*P. allanovi* Tovb.			—	
63	*P. bigoti incivilis* Glasun.			—	
64	*P. rectangularis* Kas.			—	
65	*P. quadratus* Kas.			—	
66	*P.* aff. *bigoureti* Seun.			—	
67	*P.* aff. *planidorsatus* Kas.			—	
68	*P. bogdanovae* Tovb.			—	
69	*P. abichi* Anth.			—	—
70	*P. bigoti* Seun.			—	—
71	*Acanthohoplites aschiltaensis* Anth.				—
72	*Eodouvilleiceras badkhysicum* Urmanova				—
73	*E. clansayense* Jac.				—

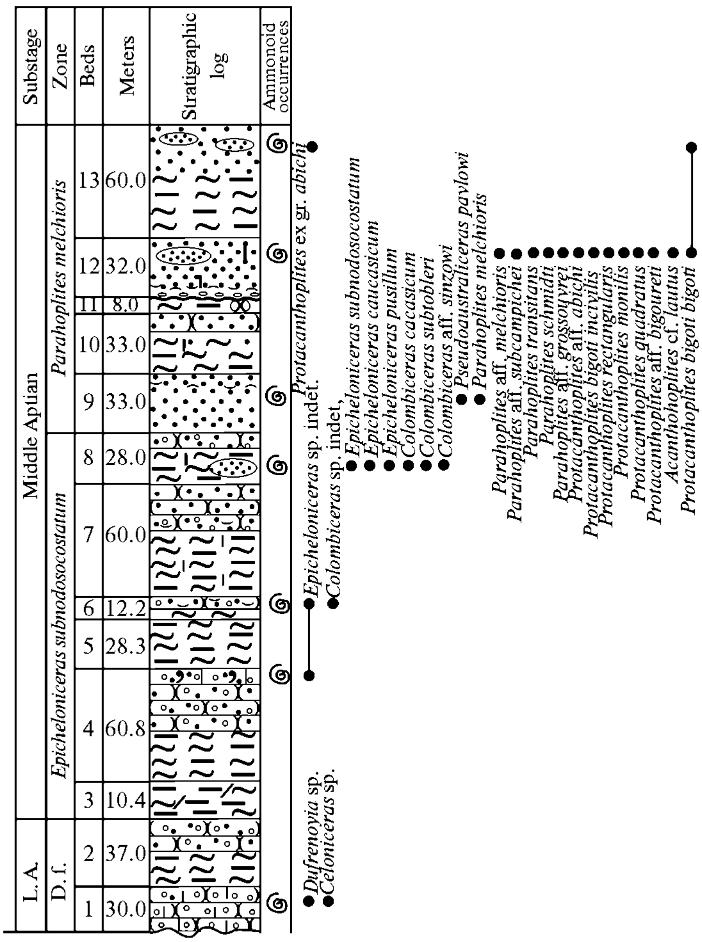


Fig. 14. Section near the Sekiz-khan spring (Adzhidere River valley, Kopet Dagh Range) (after Tovbina et al., 1985, pp. 247–252).

Bed 11. Almost black, argillaceous siltstone, with septarian concretions, covered by the talus...8.0 m thick.

Bed 12. Greenish gray, calcareous, glauconitic sandstone, with laminated interbeds. At the base of the bed, there is a layer of conglomerate (0.2–0.3 m), composed of limestone and calcareous sandstone pebbles and rounded molds of bivalve shells. The calcareous concretions in the upper part of the bed and near the very top contain mass aggregations of ammonite shells of *Parahoplites* aff. *melchioris* Anth., *P.* aff. *subcampichei* Sinz., *P. transitans* Sinz., *P. schmidti* Jac. et Tobl., *P.* aff. *grossouvrei* Jac., *Protacanthoplites* aff. *abichi* Anth., *P. bigoti bigoti* Seun., *P. bigoti incivilis* Glasun., *P. rectangularis* Kas., *P. monilis* Tovb., *P. quadratus* Kas., *P.* aff. *bigoureti* Seun., *Acanthohoplites* cf. *lautus* Glasun. and the brachiopods *Cyclothyris depressa* J. de C. Sow., *C. parvirostris* J. de C. Sow., and *Cyrtothyris middlemissi* Calzada. The bed is..32 m thick.

Bed 13. Upward in the bed, there is a gradual transition from dark gray silty clay to argillaceous siltstones and, further up, to the fine-grained irregularly bedded sandstones. At the top of the bed, there is a horizon with large (up to 1 m in diameter) calcareous concretions. The bed is............ ....60.6 m thick.

In 16 km to the west, in the vicinity of the Chalsu spring, the top of this member contained the ammonites *Protacanthoplites bigoti bigoti* Seun. and *P.* ex gr. *abichi* Anth. In the same section, the top of the *Parahoplites melchioris* Zone has traces of erosion (phosphatized conglomerate).

The *E. subnodosocostatum* Zone in this section is 199.7 m thick and the *Parahoplites melchioris* zone is 166 m thick.

***Epicheloniceras subnodosocostatum* Zone.** In the western Kopet Dagh, this zone is represented by siltstones, argillaceous siltstones, and sandstones, with thin interbeds of oolitic sandstones and oolitic limestones. This part of the Aptian section contains frequent coquina interbeds, as usual for this zone in the Tekedzhik reference section, overfilled with bivalves. The zone decreases in thickness in the eastward direction from 250 m in the Danata Kyurendag to 219 m in the Kazandzhik Kyurendag and to 168 m in the Chalsu section of the central Kopet Dagh.

In Kopet Dagh, in contrast to other regions of Transcaspia, ammonites in this part of the Aptian are considerably less common. However, despite being rare, they are relatively diverse and are represented by the species *Caspianites wassiliewskyi* Renng., *Epicheloniceras subnodosocostatum* Sinz., *Ep. tschernyschewi* Sinz., *Ep. pusillum* Kas., *Ep. buxtorfi* Jac., *Ep. stuckenbergi* Kas., *Colombiceras tobleri* Jac., *C. caucasicum* Lupp., and *C. subtobleri* Kas. *Aconeceras* has not been found in the Kopet Dagh section. Bivalves are abundant and form characteristic coquina beds similar to the coquinae of the Tededzik reference section. Although bivalves are numerous, they belong to species of wide geographic distribution, such as *Gervillella forbesi* d'Orb., *Camptonectes cottaldinus* d'Orb., *Aetostreon latissimum* Lam., *Limatula tombeckiana* d'Orb., *Pterotrigonia vectiana* Lyc., *P. aliformis* Park., *Linotrigonia archiaciana* d'Orb., *Thetironia minor circassensis* Mordv., *Th. minor transversa* Renng., and *Tellina woodsi* Mordv. Brachiopods are represented by *Sellithyris upwarensis* Walker, forming mass aggregations. Of echinoids, *Epiaster prior* Lamb. has been found in this section.

***Parahoplites melchioris* Zone.** In western Kopet Dagh, these beds are composed of siltstones, gradually becoming argillaceous siltstone, loose and compact sandstones, and calcareous sandstones with horizons of large calcareous concretions. In the region of the Kopet Dagh inner folds (basins of the Sumbar and Chandyr rivers, Palyzan and Sangudag ranges), beds of the *P. melchioris* Zone are subdivided into the lower argillaceous–silty member and upper sandstone one. In the eastward direction, sandstones gradually disappear, while compact siltstone becomes dominant. The thickness of the zone varies from 102 m in the Babasen gorge, 116 m in the Chalsu gorge, and to 226 m in the south of the area, in the Palyzan Range.

The fossil assemblage of Kopet Dagh contains ammonites of the index genera *Parahoplites* and *Protacanthoplites: Parahoplites melchioris* Anth., *P. multicostatus* Sinz., *P. debilicostatus* I. Mich., *P. luppovi* Tovb., *P. schmidti* Jac. et Tobler, *P. artschmanensis* Glasun., *P.* aff. *grossouvrei* Jac., *P.* cf. *campichei* Pict. et Renev., *Protacanthoplites abichi* Anth., *P. bigoti bigoti* Seun., *P. mirus* Tovb., and *P. monilis* Tovb. Members of *Aconeceras* characteristic of the synchronous beds of Tuarkyr, Great and Lesser Balkhans are not found here.

Bivalves in this zone of Kopet Dagh are relatively abundant and represented by species of wide stratigraphic ranges often forming beds of coquina: *Grammatodon carinatus* J. Sow., *Gervillella forbesi* d'Orb., *Aetostreon latissimum* Lam., *Astarte obovata* J. Sow., *Linotrigonia spinosa* Park., *Arctica sowerbyi* d'Orb., and *Corbula striatula* J. de C. Sow. Of brachiopods there are the usual taxa for these deposits: *Cyclothyris (Belbekella) depressa* J. de C. Sow. and *C. (C.) parvirostris* J. de C. Sow.

4.2.2. Lesser Balkhan

The Lesser Balkhan Range is a small mountainous region located to the northwest of the Danata Kyurendag, from which it is separated by a large takir. The Middle Aptian beds in the Lesser Balkhan are represented by monotonous series of siltstone and sandstone with infrequent beds of coquina and small calcareous concretions. The thickness of the deposits exceed those of Kopet Dagh, nearly 625 m instead of 130–430 m. In this region, we studied three sections in the Torengly, Portsaiman, and Chalsu gorges. Below describe the section in Torengly, the western gorge of the three named above (Fig. 15).

Lower Aptian. *Dufrenoyia furcata* Zone

Bed 1. Dark gray, silty, thinly fissured clay (lower part of the bed). The sandstone is greenish yellow, bedded. In the middle of the sandstone member, there is an interbed (0.3 m) of green compact sandstone with fragments of large ammonites *Cheloniceras* sp. indet., *Dufrenoyia* sp. indet., Desmocerataceae gen. indet. The bed is..8.6 m thick.

Middle Aptian. *Epicheloniceras subnodosocostatum* Zone

Bed 2. Dark gray, argillaceous siltstone, with thin sandstone interbeds. At the top, there is a compact, detrital limestone plate (0.15 m). The bed is...............
....21.1 m thick.

Beds 3–7. Smoky argillaceous siltstone with thin interbeds of compact sandstones................67 m thick.

Bed 8. Greenish compact sandstone.......8 m thick.

Bed 9. Gray siltstone..........................5.2 m thick.

Bed 10. Dark gray, thickly laminated sandstone. A large shell fragment of *Caspianites* (?) sp. indet is found. The bed is....................................5.5 m thick.

Bed 11. Dark gray thinly fissured siltstone.............
....14.5 m thick.

Bed 12. Greenish gray massive weakly cemented sandstone, with interbeds of compact platy sandstones...33.4 m thick.

Bed 13. Dark greenish gray siltstone.....10.2 m thick.

Bed 14. Sandstone with honeycomb weathering. In the basal part of the bed, greenish, fine-grained glauconite sandstone overlain by similar sandstones with carbonate cement. Rare fragments of large uncoiled ammonites (most likely of *Caspianites*). In the upper part of the bed, there are indistinct horizons of oval concretions, some of which contain abundant fossils: bivalves, gastropods, and poorly preserved ammonite shells of *Tetragonites* sp. indet., *Epicheloniceras* sp. indet., and *Colombiceras* sp. indet. The bed is...............
....40.2 m thick.

Bed 15. Gray compact thinly fissured siltstone........
....3 m thick.

Bed 16. Greenish sandstone with honeycomb weathering and interbeds of compact glauconitic sandstone with glass luster on broken surfaces............
....7.5 m thick.

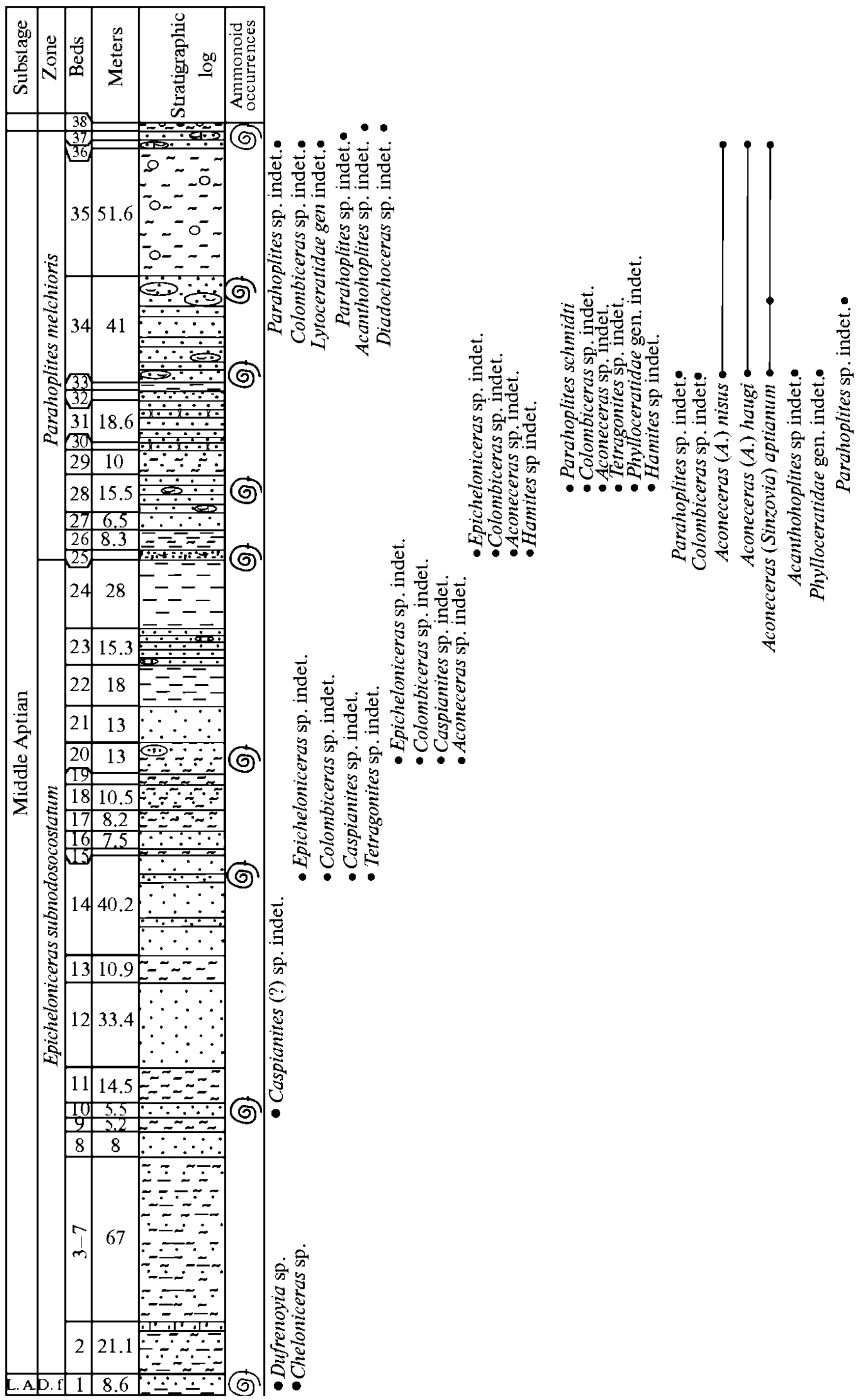


Fig. 15. Section in the Torengly gorge (Lesser Balkhan).

Bed 17. Green, thinly fissured siltstone in the basal part of the bed. Upward in the bed, plates of yellow compact ferruginous sandstone appear. The bed is...... ....8.2 m thick.

Bed 18. Greenish, compact, laminated siltstone; the number of arenaceous interbeds increases compared to Bed 17...................................10.5 m thick.

Bed 19. Grayish green siltstone............4.2 m thick.

Bed 20. Greenish yellow, massive and laminated sandstone and siltstone. Upward in the bed, greenish siltstone alternate with grayish yellow, compact laminated sandstone with detrital concretions. Some of the concretions are overfilled by shells and molds of bivalves, gastropods, and the ammonite genera *Epich-*

eloniceras sp. indet., *Colombiceras* sp. indet., *Caspianites* sp. indet., and *Aconeceras* sp. and indeterminable molds of the ammonite family Desmoceratidae. The bed is..13 m thick.

Bed 21. Greenish yellow sandstone.......13 m thick.

Bed 22. Dark gray argillites...................18 m thick.

Bed 23. Gray, greenish, yellowish, compact, massive sandstone, with honeycomb weathering. Sandstone contains concretions with detritus, shells, and molds of bivalves, gastropods, and ammonites. In the upper part of the bed, there are lenses with pebbles of sandstone and calcareous concretions with the same fossils. Near the very top of the bed, there is a layer of dirty grayish green glauconitic sandstone. The bed is capped by a layer of yellowish gray siltstone................15.3 m thick.

Bed 24. Dark green thinly fissured siltstone........... ....28 m thick.

Parahoplites melchioris Zone

Bed 25. Dark gray, compact sandstone with limestone pebbles 0.03–0.15 m in size. In the sandstone, there are nests of shells and molds of bivalves, gastropods, and ammonites of the genera *Epicheloniceras* sp. indet., *Colombiceras* sp. indet., *Hamites* sp., *Aconeceras* sp. indet., and others. The bed is 0.5 m thick.

Bed 26. Argillites with layers of yellow siltstone....... ....8.3 m thick.

Bed 27. Gray ferruginous, bedded sandstone.......... ....6.5 m thick.

Bed 28. Greenish and yellowish gray massive and bedded, glauconitic sandstone with small (up to 0.15–0.20 m in diameter) calcareous concretions with many shells and molds of bivalves, gastropods, and ammonites of the genera *Phylloceras* sp. indet., *Tetragonites* sp. indet., *Parahoplites schmidti* Jac., *Colombiceras* sp. indet., *Aconeceras* sp. indet., *Hamites* sp. indet., and others...15.5 m thick.

Bed 29. Alternation of siltstones and sandstones..... ....10 m thick.

Bed 30. Fine-grained thinly laminated, compact sandstone...1.5 m thick.

Bed 31. Banded, strongly compact thickly laminated sandstone alternating with looser sandstones forming depressions in the relief.............18.6 m thick.

Bed 32. Grayish green, compact sandstone. At the top of the bed with a conglomerate of whitish phosphoritic pebbles. The bed is......................3.3 m thick.

Bed 33. Dark gray, on the surface light bluish argillites, in places, ferruginous......................1.5 m thick.

Bed 34. Yellowish gray massive, compact sandstone alternating with weakly cemented sandstone. Calcareous compact concretions are scattered in the bed, some of them with shells and molds of bivalves, gastropods, and the ammonite genus *Parahoplites*. At the top of the bed, there are loose concretions (or "nests") overfilled by shells of the ammonites *Parahoplites* sp. indet., *Colombiceras* sp. indet., *Aconeceras (Sinzovia) aptianum* Saras., *Tetragonites* sp. indet., *Phylloceras* sp. indet., *Acanthohoplites* sp. indet., and others. The bed is.......... ....41 m thick.

Bed 35. Dark greenish gray siltstone with septarian concretions...51.6 m thick.

Bed 36. Gray, bedded, at the base loose sandstone with concretions of gray calcareous sandstone, overfilled by shells and molds of bivalves, gastropods, brachiopod, and ammonite of the genera *Parahoplites* sp. indet., *Colombiceras* sp. indet., *Aconeceras (A.) nisus* d'Orb., *A. (A.) haugi* Saras., *A. (Sinzovia) aptianum* Saras., *Lytoceras* sp. indet. and others. At the top of the bed, these concretions enclose the ammonites *Parahoplites* sp. indet. and *Acanthohoplites* sp. indet. The bed is..3.7 m thick.

Bed 37. Yellowish gray sandstone with honeycomb weathering textures, with concretions containing the ammonite *Parahoplites* sp. indet..............2.5 m thick.

Upper Aptian. *Acanthohoplites prodromus* Zone

Bed 38. Smoky siltstone; at the top, with conglomerate-like interbeds with small phosphoritic pebbles and molds of bivalves and the ammonites *Parahoplites* (?), *Acanthohoplites* sp. indet., and *Diadochoceras* sp. indet. The bed is....................................0.3 m thick.

All fossils in this section are poorly preserved and most of them indeterminable to species. However, the presence of the index genera *Epicheloniceras* (in the lower part) and *Parahoplites* (in the upper part) allow recognition of the zones.

***Epicheloniceras subnodosocostatum* Zone.** At the base of the *E. subnodosocostatum* Zone of the Lesser Balkhan, as in the western Kopet Dagh Range, there are siltstone beds. They are not separated from the total series of the overlying rocks, but contain fragments of large uncoiled ammonites most likely of the genus *Caspianites,* which is characteristic of the above-named zone (Fig. 16). The whole of the overlying part of the zone is, as mentioned above, composed of regular alternation of siltstone (rarely argillaceous siltstone) with sandstones, forming resistant ledges (Fig. 17). The coquina beds are virtually absent and fossil accumulations are usually found in calcareous concretions.

Despite relatively small distances between the above sections, the thickness of the *Ep. subnodosocostatum* Zone varies greatly from 370 to 600 m. For instance, in the Portsaiman section located between the Torengly and Chalsu sections, the zone is almost half as thick as in the neighboring sections. This could be explained by deep erosion, as a result of which the Cenomanian beds overlie the beds of this zone (as was noted by A.D. Natsky). In the same section, more coarsely-grained sandstones dominate compared to the neighboring regions. However, this could be explained by the shallower-water sedimentation in this area of the Aptian basin, resulting from the block uplift, which did not affect the adjacent areas.

In the Lesser Balkhan sections, fossil accumulations are found in the calcareous nodules. The ammo-

Fig. 16. Fragments of a large *"Caspianites"* sp. at the base of the *Epicheloniceras subnodosocostatum* Zone. Lesser Balkhan , Portsaiman gorge (collected in 1966).

nites include *Aconeceras (Sinzovia) aptianum* Saras., *Ap. (Ap.) nisus* d'Orb., *Ap. (Ap.) haugi* Saras., *Epicheloniceras subnodosocostatum* Sinz., *Ep. tschernyschewi* Sinz., *Ep. martini* d'Orb., *Ep. pusillum* Kas., *Colombiceras tobleri* Jac. In the lower part of the sections of this zone, there are fragments of large shells of uncoiled ammonites most likely of the genus *Caspianites* up to 0.7–0.8 m in diameter. In addition, there are found ammonites of the genera *Phylloceras, Tetragonites,* and *Uhligella.* Bivalves in the Lesser Balkhan are less common than in Tuarkyr or Great Balkhan. They include *Leionucula simplex* d'Orb., *Nuculana scapha* d'Orb., *Thetironia minor transversa* Renng., *Pterotrigonia aliformis* Park., and *Corbula striatula* J. de C. Sow. Brachiopods are represented by geographically widespread species: *Cyclothyris parvirostris* (J. de C. Sow.), *Sellithyris upwarensis* Walker, and *S. coxwellensis* Middl.

***Parahoplites melchioris* Zone.** Deposits of the *P. melchioris* Zone conformably overlie the underlying beds and are represented by arenaceous–silty series with horizons of large globular concretions. In the central part of the southern slope of the range, they are eroded (Portsaiman gorge) and, in the upper part of the zone, there is a slab conglomerate up to 6.5 m thick. The overlying beds are Cenomanian. The conglomerate contains rounded pebbles of marl, sandstone, siltstone, phosphoritic pebbles, nests of gravelite, redeposited concretions, with shell remains of the ammonites *Parahoplites* and *Anahoplites* and the bivalves *Birostrina sulcata* Park. and others. The zone is 148–170 m thick.

The Lesser Balkhan ammonite assemblage of this zone is almost the same as that of the Great Balkhan.

The general overview of the distribution of ammonites in the zones of the Middle Aptian of Transcaspia was shown earlier in Table 11.

4.2.3. Great Balkhan and Kuba Dagh

The Middle Aptian beds of the Lower Cretaceous sedimentary complex are exposed on the surface of the northern margin of the Great Balkhan Anticline and

Fig. 17. Alternating siltstone and sandstone of the *Epicheloniceras subnodosocostatum* Zone. Lesser Balkhan, Portsaiman gorge (1966).

Kuba Dagh Range. Although these structures are tectonically different, in the Middle Aptian Time they developed in almost the same manner. The Middle Aptian beds of these regions are very similar in thickness, lithology, and paleontology and, therefore, considered together.

For these regions, we describe two most complete and well-exposed sections near the Utuludzha and Bordzhakly wells.

The Utuludzha section is described 1.5 km northwest of the well (Fig. 18).

Lower Aptian. *Dufrenoyia furcata* Zone

Bed 1. Gray, fine-grained, arenaceous limestones. In the upper part of the bed, there are lenses of compact large-grained sandstone with gravel, infrequent flatly rounded glauconitic pebbles (apparently with phosphatic grains) of gray sandstone. The lenses are sometimes "expanded" to the entire thickness of the bed. The bed contains the ammonites *Dufrenoyia dufrenoyi* d'Orb., *D.* ex gr. *sinzovi* Lupp., *D. fursovae* Bogdanova, *Cheloniceras cornuelianum* d'Orb., the bivalve *Aucellina* sp., and the echinoid *Epiaster fourtaui* Lamb. The bed is..............................1.2 m thick.

Middle Aptian. *Epicheloniceras subnodosocostatum* Zone

Bed 2. Dark, almost black, strongly silty, shingled clay, with two lenticular beds of gray calcareous sandstone (in the middle part of the bed and at the top). The interbeds are from 0.3–0.4 to 0.7–0.9 m thick. The upper sandstone horizon contains isolated fragments of belemnite rostra. The bed is.......8.5 m thick.

Bed 3. Mostly turf-covered. Trenches at the base of the bed have revealed dark arenaceous siltstone, rapidly becoming yellowish loose sand. The bed is........... ....12.3 m thick.

Bed 4. Dark, greenish siltstone, in places, argillaceous or arenaceous................................6.5 m thick.

Bed 5. Yellowish loose sand; in the basal part of the bed with lenses of calcareous sandstone (from 0.5 to 1.5 m); the density and calcareous content of the rocks increase toward the center of the lenses. The same bed contains aggregations of small shelly detritus. Ammonites: *Cheloniceras* sp., the bivalve *Leionucula* ex gr. *albensis* d'Orb., the brachiopod *Sellithyris* cf. *coxwellensis* Middl. The bed is.................................7.2 m thick.

Bed 6. Sand, like in Bed 5. Three lenslike horizons (at the base, in the middle and at the top) of calcareous sandstone. The thickness of the lower horizons does not exceed 0.5 m, of the upper, 1 m. The upper horizon contains aggregations of shelly detritus. The sandstone lenses are commonly fused together to form layers varying in thickness. Traces of bioturbation may be observed. The following taxa have been determined: the ammonites *Epicheloniceras subnodosocostatum* Sinz., *Ep. tschernyschewi* Sinz., *Ep. orientale* Jac., *Colombiceras tobleri* Jac. et Tobl., *C. discoidalis* Sinz., *C. subtobleri* Kas., *C. subpeltoceroides* Sinz., *Aconeceras (Sinzowia) aptianum* Saras., *Aconeceras (Ap.) nisus* d'Orb., *A. (Ap.) haugi* Saras., *Tropaeum* sp., *Hamites* sp., the bivalves *Leionucula planata* Leym., *Idonearca* ex gr. *glabrae* Park., *Camptonectes cottaldinus* d'Orb., *Lucina pissum* J. de C. Sow., the brachiopods *Sellithyris* cf. *coxwellensis* Middl., and the echinoids *Epiaster fourtaui* Lamb. The bed is....................................3.5 m thick.

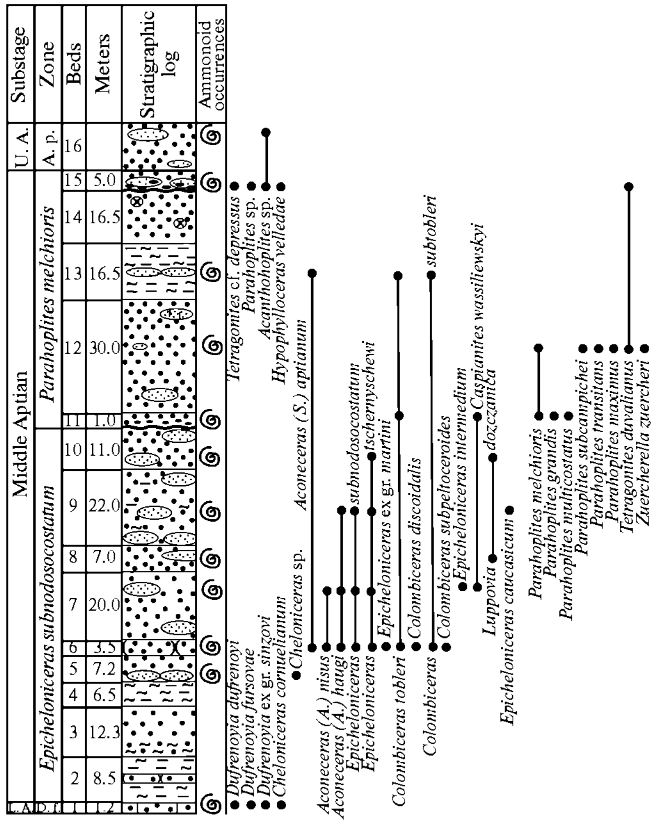


Fig. 18. Section near the Utuludzha well (Great Balkhan).

Bed 7. Gray with yellowish or greenish hue, massive, medium-grained, loosely cemented sandstone. There are two horizons of large (up to 1.5–2 m) globular or lenticular concretions of compact calcareous sandstone. The concretions are overfilled by shelly detritus, wood fragments, and numerous fossils: the ammonites *Epicheloniceras subnodosocostatum* Sinz., *Ep. intermedium* Kas., *Ep. tschernyschewi* Sinz., *Colombiceras* sp., *Caspianites wassiliewskyi* Renng., *Aconeceras (Ap.) nisus* d'Orb., Ap. (Ap.) haugi Saras., the bivalves *Glycymeris umbonatus* J. Sow., *Lucina pissum* J. de C. Sow., *Thetironia minor transversa* Renng., *Corbula striatula* J. de C. Sow. The bed is............................20 m thick.

Bed 8. Dark yellow, fine-grained, argillaceous-silty sandstone with one horizon of lenticular concretions of gray calcareous sandstone with numerous remains of poorly preserved ammonites: *Epicheloniceras* sp., *Luppovia dozczanica* Bogd., Kakab., I. Mich., belemnites, bivalves, and echinoids. The bed is.................7 m thick.

Bed 9. Sandstone, similar to that of Bed 8, with three horizons of large lenticular concretions. At the base of

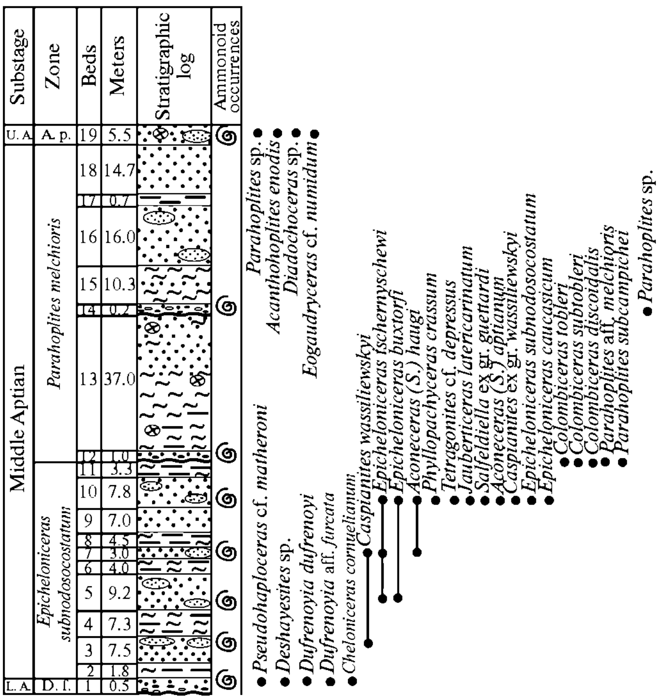


Fig. 19. Section near the Bordzhakly well (Great Balkhan).

the bed, the concretions are flattened forming a continuous horizon; in the middle part, the concretions are spherical up to 1 m in diameter and, at the top, they are of irregular shape up to 2 m in diameter. The globular concretions contain nests or lenses with fossils: the ammonites *Epicheloniceras subnodosocostatum* Sinz., *Ep. tschernyschewi* Sinz., *Ep. caucasium* Anth., *Ammonitoceras* sensu lato, *Aconeceras (Ap.) haugi* Saras., belemnites, the bivalves *Idonearca glabrae* Park., *Ctenoides undatus* Desh., *Thetironia minor transversa* Renng., and echinoids. The bed is...............22 m thick.

Bed 10. Yellowish greenish, medium-grained, glauconitic sandstone, with four horizons of large lenticular concretions of calcareous sandstone, with wood fragments and shelly detritus. Large concretions commonly form continuous beds. Small concretions contain abundant fossils: the ammonites *Epicheloniceras tschernyschewi* Sinz., *Colombiceras* sp., *Luppovia dozczanica* Bogd., Kakab., I. Mich., belemnites, the bivalves *Leionucula albensis* d'Orb., *L. planata* Leym., *Idonearca glabrae* Park., *Glycymeris sublaevis* J. de C. Sow., *Gervilaria forbesiana* d'Orb., *Plicatula carteroni* d'Orb., *Mytilus lanceolatus* J. de C. Sow., *Lucina pissum* J. de C. Sow., *Thetironia minor transversa* Renng., and the brachiopod *Cyclothyris parvirostris* J. de C. Sow. The bed is.......................11 m thick.

Parahoplites melchioris Zone

Bed 11. Gray, on weathered surface purple, medium-grained sandstone, with small and relatively large (up to 0.2 m but rarely pebbles) phosphoritic gravel, phosphoritic sandstone, covered by glauconitic taint. In the middle of the bed, there are lenses of calcareous sandstone, with varying content of phosphoritic gravel and smaller compact calcareous concretions with fossils: the ammonites *Parahoplites melchioris* Anth., *P. grandis* Sinz., *P. multicostatus* Sinz., *Colombiceras tobleri* Jac., *Caspianites wassiliewskyi* Renng., *Phylloceras* sp., *Tetragonites* sp., *Hamites* sp., the bivalve *Fenestricardita tenuicostata* J. de C. Sow., the brachiopods *Praelongithyris lankesteri* Walker, *Cyclothyris parvirostris* J. de C. Sow., and *Sellithyris upwarensis* Walker. The bed is......................1 m thick.

Bed 12. Yellow, weakly cemented sandstone, with several layers of large (up to 1 m in diameter) and smaller concretions of gray calcareous compact sandstone with abundant fossils: the ammonites *Parahoplites melchioris* Anth., *P. subcampichei* Sinz., *P. transitans* Sinz., *P. maximus* Sinz., *Tetragonites duvalianus* d'Orb., *Zuercherella zuercheri* Jac., fragments of uncoiled ammonites, bivalves *Pectinucula tenuicostata* Mordv. The bed is....................................30 m thick.

Bed 13. Dark gray, almost black, argillaceous siltstone covered by talus with greenish and reddish stains. The bed is easily recognized in the section by a grayish band between the layers of yellow sandstones with concretions. Ammonites *Colombiceras tobleri* Jac., *C. subtobleri* Kas., *Aconeceras (Sinzowia) aptianum* Saras. The bed is....................................16.5 m thick.

Bed 14. Turf-covered. Pits expose yellowish loose sandstone with numerous small (up to 0.2 m) septarian concretions. The bed is.....................14.7 m thick.

Bed 15. Greenish yellow loose sandstone, with several layers of large lenticular concretions of gray calcareous sandstone (some of the concretions form continuous horizons). The concretions contain nests and continuous lenses of conglomerates with phosphoritic pebbles and many fossils: ammonites of the genera *Parahoplites* and *Acanthohoplites* (not identifiable to species), and also *Phylloceras velledae* Mich., *Tetragonites* cf. *depressus* Rasp., *T. duvalianus* d'Orb., belemnites, bivalves, brachiopods, echinoids. The bed is 5 m thick.

Upper Aptian. *Acanthohoplites prodromus* Zone

Bed 16. Gray and yellowish sandstone with concretions of compact gray sandstone. The concretions contain nests with fossils (*Acanthohoplites* sp. and others). The bed is..................................7.3 m thick.

The *Epicheloniceras subnodosocostatum* Zone is 98.0 m thick and the *Parahoplites melchioris* Zone is 67.2 m thick.

The Bordzhakly section is located on the southern slope of the Great Balkhan Range, 7–8 km east of the Bordzhakly well (Fig. 19).

Lower Aptian. *Dufrenoyia furcata* Zone

Bed 1. At the base of the bed, there is a layer of conglomerate, containing small (up to 2–3 cm) pebbles of compact calcareous phosphatized sandstone, some pebbles are covered by greenish glauconitic stains. The upper part of the bed is composed of yellowish fine-grained sandstone. Pebbles and sandstone contain numerous (sometimes rounded) shells and molds of fossils: *Dufrenoyia dufrenoyi* d'Orb., *D.* aff. *furcata* J. de C. Sow., *Deshayesites* sp., *Cheloniceras cornuelianum* d'Orb., *Pseudohaploceras* cf. *matheroni* d'Orb., *Sulcirhynchia hythensis* Owen, belemnites, bivalves, gastropods. The bed is............................0.5 m thick.

Middle Aptian. *Epicheloniceras subnodosocostatum* Zone

Bed 2. Turf-covered. In places there are exposures of dark gray, almost black, silty clay. The bed is..1.8 m thick.

Bed 3. Yellow sand; at the top, two horizons of joined concretions (0.5–0.7 and 1.0–1.5 m) of compact laminated sandstone with glauconitic grains. Concretions contain the ammonite *Caspianites wassiliewskyi* Renng. and rare bivalves. The bed is ....7.5 m thick.

Bed 4. Siltstone argillaceous, black, nodular...7.3 m thick.

Bed 5. Yellowish, loosely cemented fine-grained sand, with two horizons of large (up to 1–2 m) lenticular concretions in the upper part of the bed. The concretions contain the ammonites *Epicheloniceras tschernyschewi* Sinz., *E. buxtorfi* Jac., *Caspianites* sp., bivalves *Leionucula albensis* d'Orb., belemnites, and gastropods. The bed is............................9.5 m thick.

Bed 6. Dark gray, argillaceous siltstone.....4 m thick.

Bed 7. Brownish yellow loose sandstone, toward the top becoming a horizon of concretions of gray, compact sandstone, with brownish "desert tan" and honeycomb weathering. Lenses of concretions contain the ammonites *Epicheloniceras tschernyschewi* Sinz., *Caspianites* cf. *wassiliewskyi* Renng., *Aconeceras (Ap.) haugi* Saras., bivalves, and gastropods. The bed is..............3 m thick.

Bed 8. Dark gray, silty clay, in places, weakly arenaceous..4.5 m thick.

Bed 9. Yellow, loose sand.......................7 m thick.

Bed 10. Yellow loose sand, at the base and at the top, with lenses of compact calcareous sandstone with phosphoritic pebbles and pebbles covered by glauconite. The lenses contain abundant ammonites *Phyllopachiceras crissum* Drushits, *Colombiceras* sp., *Epicheloniceras tschernyschewi* Sinz., *E. subnodosocostatum* Sinz., *E. buxtorfi* Jac., *E. caucasicum* Anth., *Caspianites* ex gr. *wassiliewskyi* Renng., *Salfeldiella* ex gr. *guettardi* Rasp., *Jauberticeras latericarinatum* Anth., *Zuercherella* sp., *Tetragonites* cf. *depressus* Rasp., *Aconeceras (Sinzowia) aptianum* Saras., *Ap. (Ap.) haugi* Saras., bivalves *Grammatodon carinatus* J. Sow., *Arca dupiniana* d'Orb., *Idonearca cornuelliana* d'Orb., the brachiopods *Sellithyris upwarensis* Walker, *Cyclothyris* cf. *parvirostris* J. de C. Sow., belemnites, and gastropods. The bed is.....................................7.8 m thick.

Bed 11. Dark silty clay, with gypsum.......3.3 m thick.

Parahoplites melchioris Zone

Bed 12. Greenish gray calcareous sandstone, with nests of shelly detritus. At the top, there is a bed of phosphoritic conglomerate, forming lenses varying in thickness, with numerous small phosphoritic pebbles and phosphatized molds of the ammonites *Colombiceras discoidalis* Kas., *C. subtobleri* Kas., *Parahoplites* aff. *melchioris* Anth., P. *subcampichei* Sinz.; rare bivalves *Plicatula placunea* Lam., and the brachiopod *Praelongithyris lankesteri* Walker. The bed is.......................1 m thick.

Bed 13. Dark gray, argillaceous siltstone, in the upper part of the bed becoming yellow arenaceous. Septarian concretions are found throughout the bed, at the base, small (0.3 m in diameter), at the top, larger (0.6–0.8 m in diameter). The bed is.....................37 m thick.

Bed 14. Conglomerate. Cement is gray fine-grained calcareous sandstone; numerous pebbles varying in shape (oval, flattened, irregularly rounded) and size (from 2 to 7 cm) and composed of phosphatized sandstone with brownish ferruginous and, less commonly, greenish glauconitic stains and numerous burrowing traces. Rare occurrences of the ammonite *Parahoplites* sp. indet. The bed is..............0.2 m thick.

Bed 15. Brownish gray siltstone with layers of yellowish gray and gray sandstones with numerous bioturbations filled by whitish argillaceous material. The bed is..10.3 m thick.

Bed 16. Grayish yellow weakly cemented sandstone with horizons of large concretions of gray compact sandstone. The bed is..............................16 m thick.

Bed 17. Dark gray clay........................0.7 m thick.

Bed 18. Light greenish gray, weakly cemented sandstone...14.7 m thick.

Upper Aptian. *Acanthohoplites prodromus* Zone

Bed 19. Yellow loosely cemented sandstone with three layers lens-shaped or compact concretion-like sandstones. The middle layer contains septarian concretions with the ammonites *Parahoplites* sp., *Diadochoceras* sp., *Acanthohoplites enodis* Tovb., *Eogaudriceras* cf. *numidum* Coq. and infrequent bivalves. The bed is..5.5 m thick.

The *Epicheloniceras subnodosocostatum* Zone is 55.4 m thick and the *Parahoplites melchioris* Zone is 79.9 m thick.

***Epicheloniceras subnodosocostatum* Zone.** The Great Balkhan and Kuba Dagh beds of this zone are lithologically divided into two parts: the lower is dark silty clay and argillaceous siltstone with beds of calcareous sandstone, the upper part is loose fine-grained sandstone with numerous concretions and aggregations of phosphoritic gravel in the upper part. In the eastward direction in this region, the role of sandy material decreases. Oyster coquina, frequent in Tuarkyr, is absent here. The deposits are thickest in Kuba Dagh (85–100 m), whereas in the Great Balkhan, they do not exceed 52–98 m.

The Great Balkhan and Kunba Dagh ammonite assemblages of this zone differ from the Tuarkyr assemblage in the frequent and well-preserved fossils, the presence of phylloceratids, tetragonitids, and desmoceratids. The assemblage contains *Phyllopachyc-*

eras crassum Drushits, *Tetragonites depressus* Rasp., *Jauberticeras latericarinatum* Anth., *Salfeldiella guettardi* Rasp., *Aconeceras (Sinzowia) aptianum* Saras., *Ap. (Ap.) nisus* d'Orb., *Ap. (Ap.) haugi* Saras., *Caspianites wassiliewskyi* Renng., *Luppovia dotshanensis* Bogd., Kakab., et I. Mich., *Epicheloniceras subnodosocostatum* Sinz., *Ep. tschernyschewi* Sinz., *Ep. intermedium* Kas., *Ep. caucasicum* Anth., *Ep. buxtorfi* Jac., *Colombiceras tobleri* Jac. et Tobler, *C. subtobleri* Kas., *C. subpeltoceroides* Sinz. Of bivalves, the bed contains *Leionucula planata* Leym., *L. cornueliana* d'Orb., *Gervillella forbesiana* d'Orb., *Plicatula carteroniana* d'Orb., *Mytilus lanceolatus* J de C. Sow., *Ctenostreon undatus* Desh., *Lucina pissum* J. de C. Sow., *Corbula striatula* J. de C. Sow. Brachiopods are represented by almost the same species as in Tuarkyr: *Cyclothyris parvirostris* J. de C. Sow., *Sellithyris upwarensis* Walker, and *S. coxwellensis* Middl. Echinoids are represented by *Holaster benstedi* Forb., *Epiaster prior* Lamb. and gastropods, by *Proscala gurgites* Pict. et Raux.

***Parahoplites melchioris* Zone.** In the Great Balkhan and Kuba Dagh ranges, these beds overlie the beds with small erosion represented by a thin conglomerate. In Kuba Dagh, beds of this zone are represented by loose siltstones and calcareous sandstones. Easterly, the number of sandy layers increases and, in Great Balkhan, the lower part of the zone is composed of loose massive sandstones with horizons of large globular concretions, banded stained siltstones, and argillaceous–silty sandstones. Coquina interbeds, as in the underlying beds, are absent. In Kuba Dagh, the zone is 45–50 m thick and, in Great Balkhan, it ranges from 80 to 100 m.

The fossil assemblage of this zone shows a large diversity of abundant ammonites. In addition to the index species occurring in the area of the Tekedhik section, it includes *Parahoplites melchioris* Anth., *P. multicostatus* Sinz., *P. irregularis* Casey, *P. subcampichei* Sinz., *P. debilicostatus* I. Mich., *P. luppovi* Tovb., *P.* aff. *melchioris* Anth., *P.* aff. *grossouvrei* Jac., *Protacanthoplites abichi* Anth., *P. monilis* Tovb., *Aconeceras (Sinzowia) aptianum* Saras., *Ap. (Ap.) haugi* Saras. and *Phylloceras anthulai* Kas., *Ph. aptiense* Sayn, *Tetragonites depressus* Rasp., *Aconeceras (Ap.) nisum* d'Orb., *Zuercherella zuercheri* Jac. Of bivalves, which here are relatively rare, the following taxa are identified: *Pectinucula tenuicostata* Mordv., *Idonearca* ex gr. *cornueliana* d'Orb. Large oysters, numerous in the Tuarkyr sections, are completely absent. Brachiopods are common here and represented by *Cyclothyris (Belbekella) depressa* (J. de C. Sow.), *P. (P.) parvirostris* (J. de C. Sow.), *Burrirhynchia grasiana* (d'Orb.), *B. sulcata* (d'Orb.), *Praelongithyris praelongiforma* Middlemiss. Gastropods are found less commonly, *Nummocalcar dentatum* d'Orb. and *Tessarolax ebrayi* Lor.

4.2.4. Tuarkyr

In 1969, a large team of stratigraphers and paleontologists from VSEGEI studied the reference sections of the Aptian and Albian stages, the descriptions of which unfortunately remained unpublished.[5] For the Aptian Stage, the section on the Tekedzhik Uplift on the southwestern margin of the Tuarkyr Anticline was chosen as the reference section. This is a readily accessible and completely exposed section of this stage, but the Middle Aptian beds in it are unfortunately insufficiently characterized by ammonites. Therefore, two other sections of Tuarkyr are described below, Umokdere and Babashi, in which both Middle Aptian zones are reasonably well characterized.

The section in the Umokdere gorge is located on the southeastern wing on the Tuarkyr Anticline, on the eastern slope of the Akkyr Range, near the topographic mark 216 m (Figs. 20, 21).

Lower Aptian. *Dufrenoyia furcata* Zone

Bed 1. Yellowish gray and greenish gray, massive, weakly cemented sandstone, with horizons of arenaceous concretions. The ammonite *Dufrenoyia* ex gr. *furcata* J. de C. Sow., the bivalves *Leionucula albensis* d'Orb., *Inoceramus* sp., and gastropods are recorded. The bed is..22.7 m thick.

Middle Aptian. *Epicheloniceras subnodosocostatum* Zone.

Bed 2. On the surface of the bed, there are fragments of strongly fragmented oyster coquina, rarely with pebbles covered by a glauconitic crust. There are poorly preserved ammonites *Colombiceras* aff. *crassicostatum* d'Orb., *Epicheloniceras* ex gr. *martini* d'Orb., bivalves *Septifer lineatus* J. de C. Sow., *Pterotrigonia aliformis* Park., the brachiopod *Platythyris moutoniana* d'Orb., belemnites, gastropods, and echinoids. The bed is..0.3 m thick.

Bed 3. Dark green silty clay with infrequent fragments of shells of bivalves and gastropods.................. ....3.9 m thick.

Bed 4. Gray sandstone, with small concretions (up to 0.1–0.15 m in diameter) of calcareous sandstone, overfilled by small bivalves, dominated by *Corbula striatula* J. de C. Sow., *Thetironia minor transversa* Renng. Upward in the bed, sandstone becomes loosely cemented. In the bed, there are heteromorphic ammonites, *Caspianites wassiliewskyi* Renng. The bed is......... ....8.2 m thick.

Bed 5. Greenish gray, fine-grained, loose sandstone. The bed contains three horizons of compact lenticular or concretionary sandstones; it is.............27.6 m thick.

Bed 6. Greenish gray, fine-grained cross-bedded sandstone...3 m thick.

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[5] The study of the reference sections were performed by E.Ya. Yakhnin (lithology), fossils were identified by S.Z. Tovbina (ammonites), T.N. Bogdanova (ammonites, bivalves), and S.V. Lobacheva (brachiopods, echinoids). The studies were headed by Professor N.P. Luppov.

Bed 7. Greenish, argillaceous siltstone. In the talus of the bed, there are small calcareous–arenaceous concretions overfilled with bivalves and gastropods: *Leionucula impressa* J. de C. Sow., *Idonearca nana* d'Orb., *Cardium subhillanum* Leym. and others. The bed is..15.6 m thick.

Parahoplites melchioris Zone

Bed 8. At the base, conglomerate with pebbles, covered by glauconitic stains. The conglomerate is overlain by sandstone with numerous shells of bivalves: *Leionucula impressa* J. de C. Sow., *Idonearca glabra* Park., *Pseudolimea royeriana* d'Orb., *Linotrigonia archiaciana* d'Orb., *Thetironia minor transversa* Renng., *Ptychomya robinaldina* d'Orb., brachiopods, and corals. The bed is................................1 m thick.

Bed 9. Yellow sandstone, with several horizons with large concretions and, less commonly, small concretions with the ammonites *Caspianites wassiliewskyi* Renng., bivalves *Idonearca glabra* Park., *Modiolus bipartitus* Sow., *Lucina dawnesi* Woods, *Corbula striatula* J. de C. Sow., *Thracia robinaldina* d'Orb., *Goniomya carre* Ag., the brachiopod *Belbekella bertheloti* Kil., and echinoids. The bed is.................11 m thick.

Bed 10. At the base, the sandstone is greenish yellow medium-grained; upward in the bed, the sandstone contains argillaceous material, gradually becoming dark gray clay. The bed is...........4.5 m thick.

Bed 11. Dark, almost black, bedded clay with considerable gypsum content......................11.3 m thick.

Bed 12. Dark gray, very compact siltstone, with infrequent argillaceous pebbles and shell fragments of indeterminable ammonites and shells of bivalves: *Nuculana* ex gr. *mariae* d'Orb., *Grammatodon carinatus* J. Sow., *Cardium* ex gr. *subhillanum* Leym. The bed is.... ....0.3 m thick.

Bed 13. Dark gray, silty clay.................7.9 m thick.

Bed 14. Yellow, laminated siltstone, with septarian concretions at the top. The bed is...............3.8 m thick.

Bed 15. Gray loosely cemented siltstone, with infrequent concretions of denser siltstone; 6.2 m thick.

Bed 16. Brownish yellow, massive, compact sandstone, with large concretions...................4.2 m thick.

Bed 17. Dark, dense clay, in places banded. The banded texture is caused by inclusions of thin lenses of siltstone. Upward the bed, the clay becomes thinly laminated. The bed is..............................6.0 m thick.

Bed 18. At the base, -there is oyster coquina with abundant shells of the oysters *Aetostreon latissimum* Lam., *Ceratostreon* ex gr. *minos* Coq., *Lopha macroptera* J. de C. Sow. and belemnite rostra. Upward in the section, sandstone is laminated, banded with infrequent, strongly decayed by septarian concretions. The bed is...8.0 m thick.

Bed 19. Conglomerate with light yellow variously rounded, mainly small pebbles. The fossils are very poorly preserved: the ammonite *Parahoplites* sp. indet., the bivalves *Plicatula* ex gr. *inflata* J. de C. Sow., *Aucellina* sp., *Linotrigonia* cf. *archiaciana* d'Orb., the

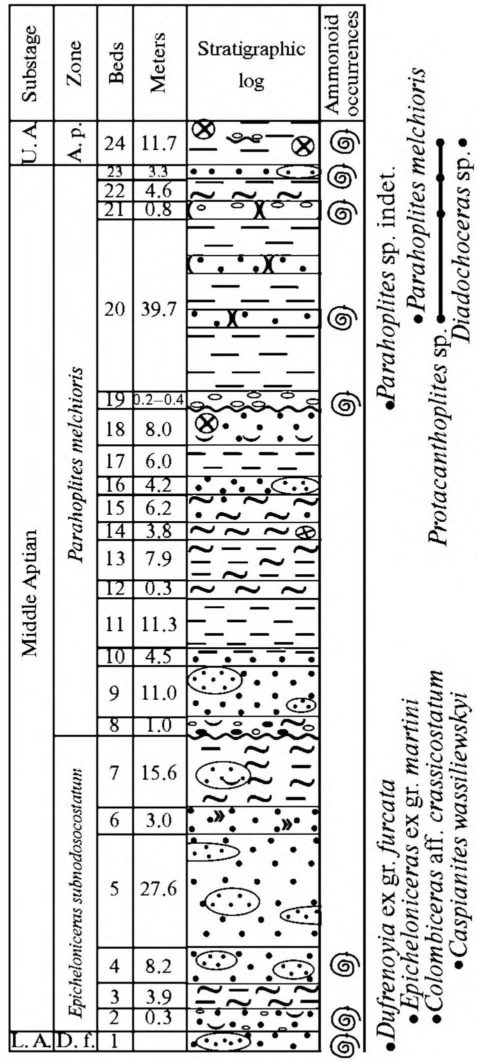


Fig. 20. Section in the Umokdere gorge, eastern slope of the Akkyr Range (Tuarkyr).

Fig. 21. A range of Aptian deposits in the Umokdere gorge, Tuarkyr (1960).

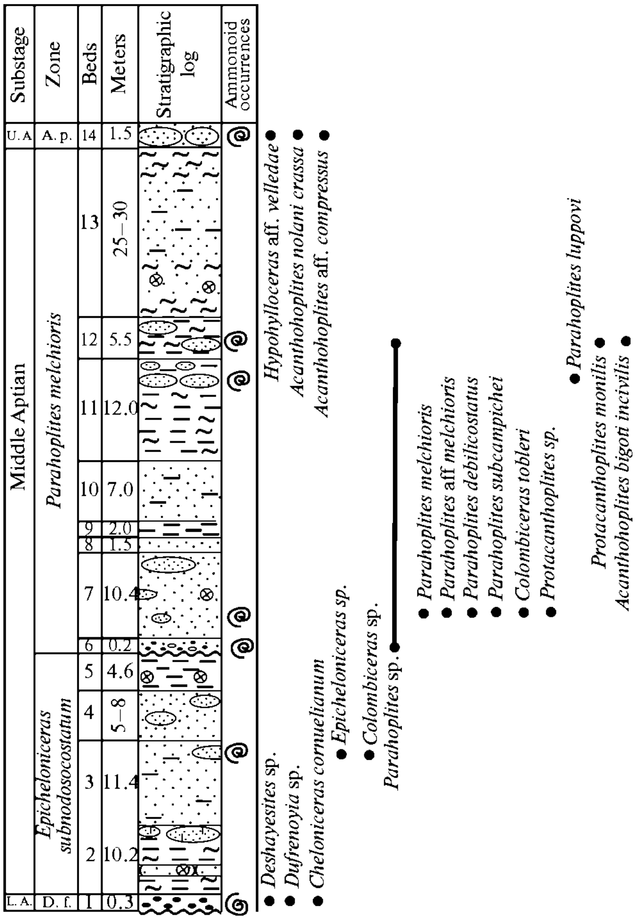


Fig. 22. Section near the Babashi well (northeastern termination of the Tuarkyr Anticline).

brachiopod *Praelongithyris lankesteri* Kil., and echinoids. The bed is..............................0.2–0.4 m thick.

Bed 20. Dark, greenish gray oily, soft, bedded clay alternating with light gray, compact ferruginous clays; contains gypsum and layers of gray compact sandstones. The lower layer has yielded the ammonites *Parahoplites melchioris* Anth. and *Protacanthoplites*[6] sp. nov., and bivalve shells. The bed is........................39.7 m thick.

Bed 21. Greenish yellow hard sandstone with fragments of fossilized wood and very poorly preserved fragments of ammonite and bivalve shells. At the top, there are frequent, small, well-rounded pebbles. The same level contains poorly preserved ammonites (*Protacanthoplites* sp.) and bivalves (*Nuculana scapha* d'Orb., *Linotrigonia rectaespinosa* Savel. and others). The bed is.......................................0.5–0.8 m thick.

Bed 22. Alternation of grayish yellow siltstone and black clay...4.6 m thick.

[6] I.A. Mikhailova considers the genus *Protacanthoplites* Tovbina invalid and assigns its species to *Acanthohoplites* Sinzow, 1907.

Bed 23. Yellow sandstone with large and small concretions. Small concretions at the base contain *Protacanthoplites* sp. The bed is........................3.3 m thick.

Upper Aptian. *Acanthohoplites prodromus* Zone

Bed 24. Black clay with septarian concretions. There are loose phosphoritic pebbles, with fragments of ammonite molds (*Diadochoceras* sp.), bivalves, and brachiopods. The bed is.........................11.7 m thick.

The Babashi section (Fig. 22) is located in the northwestern margin of the Tuarkyr Anticline, near the Babashi well, in a ravine to the east of the motorway from the southeast (from the village of Kizyl-kiya) to northwest, to Ustyurt.

Lower Aptian. *Dufrenoyia furcata* Zone

Bed 1. Conglomerate with large and small pebbles. The bed contains redeposited concretions of underlying sandstones with the ammonites *Deshayesites* sp., *Dufrenoyia* sp., *Cheloniceras cornuelianum* d'Orb., belemnites, the bivalves *Pseudolimea royeriana* d'Orb., *Cardium subhillanum* Leym., and the brachiopod *Praelongithyris lankesteri* Walker. The bed is...............
....0.2–0.3 m thick.

Middle Aptian. *Epicheloniceras subnodosocostatum* Zone

Bed 2. Dark gray silty clay with beds of gray compact sandstone and septarian concretions. At the top of the bed, there is a layer of large elongated concretions of compact sandstone, strongly weathered and decayed. The bed is...............................10.2 m thick.

Bed 3. Brownish yellow, weakly cemented sandstone with infrequent layers of clay. In the upper part, the sandstone becomes variegated and is terminated with a horizon of lenticular sandstone with nests of poorly preserved oyster shells. The bed contains rare shells of ammonites of the genera *Epicheloniceras* and *Colombiceras*, numerous bivalves *Leionucula* ex gr. *impressa* J. de C. Sow., *Grammatodon carinatus* J. Sow., *Thetironia minor circassensis* Mordv., *Opis neocomiensis* d'Orb., *Corbula* ex gr. *striatula* J. de C. Sow., *Pholadomya* ex gr. *semicostata* Ag., and the brachiopod *Cyrtothyris cantabrigiensis* (Walker), *"Rhynchonella" parvirostris* Sow. The bed is.....................11.4 m thick.

Bed 4. Loose sandstone with large decayed concretions. Concretions of the upper part of the bed contain shell fragments of very large heteromorphic ammonites, large oysters *Aetostreon latissimum* Lam., and terebratulids. The bed is.........................5–8 m thick.

Bed 5. Black bedded, thinly laminated clay with horizons septarian concretions................4.6 m thick.

Parahoplites melchioris Zone

Bed 6. Conglomerate with well-rounded relatively large pebbles, often covered by greenish glauconitic film. Upper part of the bed contains a lens of very dark, almost black sandstone with phosphoritic gravelite. Fossils include very rare and poorly preserved shells of the ammonite genus *Parahoplites* and the bivalve *Thetironia minor transversa* Renng. The bed is..................
....0.2 m thick.

Bed 7. Brownish gray massive sandstone; the upper part of the bed contains septarian concretions. Apart from those, there are small concretions of calcareous sandstone with abundant ammonites, *Parahoplites melchioris* Anth., *P.* aff. *melchioris* Anth., *P. debilicostatus* I. Mich., *P. subcampichei* Sinz., *Colombiceras tobleri* Jacob, *Acanthohoplites* sp. nov., the bivalves *Leionucula albensis* d'Orb., *Pectinucula cretae* Gardn., *Nuculana scapha* d'Orb., *N. solea* d'Orb., *N. mariae* d'Orb., *Thetironia laevigata* J. Sow., *Thracia* cf. *robinaldina* d'Orb., and gastropods. Near the top of the bed, there is a layer of dark gray strongly decayed sandstone, laterally replaced by very large (up to 1.5 m in diameter) complexly shaped concretions. The bed is........10.4 m thick.

Bed 8. Brown sandstone......................1.5 m thick.

Bed 9. Dark, bedded clay......................2.0 m thick.

Bed 10. Brown, weakly cemented sandstone, with lenses of clay..7.0 m thick.

Bed 11. Dark gray, compact, silty clay. Near the top of the bed, there is a horizon of large arenaceous strongly decayed concretions with weathered brown surface. Somewhat higher than these large concretions, there are small concretions overfilled by the ammonite *Parahoplites luppovi* Tovb. and the bivalves *Pectinucula planata* Leym., *Pterotrigonia* cf. *aliformis* Park., *Thetironia minor transversa* Renng., *Thracia robinaldina* d'Orb., *Goniomya carre* Ag. The bed is.......................
....12.0 m thick.

Bed 12. Dark compact bedded clay and dark brown weakly cemented siltstone. In the top, there are strongly decayed large concretions with the ammonites *Parahoplites* sp., *Protacanthoplites monilis* Tovb., *Acanthohoplites bigoti incivilis* Glasun., the bivalves *Nuculana scapha* d'Orb., *Grammatodon carinatus* J. Sow., *Idonearca glabra* Park., and the brachiopod *Belbekella* sp. The bed is..........................5.5 m thick.

Bed 13. The lower part is composed of compact siltstone and sandstone with septarian concretions; upward in the section, there is greenish brown loose sand with lenses of dark clay, which gradually become siltstone..25–30 m thick.

Upper Aptian. *Acanthohoplites prodromus* Zone

Bed 14. A horizon of large strongly decayed arenaceous concretions with the ammonites *Hypophylloceras* aff. *velledae* Mich., *Acanthohoplites nolani crassus* Sinz., *A.* aff. *compressus* Kas. and the brachiopod *Belbekella caseyi* Owen. The bed is........1–1.5 m thick.

The *Epicheloniceras subnodosocostatum* Zone in the Umokdere section is 56.8 m thick. Toward the northern margin of the Tuarkyr Anticline, the thickness of the zone is almost halved and, in the Babashi section, it is 34.2 m thick. The *Parahoplites melchioris* Zone in the Umokdere section is 112.9 m thick, but it is reduced near the Babashi well, as well as the thickness of the lower zone, and becomes 68.6 m thick.

***Epicheloniceras subnodosocostatum* Zone.** Beds of this zone in the reference section are lithologically divided into three parts: lower argillaceous member, middle member represented mostly by siltstones with numerous layers of relatively thick coquinae and very large sandy concretions, and the upper argillaceous–siltstone member. Small calcareous concretions in these beds are rare compared to other horizons of the substage.

Mostly argillaceous–silty composition of these beds and layers of coquina typical of the reference section remain across the entire area, but on the whole this series shows rapid lateral change in the lithology of the members and their thickness and, hence, it is not possible to trace isolated beds from section to section. The composition of the middle member to the northwest of the reference section changes noticeably, showing the appearance of sandstone horizons and redbeds, whereas the coquina beds with various bivalves are replaced in the same direction by oyster banks. The thickness of the zone in the Tekedzhik Range is 65 m, near the village of Geokdere, 70 m, near the Umokdere gorge, 85 m, and near the Tuar well, about 90 m.

The Tekedzhik reference section contains relatively few ammonites; these are *Epicheloniceras* sp., and *Caspianites* sp. The coquinae contain numerous bivalves: *Pectinucula simplex* d'Orb., *Idonearca glabra* Park., *Gervillella sublanceolata* J. Sow., *Ceratostreon subsinuatum* Leym., *Aetostreon latissimum* Lam., *Modiolus* ex gr. *ligeriensis* d'Orb., *Quadratotrigonia karakaschi* Mordv., *Linotrigonia* ex gr. *ornata* d'Orb., *L. archiaciana* d'Orb., *L. rectaespinosa* Savel., *Ptychomya robinaldina* d'Orb., rare gastropods *Confusiscala dupiniana* d'Orb., and the brachiopod *Sellithyris upwarensis* Walker.

The ammonite assemblage in Tuarkyr in general includes the index zonal species: *Epicheloniceras subnodosocostatum* Sinz., *Ep.* ex gr. *martini* d'Orb., *Ep. intermedium* Kas., *Ep. pusillum* Sinz., *Colombiceras crassicostatum* d'Orb., and also species of wide stratigraphic distribution, *Colombiceras subtobleri* Kas., *Aconeceras (Sinzovia) aptianum* Saras., *A. (Aconeceras) haugi* Saras. In addition, this zone typically contains large heteromorphic ammonites *Caspianites wassiliewskyi* Renng., and *Pseudoaustraliceras pavlowi* Wassil. The bivalve assemblage contains many taxa with thick-walled shells, often forming coquinae characteristic of the middle part of the zone. Usually, these are true oyster banks reaching 2–3 m in thickness and composed of shells of *Idonearca glabra* Park., *Gervillella sublanceolata* d'Orb., *Aetostreon latissimum* Lam., *Astarte obovata* J. Sow., *Pterotrigonia geokderensis* Savel., and *Linotrigonia archiaciana* d'Orb. Small calcareous concretions are full of the bivalves *Cymbula gardneri* Nik., *Thetironia minor transversa* Renng., and *Th. minor circassensis* Mordv. Of brachiopods, shells of *Cyclothyris parvirostris* J. de C. Sow., *Sellithyris upwarensis* Walker, and *Praelongithyris praelongiforma* Middl. are common. Gastropods are represented by *Confusiscala dupiniana* d'Orb. and *Turbo glabrus* Pčel.

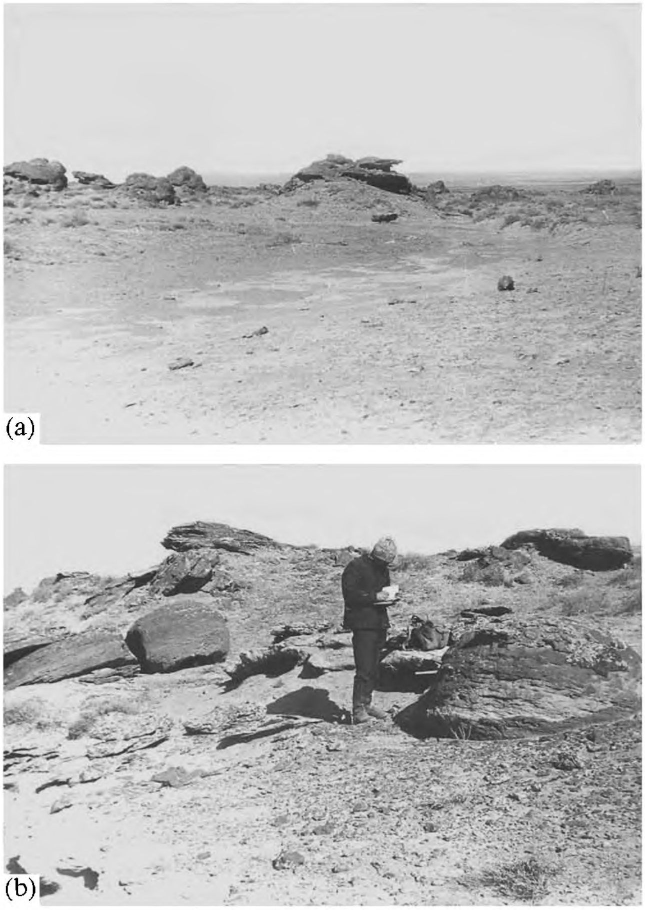


Fig. 23. Sandstone with large concretions in the *Parahoplites melchioris* Zone of the Tekedzhik Range, Tuarkyr (1967).

***Parahoplites melchioris* Zone.** The boundary with the underlying beds, i.e., between the *subnodosocostatum* and *melchioris* zones, is drawn based on the first appearance in the sections of the genus *Parahoplites*. However, as in the Kopet Dagh sections, *Parahoplites* in this region does not always occur at the very base of the zone and, in some sections (for instance, in those described in this work), they are not found at the very base of the zone.

In the reference Tekedzhik section, the *melchioris* zone shows a distinct bifid structure. The lower part is a thick sandstone member with numerous concretions (Figs. 23a, 23b), which has a clear boundary with underlying argillaceous siltstones of the *Ep. subnodosocostatum* Zone. The upper part is composed mostly by argillaceous siltstone with frequent coquina layers. The latter usually lie with traces of clear erosion on the underlying beds and contain at the base scattered pebbles of these rocks. In the adjacent areas, the *Parahoplites* beds are poorly exposed and it is possible to suggest that the subdivision of the zone into two parts most likely spread over a large part of the Tuarkyr region. However, in places, the role of sandstone in the composition of the lower member is insignificant, whereas coquinae in the upper part of the zone are not widespread and sometimes replaced by thin intraformational conglomerates or even completely wedge out. In the reference section, the zone is 115 m thick; in the section of the Umokdere gorge, it is 113 m thick.

In Tuarkyr in general, these beds are relatively weakly characterized by ammonites. However, some sections (including the above Babashi section) contain numerous species of the index genus *Parahoplites: P. melchioris* Anth., *P.* aff. *melchioris* Anth., *P. campichei* Pict. et Renev., *P. subcampichei* Sinz., *P.* cf. *maximus* Sinz., *P. debilicostatus* I. Mich., *P.* aff. *multicostatus* Sinz., *P.* aff. *grossouvrei* Jac., *P. luppovi* Tovb. In addition, the bed contains *Aconeceras (Sinzowia) aptianum* Saras., *Ap. (Ap.) haugi* Saras., *Protacanthoplites abichi* Anth., *P. monilis* Tovb., *P. bigoti* Seun., and *P. bigoti incivilis* Glasun. The ammonite assemblage does not contain phylloceratids, tetragonitids, and desmoceratids, which appear in the southerly Balkhan and Kopet Dagh sections. Bivalves are represented by large oysters *Aetostreon latissimum* Lam. and *Lopha macroptera* J. de C. Sow., the shells of which form oyster coquinae and also smaller shells of *Cyclorisma cornueliana* d'Orb. Shells of the latter species are often very abundant in small concretions. Brachiopods are represented by the rhynchinellid species *Cyclothyris (Belbekella) depressa* J. de C. Sow., *P. (P.) parvirostris* J. de C. Sow., *C. (Lamellaerhynchia) caseyi* Owen, and long-looped *Gemmarcula truncata* J. de C. Sow. Echinoids are represented by *Holaster benstedi* Forb., *H. prestensis* Des. in Lor. Gastropods are relatively frequent, represented by *Nummocalcar dentatum* d'Orb., *Confusiscala dupiniana* d'Orb., *Tessarolax obrayi* Lor., and *Ringinella multilineata* Natz.

5. AMMONOID-BASED MIDDLE APTIAN CORRELATION

Marine Middle Aptian beds are widespread in almost all continents of the globe. In Europe, these include sections of France, England, Germany, Romania, Bulgaria, Hungary, Austria, Spain, Italy, northern Caucasus, Volga Region, and Georgia. In Asia, in Turkmenistan, Uzbekistan, Tajikistan, Iran, China, and Japan. Middle Aptian beds are also present in North and South America, Africa, and Australia; not everywhere in the above region, they are well studied. They are unequally characterized by the index group, ammonites, and, hence, differ in detail and degree of substantiation of stratigraphic subdivision. Before characterizing the beds in the above regions and correlation of the zonal strata recognized in these beds, it is necessary to consider the position of the lower boundary with the Bedoulian Substage, or Lower Aptian.

As known from many publications on the Aptian, this boundary was at various times drawn at different levels: at the base or at the top of the *Dufrenoyia furcata* Zone or (while the name of this biostraton varied) at the base of the beds with *Dufrenoyia* or at the top of these beds. In most regions of the development of the boundaries beds of the Bedoulian and Gargasian substages, the boundary between them is accepted at the top of the *Dufrenoyia* beds. France was almost the only region in Europe where this boundary was for a long time drawn at the base of the *Dufrenoyia* beds. In other words, French stratigraphers retained the original position of this boundary, which existed from the 19th century, from the time of the recognition of the Bedoulian and Gargasian horizons. When correlating the boundary beds of these substages in all regions of France, they always noted various levels of this boundary and, as a consequence, an incongruence between their ranges and those of the above horizon (Luppov, 1956; Bogdanova, 1978; Egoian, 1984; Conte, 1994; and others).

Principles of the boundaries between the strata of various ranks and definition of these boundaries have always been a focus of stratigraphic research. The universally accepted principles include (1) rule of priority, i.e., the position of the boundary should agree with its position in the stratotype; (2) its base should be defined by the first appearance datum of a new zonal species (Sazonova and Sazonov, 1979). Egoian (1984), while accepting for some cases the first rule and criticising the second, gave his definition of the biostratigraphic boundaries (in particular the stage boundaries): "... the stage boundary is the level of the change in the taxa by which these stages are distinguished" (Sazonova and Sazonov, 1979, p. 83)). This definition of the boundary should also exist in reference to smaller biostrata, i.e., substages and even zones.

French stratigraphers and paleontologists, as shown above, conform to the first rule, i.e., they currently draw the boundary between the Bedoulian and Gargasian (or Lower and Upper Aptian as they understand it), as it was once drawn by d'Orbigny at the base of the beds with *Dufrenoyia*. By "currently" we mean the beginning of the 21st century, when the stratotype of the Gargasian Substage was studied in detail. At the end of the 20th century after the study of the Bedoulian stratotype, this boundary was transferred to the top of the *Dufrenoyia* and *Tropaeum bowerbanki* Zone, mainly to eliminate the incongruence of the ranges of the Bedoulian or Lower Aptian and Gargasian or Middle Aptian.

In the Russian stratigraphic schemes, the beds with *Dufrenoyia* were for the first time placed in the Lower Aptian (Renngarten, 1951). Renngarten based this decision on the associated records of the ammonite genera *Dufrenoyia, Deshayesites,* and *Cheloniceras.* Luppov (1956) also emphasized a close connection of the ammonite fauna of the beds with *Dufrenoyia* with that of the underlying beds and a sudden change in the fauna at the boundary of the beds with *Dufrenoyia* and overlying beds of the Aptian.

What is the true boundary of the Lower and Middle Aptian? In our understanding, following the definition of Egoian, this is the level at which representatives of the ammonite superfamily Deshayesitoidea disappear and abundant ammonites of the superfamily Parahoplitoidea appear; in the family Douvilleiceratidae, the ammonite genus *Cheloniceras* (a subgenus according to some specialists) disappears and the genus *Epicheloniceras* appears. Within other ammonite taxa, species assemblages change: in the genera of the superfamily Ancyloceratoidea also among phylloceratids, tetagonitids, and desmoceratids. Changes in compositions of ammonite assemblages (change in superfamilies) are almost synchronous in sections of all regions of Europe and Central Asia, somewhat differing in the compositions of genera and species, depending on paleobiogeographic provinces (Table 12). In our understanding, this is the boundary between the *Dufrenoyia furcata* and *Colombiceras crassicostatum* and *Epicheloniceras subnodosococtatum* (or *Epicheloniceras subnodosocostatum*) zones.

Lower Aptian. The boundary between the Lower and Middle (or Upper) Aptian is drawn at different levels, hence, the consideration and correlation of the boundary beds of these substages should begin from a characterization of the bed directly overlying the Lower Aptian beds with *Deshayesites* (Report on the 4th ..., 2011), the Early Aptian age of which is similarly understood by all workers. The *Dufrenoyia furcata* Zone is recognized above the upper zone with *Deshayesites deshayesi.* The *Dufrenoyia furcata* Zone was (Report on the 4th ..., 2011) accepted as including two subzones, *D. furcata* and *D. dufrenoyi* at a Kilian Group meeting. These subzones, as was established at the Kilian Group meeting, are found in France (Dutour, 2005), Spain (Moreno-Bedmar et al., 2010), and Mexico (Barragán-Manzo and Mendes-Franco, 2005). Beds with *Dufrenoyia* reffered to as the "*Dufrenoyia furcata* Zone" are recognized in most regions of Europe, Asia, and America. However, in some regions, they are referred to as the *Tropaeum bowerbanki–Dufrenoyia furcata* Zone (Germany) or *Tropaeum bowerbanki* Zone [England, Russia (Ulyanovsk–Saratov Volga Region)]. This depends on the predominance of a particular genus in the sections. The distribution of ammonites in the *Dufrenoyia furcata* Zone is shown in Table 13.

The western Caucasus region is the nearest region to Central Caucasus, and many workers place the boundary between the regions along the Pshekha River. Very scarce data exist on the upper horizons of the Lower Aptian, which could be recognized in the *Dufrenoyia furcata* Zone. For instance, in the review of the Cretaceous System (Egoian, 1986), the author did not name any of the characteristic zonal ammonite species, whereas in the stratigraphic scheme (Egoian, 1986, p. 147, text-fig. 24), this part of the Lower Aptian section does not have a name. In a later work, Egoian (1989) showed "Beds with *Dufrenoyia furcata*"

Table 12. Distribution of Aptian ammonites in the world

		Turkmenistan	Kazakhstan	Dagestan	Northern Caucasus	Volga Region	Georgia	Ukraine	Bulgaria	Romania	Hungary	Austria	France	Switzerland	Germany	England	Italy	Spain	Morocco	Tunis	Madagascar	California	Texas	Mexico	Colombia	Venezuela	Argentina	Australia	Japan	China	Iran
1	*Phylloceras*																				+										
2	*Phyllopachyceras*	+		+									+								+	+									
3	*Hypophylloceras*	+		+			+				+	+	+									+					+				
4	*Euphylloceras*				+		+	+		+											+										
5	*Holcophylloceras*	+			+					+	+						+					+									
6	*Salfeldiella*												+								+										
7	*Argonauticeras*						+																								
8	*Protetragonites*												+								+										
9	*Eugaudryceras*								+				+																		
10	*Eotetragonites*																				+										
11	*Tetragonites*	+		+	+		+			+	+																				
12	*Gabbioceras*										+		+									+									
13	*Jauberticeras*	+									+		+																		
14	*Aconeceras*	+		+	+				+				+		+	+		+			+					+		+		+	
15	*Sinzowia*												+														+				
16	*Falciferella*																				+										
17	*Doridiscus*																														
18	*Notodiscus*															+					+										
19	*Sanmartinoceras*	+														+			+		+					+	+	+			
20	*Pseudosaynella*	+			+																					+	+				
21	*Aioloceras*																										+	+			
22	*Valdedorsella*										+		+				+				+				+	+					
23	*Pseudohaploceras*	+		+					+	+			+											+	+				+		
24	*Ferruglioceras*																										+				
25	*Callisoniceras*														+																
26	*Melchiorites*			+			+					+	+				+				+	+			+	+					
27	*Puzosia*			+			+		+	+		+									+				+						
28	*Zuercherella*	+			+		+				+	+	+		+										+	+					
29	*Uhligella*										+		+								+			+		+					+
30	*Desmoceras*						+				+	+										+									
31	*Cortesiceras*																								+						
32	*Silesitoides*										+																				
33	*Parasilesites*										+																				
34	*Neosilesites*										+																		+		
35	*Silesites*									+																	+				
36	*Ancyloceras*										+																+				
37	*Lithancylus*															+											+				
38	*Australiceras*															+					+	+					+	+			

Table 12. (Contd.)

		Turkmenistan	Kazakhstan	Dagestan	Northern Caucasus	Volga Region	Georgia	Ukraine	Bulgaria	Romania	Hungary	Austria	France	Switzerland	Germany	England	Italy	Spain	Morocco	Tunis	Madagascar	California	Texas	Mexico	Colombia	Venezuela	Argentina	Australia	Japan	China	Iran
39	*Pseudoaustraliceras*	+		+			+		+																				+		
40	*Tropaeum*	+	+	+			+		+						+	+					+	+					+	+	+		
41	*Ammonitoceras*						+			+					+	+								+							
42	*Caspianites*	+														+															
43	*Toxoceratoides*	+					+		+	+						+											+	+		+	
44	*Tonohamites*						+				+					+		+									+			+	
45	*Helicancylus*																										+			+	
46	*Luppovia*	+																													
47	*Hamiticeras*						+		+	+		+															+				
48	*Ptychoceras*				+		+			+	+																+				
49	*Peltocrioceras*																									+	+				
50	*Macroscaphites*						+			+																					
51	*Cicatrites*				+		+																								
52	*Metahamites*																				+										
53	*Protanisoceras*										+																				
55	*Ephamulina*										+										+										
56	*Hamites*										+																	+			
57	*Roloboceras*	+																								+					
58	*Megatiloceras*																							+							
59	*Cheloniceras*	+		+	+		+		+		+		+		+				+			+	+	+		+	?		+		+
60	*Epicheloniceras*	+		+	+		+		+	+	+	+	+					+	+		+	+			+	+			+	+	+
61	*Paracheloniceras*						+				+										+										
62	*Paracanthoplites*						+				+																				
63	*Diadochoceras*	+		+	+		+		+		+	+	+																		
64	*Walpenites*															+															
65	*Vectisites*															+		+							+						
66	*Eodouvilleiceras*	+		+	+						+																				
67	*Deshayesites*	+	+	+	+	+		+	+	+			+				+	+								+					+
68	*Dufrenoyia*	+	+	+	+		+		+		+	+	+		+	+		+					+	+	+	+			+		
69	*Burckhardtites*	+								+														+		+					
70	*Mathoceras*								+		+															+					
71	*Colombiceras*	+		+	+		+	+	+	+	+	+	+				+	+	+					+	+	+				+	+
72	*Riedelites*																			+					+						
73	*Gargasiceras*	+							+				+												+	+					
74	*Hypacanthoplites*	+		+	+						+	+			+						+	+	+	+			+				+
75	*Parahoplites*	+	+	+	+			+	+	+	+	+			+	+		+	+	+	+	+	?	+	+					?	+
76	*Acanthohoplites*	+	+	+	+		+	+	+	+	+	+			+		+		+		+	+	+	+	+					+	
77	*Protacanthoplites*	+					+																		+						
78	*Chaschupseceras*						+																								

Table 13. Ammonite distribution in the *Dufrenoyia furcata* Zone and its equivalents

		Southeastern France			England		Germany	Georgia	Central region of Northern Caucasus	SE part of N Caucasus	Turkmenistan
		Dufrenoyia furcata Zone			*Tropaeum bowerbanki* Zone		*Trop. bowerbanki* + *Dufrenoyia furcata* Zone	*Dufrenoyia furcata* Zone			
		Furcata Subzone	*Dufrenoyi* Subzone		*Dufrenoyia transitoria* Subzone	*Cheloniceras meyendorfi* Subzone					
			Praedufrenoyi Horizons	*Dufrenoyi* Horizons							
1	*Phylloceras (Hypophylloceras) aptiense* Fallot	—	—	—							
2	*Phylloceras (Hypophylloceras) morelanum* d'Orb.		—	—							
3	*Phyllopachyceras baborense* Coq.	—	—	—				—			
4	*Salfeldiella (Gyrophyllites) paquieri* Sayn	—	—	—							
5	*Salfeldiella (S.) opegana* Sayn	—	—	—							
6	*Protetragonites strangulatum* d'Orb.	—	—	—							
7	*Eogaudryceras (E.) blieuxiensis* Breistr.	—									
8	*Eogaudryceras (E.) numidum* Coq.	—	—	—							
9	*Eogaudryceras (E.) ambiquus* Breistr.		—	—							
10	*Aconeceras nisum* d'Orb.	—	—	—							
11	*Pseudohaploceras liptoviense* Zeuschn.	—	—	—				—			
12	*Zuercherella zuercheri* Jacob et Tobler	—	—	—							
13	*Cheloniceras seminodosum* Sinz.	—	—	—			—			—	—
14	*Cheloniceras cornuelianum cornuelianum* d'Orb.	—	—	—			—	—			—
15	*Cheloniceras meyendorfi* d'Orb.	—	—	—		—		—	—		
16	*Dufrenoyia furcata* J. de C. Sow.	—			—	—	—	—		—	—
17	*Dufrenoyia dufrenoyi* d'Orb.		—	—				—		—	—
18	*Dufrenoyia praedufrenoyi* Casey		—		—	—		—			
19	*Colombiceras crassicostatum* d'Orb.	—	—	—							—
20	*Gargasiceras gargasense* d'Orb.	—	—	—							—
	England										
21	*Aconeceras (A.) nisoides* Saras.				—	—	—				
22	*Aconeceras (Sinzovia) trautscholdi* Sinz.				—	—					
23	*Aconeceras (Sinzovia) haugi* Saras.					—					
24	*Tropaeum bowerbanki bowerbanki* J. de C. Sow.				—	—					
25	*Tropaeum (T.) bowerbanki densicostatum* Casey				—						

Table 13. (Contd.)

		Southeastern France			England		Germany	Georgia	Central region of Northern Caucasus	SE part of N Caucasus	Turkmenistan
		Dufrenoyia furcata Zone			*Tropaeum bowerbanki* Zone		*Trop. bowerbanki* + *Dufrenoyia furcata* Zone	*Dufrenoyia furcata* Zone			
		Furcata Subzone	*Dufrenoyi* Subzone		*Dufrenoyia transitoria* Subzone	*Cheloniceras meyendorfi* Subzone					
			Praedufrenoyi Horizons	*Dufrenoyi* Horizons							
26	*Tropaeum drewi spinosum* Kemper				—	—	—				
27	*Toxoceratoides proteus* Spath				—	—					
28	*Tonohamites limbatus* Casey				—	—					
29	*Tonohamites* (*T.*) *hunstantonensis* Casey					—					
30	*Cheloniceras crassum* Spath				—	—					
31	*Cheloniceras kiliani obesum* Casey					—					
32	*Cheloniceras gottchei* Kil.				—	—			—		
33	*Cheloniceras proteus* Casey				—	—					
34	*Cheloniceras rotundum* Casey				—	—					
35	*Dufrenoyia lurensis* Kil.				—	—			—		—
36	*Dufrenoyi scalata* Casey				—						—
37	*Dufrenoyia notha* Casey				—						
38	*Dufrenoyia mackesoni* Casey				—						
40	*Dufrenoyia transitoria* Casey				—						
41	*Dufrenoyia truncata* Spath				—						
42	*Dufrenoyia discoidalis* Casey				—						
43	*Dufrenoyia formosa* Casey				—						
	Germany										
44	*Aconeceras* (Sinzovia) *stollei* Casey						—				
45	*Tropaeum drewi drewi* Casey				—		—				
46	*Tropaeum logteri* Kemper						—				
47	*Cheloniceras cornuelianum latispinosum* Nikch.						—	—			
48	*Cheloniceras kiliani* Koen.						—				
	Georgia										
50	*Phylloceras* (*Hypophylloceras*) ex gr. *cyprus* Fall. et Term.							—			
51	*Phyllopachyceras crassum* Drushits							—			—
52	*Puzosia* aff. *belus* d'Orb.							—			
53	*Desmoceras lakhepaense* Rouch.							—			

Table 13. (Contd.)

		Southeastern France			England		Germany	Georgia	Central region of Northern Caucasus	SE part of N Caucasus	Turkmenistan
		Dufrenoyia furcata Zone			*Tropaeum bowerbanki* Zone		*Trop. bowerbanki* + *Dufrenoyia furcata* Zone	*Dufrenoyia furcata* Zone			
		Furcata Subzone	*Dufrenoyi* Subzone								
			Praedufrenoyi Horizons	*Dufrenoyi* Horizons	*Dufrenoyia transitoria* Subzone	*Cheloniceras meyendorfi* Subzone					
54	*Tropaeum* (*T.*) *longus* Kakab.							—			
55	*Toxoceratoides royerianus* d'Orb.							—			
56	*Ptychoceras puzosianum* d'Orb.							—			—
57	*Macroscaphites nodosocostatus nunui* Erist.							—			
58	*Macroscaphites abchasiense* Kakab.							—			
59	*Macroscaphites recticostatus* d'Orb.							—			
60	*Macroscaphites microcostatus* Sim., Bac., Sor.							—			
61	*Cheloniceras seminodosum naltschikensis* Niksch.							—			
62	*Cheloniceras sporadicum* Rouch.							—			
63	*Cheloniceras crassum* Spath							—			
64	*Cheloniceras disparile* Casey							—			
65	*Cheloniceras asper* Scharik.							—			
66	*Euphylloceras aptiense* Sayn							—			
	Central region of Northern Caucasus										
67	*Deshayesites terminalis* Bogdanova								—		—
68	*Dufrenoyia subfurcata* Kas.							—	—		
	Dagestan										
69	*Pseudohaploceras matheroni* d'Orb.									—	—
70	*Epicheloniceras* ex gr. *tschernyschewi* Sinz.									—	
71	*Epicheloniceras waageni* Anth.									—	
	Turkmenistan										
72	*Holcophylloceras guettardi* Rasp.										—
73	*Tetragonites depressus* Rasp.										—
74	*Jauberticeras latericarinatum* Anth.										—
75	*Dufrenoyia sinzovi* Lupp.										—
76	*Dufrenoyia fursovae* Bogdanova										—
77	*Burckhardtites palumbes* Humphrey										—
78	*Burckhardtites gregoriensis* Humphrey										—

in the log of the western Caucasus (p. 139) in the upper part of the *Deshayesites deshayesi* Zone, without indicating any characteristic ammonite assemblage from these beds.

In most of the Mangyshlak Peninsula (Kazakhstan), in sections of the West Karatau and East Karatau ranges, the *Dufrenoyia furcata* Ammonite Zone is found in a thin layer of calcareous phosphoritic sandstone, the so-called "slab" with Lower Aptian ammonites of the *Paradeshayesites weissi, Deshayesites deshayesi,* and *Dufrenoyia furcata* zones (Saveliev and Vasilenko, 1963; Bogdanova, 1999).

The *Dufrenoyia furcata* Zone in **France,** as shown above (see Table 2), begins the Gargasian Substage (or horizon) (Atrops and Dutour, 2005). Atrops and Dutour write that they "... restored the *Furcata* Zone at the base of the Gargasian Substage ... based on historical and paleontological data" (Atrops and Dutour, 2005, p. 7). Its lower boundary is placed at the level of the disappearance of the species *Deshayesites grandis* Spath and *Sinzovia nisoides* Saras. and the appearance of the genera *Dufrenoyia, Gargasiceras, Aconeceras, Colombiceras, Zuercherella,* and *Eogaudryceras.* This boundary is considered as a level based on a significant faunal change. In the generalized section of the stratotype, the zone under consideration is relatively thick (45 m) and contains a representative collection of the genus *Dufrenoyia.* Based on this material, French paleontologists tracked the evolution of morphological characters of various *Dufrenoyia* and recognized two subzones, *furcata* and *dufrenoyi.* Two horizons distinguished within the *dufrenoyi* Zone correspond to the intrageneric morphological groups: *praedufrenoyi* and *dufrenoyi.*

Of the relatively large number of known species of the genus *Dufrenoyia,* the stratotype section contains only the three above species. The assemblage contains numerous smooth ammonites of the genera *Phylloceras, Salfeldiella, Eugaudryceras,* and weakly ornamented *Aconeceras, Sinzovia, Pseudohaploceras,* and others. Three species are represented by typical Early Aptian *Cheloniceras* (*Ch. cornuelianum* and *Ch. seminodosum*). *Aconeceras nisus,* which in other regions is usually found in the higher beds of the Aptian, is here present from the base of the *Furcata* Zone, while *Gargasiceras gargasense* and *Colombiceras crassicostatum* characteristic of the Middle Aptian are found in the upper part of the *Dufrenoyi* horizon. Dauphin (2002, p. 117) recorded in this interval, the Barremian ammonites *Pseudohaploceras liptoviense* and *Melchiorites melchioris,* which disappear in the upper part of the zone. In general, the composition of the ammonite assemblage suggests that the stratotype section contains a mixed assemblage of the eastern and western types, which had been known from the time of V. Kilian (smooth forms in association with ornamented shells, which allowed the detailed subdivision of this part of the section).

In **England** (Table 14), this interval is referred to as the *Tropaeum bowerbanki* Zone, which Casey (1961b) subdivided into two subzones, *Dufrenoyia transitoria* (lower) and *Cheloniceras meyendorfi* (upper). The lower subzone has most species of the genus *Dufrenoyia,* all of which, except one, *D. formosa,* found in Georgia, are restricted to this region. In France, these species of *Dufrenoyia* are absent. Dauphin (2002, p. 119) considers that *Dufrenoyia* species characteristic of the lower zone of England, are characteristic of the older beds, which are most likely absent in France, and that it is incorrect to draw the base of the *Dufrenoyia furcata* Zone of France at the base of the *Tropaeum bowerbanki* Zone of England. In addition to a large number of species of the genus *Dufrenoyia,* beds of this age in England contain a rich assemblage of uncoiled ammonite genera *Tropaeum, Toxoceratoides, Tonohamites,* and relatively frequent representatives of *Cheloniceras.* It should be said that, in the English sections of this interval, *Aconeceras (A.) nisus* has not been recorded, which, in contrast to French sections., occurs in England higher in the section, i.e., in the Upper Aptian *Epicheloniceras martinioides* Zone.

The stratigraphy of this part of the section in **Germany** (Table 15) is given according to early works of Kemper (1971, 1976). In these papers, the interval under consideration corresponds to the *Dufrenoyia furcata* Zone (J. de C. Sow) and *Tropaeum bowerbanki* Zone (J. de C. Sow.) (Kemper, 1971). Kemper wrote later that subdivision into zones in its direct sense was impossible, while it was possible to name the succession of important species (Kemper, 1995, p. 172). One of the index species of the zone, *T. bowerbanki,* is not figured nor mentioned in any known works of Kemper on the Aptian of Germany. A single specimen of *D. furcata* is figured in Kemper's 1971 paper (p. 381, pl. 26, fig. 2) and the same specimen was also photographed in 1995 (p. 193, pl. 3, fig. 2). In Germany, there are also several geographically widespread species of *Cheloniceras* and uncoiled ammonite genus *Tropaeum,* which are present in England. It is difficult to interpret the range of this zone and correlation of its boundaries with the zones in France and England. It is possible that it, like the French *D. furcata* Zone, approximately corresponds to the upper part of the English *T. bowerbanki* Zone based on the presence of *Tropaeum.*

The *Dufrenoyia furcata* Zone of **Georgia** (Table 16), which was originally recognized as a stratigraphic biounit of this rank by Kotetishvili (1986, p. 53), is characterized by the presence of geographically widespread members of the genera *Dufrenoyia* and *Cheloniceras.* One of the *Dufrenoyia* species is similar to the English species *D. formosa,* which is found in the lower *D. transitoria* Subzone of England. The ammonite assemblage of this zone in Georgia contains virtually no phylloceratids and tetragonitids, numerous in France, as well as *Tropaeum* characteristic of the English sections, but a large percent in this assemblage

Table 14. Stratigraphic distribution of ammonite species in the Upper Aptian England (after Casey, 1961–1998)

No.	Ammonites species	Lower Aptian		Upper Aptian				
		Tropaeum bowerbanki Zone		*Cheloniceras martiniodes* Zone			*Parahoplites hutfieldiensis* Zone	
		Dufrenoyia transitorius Subzone	*Cheloniceras meyendorfi* Subzone	*Cheloniceras debile* Subzone	*Cheloniceras gracile* Subzone	*Cheloniceras buxtorfi* Subzone	*Tropaeum subarcticum* Subzone	*P. cunningtoni* Subzone
1	*Lithancylus grandis* J. de C. Sow.	◄—	—					
2	*L. fustis* Casey	◄—	—					
3	*Tropaeum* (*T.*) *hilsi* J. de C. Sow.	—	—					
4	*Tonohamites decurrens* Spath	◄—	—					
5	*Cheloniceras* (*Ch.*) *cornuelianum* d'Orb.	◄—	—					
6	*Ch.* (*Ch.*) *crassum* Spath	◄—	—					
7	*Ch.* (*Ch.*) *quadrarium dispansum* Casey	◄—	—					
8	*Ch.* (*Ch.*) *mackesoni norfolkense* Casey	◄—	—					
9	*Tropaeum* (*T.*) *bowerbanki densistriatum* Casey	—						
10	*Tonohamites* cf. *koeneni* Casey	—						
11	*Dufrenoyia formosa* Casey	—						
12	*D. scalata* Casey	—						
13	*D. noma* Casey	—						
14	*D. mackesoni* Casey	—						
15	*D. transitoria* Casey	—						
16	*D. truncata* Spath	—						
17	*D. discoidalis* Casey	—						
18	*Aconeceres nisoides* Sarasin	—	—					
19	*Sanmartinoceras* (Sinzovia) *trautscholdi* Sinz.	—	—					
20	*Doridiscus* sp. nov.	—	—					
21	*Tropaeum* (*T.*) *drewi* Casey	—	? —					
22	*Toxoceratoides proteus* Spath	—	—					
23	*Tonohamites limbatus* Casey	—	? —					
24	*T.* (*T.*) *hunstantonensis* Casey	—	—					
25	*Cheloniceras* (*Ch.*) *proteus* Casey	—	—					
26	*Ch.* (*Ch.*) *rotundum* Casey	—	? —					
27	*Ch.* (*Ch.*) *gottschei* Kilian	—	—					
28	*Dufrenoyia furcata* J. de C. Sow.	—	—					
29	*D. lurensis* Kilian	—	—					
30	*D. praedufrenoyi* Casey	—	—					
31	*Aconeceras haugi* Sarasin		—					
32	*Tonohamites aequicingulatus* Koenen		—					
33	*Cheloniceras* (*Ch.*) *meyendorfi* d'Orb.		—					
34	*Ch.* (*Ch.*) *kirkaldi* Casey		—					
35	*Ch.* (*Ch.*) *kiliani obesum* Casey		—					
36	*Tropaeum* (*T.*) *pseudohillsi* Casey			—				
37	*T.* (*T.*) *benstedi* Casey			—				

Table 14. (Contd.)

No.	Ammonites species	Lower Aptian		Upper Aptian				
		Tropaeum bowerbanki Zone		*Cheloniceras martiniodes* Zone			*Parahoplites hutfieldiensis* Zone	
		Dufrenoyia transitorius Subzone	*Cheloniceras meyendorfi* Subzone	*Cheloniceras debile* Subzone	*Cheloniceras gracile* Subzone	*Cheloniceras buxtorfi* Subzone	*Tropaeum subarcticum* Subzone	*P. cunning-toni* Subzone
38	*T.* (*Ancylotropaeum*) *baylissi* Casey			—				
39	*T.* (*A.*) *pondorosum* Casey			—				
40	*Ammonitoceras* rex Casey			—				
41	*Cheloniceras* (*Epicheloniceras*) *eotypicum* Casey			—				
42	*Ch.* (*E.*) *debile* Casey			—				
43	*Ch.* (E.) *debile paucenodum* Casey			—				
44	*Vectisites simplex* Casey			—				
45	*Cheloniceras* (*Epicheloniceras*) *subvolgense* Casey			—	—			
46	*Aconeceras nisus* d'Orb.			—	—	—		
47	*Tropaeum* (*T.*) *rossicum* Casey			—	—	—		
48	*Ammonitoceras tovilense* Crikm.			—	—	—		
49	*A. boughtonense* Casey			—	—	—		
50	*A. sowerbyi* Casey			—	—	—		
51	*Cheloniceras* (*Epicheloniceras*) *tschernyschewi* Sinz.			—	—	—		
52	*Ch.* (*E.*) *martinioides* Casey			—	—	—		
53	*Ch.* (*E.*) *martioides alternatum* Casey			—	—	—		
54	*Ch.* (*E.*) *cantianum* Casey			—	—	—		
55	*Vectisites caprotinus* Casey			—				
56	*Caspianites vectensis* Casey			—	—			
57	*Walpenites tardesulcatus* Casey				—			
58	*Cheloniceras* (*Epicheloniceras*) *claudi* Casey				—			
59	*Ch.* (*E.*) *gracile* Casey				—			
60	*Ch.* (*E.*) *gracile rugatum* Casey				—			
61	*Ch.* (*E.*) *sellindgense audax* Casey				—			
62	*Doridiscus rotulus* Casey				—			
63	*Australiceras* sp.				—			
64	*Cheloniceras* (*Epicheloniceras*) *buxtorfi* Jacob					—		
65	*Parahoplites maximus* Sinz.						—	
66	*Parahoplites irregularis* Casey						—	
67	*Tropaeum* (*T.*) *subsimbirskense* Sinz.						—	—
68	*T.* (*Epitropaeum*) *subarcticum* Casey						—	—
69	*Parahoplites nutfieldiensis* Casey						—	—
70	*P. daveyi* Casey						—	? —
71	*Colombiceras tobleri* Sinz. (non Jacob)						—	—
72	*Parahoplites cunningtoni* Casey							—
73	*P. depressus* Casey							—
74	*P. vectensis* Casey							—

Table 15. Stratigraphic distribution of ammonite species in the Middle Aptian of Germany (after Kemper, 1971, 1976, 1995)

No.	Ammonites species	Lower Aptian (Bedoulian)	Middle Aptian (Gargasian)				Upper Aptian (Clansayesian)
		Tropaeum bowerbanki + *Dufrenoyia furcata* Zone	*Tropaeum drewi* + *T. tenuinodosum* Zone	*Cheloniceras laticostatum* + *Ch. tschernyschewi* Zone	*Cheloniceras buxtorfi* Zone	*Parahoplites nutfieldiensis* & *P. melchioris* Zone	*Hypacanthoplites jacobi* Zone
1	*Aconeceras* (*A.*) *nicoides* (Sarasin)	—					
2	*Cheloniceras cornuelianum cornuelianum* (d'Orbigny)	—					
3	*Cheloniceras cornuelianum latispinosum* (Nikchitch)	—					
4	*Cheloniceras kiliani* (Koenen)	— ?					
5	*Dufrenoyia furcata* J. de C. Sowerby	—					
6	*Cheloniceras seminodosum* (Sinzow)	—	—				
7	*Aconeceras (Sinzovia) stolleyi* Casey	- -	- -	- -	- -	- -	
8	*Zuercherella zuercheri* (Jacob)		—				
9	*Tropaeum drewi drewi* Casey		—				
10	*Tropaeum drewi spinosum* Kemper		—				
11	*Tropaeum logteri* Kemper		—				
12	*Tropaeum tenuinodosum* Kemper		—				
13	*Cheloniceras* aff. *mackesoni* Casey		—				
14	*Cheloniceras* (*Epicheloniceras*) *tschernyschewi* (Sinzow)			—			
15	*Cheloniceras subnodosocostatum* (Sinzow)			—	—		
16	*Cheloniceras laticostatum* (Sinzow)			—	—		
17	*Ammonitoceras transcaspium* (Sinzow)			—	—	—	
18	*Tropaeum subarcticum* Casey				—		
19	*Cheloniceras* (*Epicheloniceras*) *buxtorfi* (Jacob & Tobler)				—		
20	*Parahoplites multicostatus* Sinzow				—	— ?	
21	*Aconeceras* (*S.*) aff. *trautscholdi* (Sinzow)					—	
22	*Tropaeum arcticum* Stolley					—	
23	*Parahoplites nutfieldiensis nutfieldiensis* (Sowerby)					—	
24	*Parahoplites nutfieldiensis cunningtoni* Casey					—	
25	*Parahoplites melchioris* Anthula					—	
26	*Parahoplites irregularis* Casey					—	
27	*Acanthohoplites aschiltaensis* (Anthula)					—	
28	*Callizoniceras* (*Wollemanniceras*) *keilhacki keilhacki* (Wollemarm)						—
29	*Callizoniceras* (*W.*) *keilhacki anterior* (Brinkmann)						—
30	*Hypacanthoplites* aff. *bigoureti* (Seunes)						—
31	*Hypacanthoplites* aff. *bergeroni* (Seunes)						—
32	*Hypacanthoplites nolaniformis* (Glasunova)						—
33	*Hypacanthoplites elegans* (Fritel)						—
34	*Hypacanthoplites anglicus* Casey						—
35	*Hypacanthoplites spafhi* (Dutertre)						—
36	*Hypacanthoplitus clavatus* (Fritel)						—
37	*Hypacanthoplites evolutus* (Sinzow)						—
38	*Hypacanthoplites jacobi* (Collet)						—
39	*Hypacanthoplites sarasini* (Collet)						—

Table 16. Stratigraphic distribution of ammonite species in the Middle Aptian of Georgia

No.	Ammonite species	Lower Aptian	Middle Aptian		Upper Aptian
		Dufrenoyia furcata Zone	*Epicheloniceras subnodosocostatum* Zone	*Colombiceras tobleri* Zone	*Acanthohoplites nolani* Zone
1	*Macroscaphites abchasiense* Kakab.	——			
2	*M. recticostatus* d'Orb.	——			
3	*M. microcostatus* Sim., Bač., Sor.	——			
4	*Ptychoceras puzosianum* d'Orb.	– –			
5	*Cheloniceras seminodosum naltschikensis* Niksch.	——			
6	*Ch. cornuelianum cornuelianum* d'Orb.	——			
7	*Ch. cornuelianum latispinosum* Niksch.	——			
8	*Ch. sporadicum* Rouch.	——			
9	*Ch. meyendorffi* d'Orb.	——			
10	*Ch. crassum* Spath	——			
11	*Ch. disparile* Casey	——			
12	*Ch. asper* Scharik.	——			
13	*Dufrenoyia praedufrenoyi* Casey	——			
14	*D. furcata* Sow.	——			
15	*D. subfurcata* Kas.	——			
16	*D. cf. formosa* Casey	——			
17	*D. dufrenoyi* d'Orb.	——			
18	*Euphylloceras* ex gr. *cyprus* Fall. et Term.	——			
19	*Tropaeum* (*T.*) *longus* Kakab.	——			
20	*Toxoceratoides royerianus* d'Orb.	– –			
21	*Macroscaphites nodosostriatus nunui* Erist.	——	– –		
22	*Euphylloceras aptiense* Sayn	——	——	——	
23	*Phyllopachyceras crassum* Drushits	——	——	——	
24	*Pseudohaploceras liptoviense* Zuerch.	——	——	——	
25	*Desmoceras lakhepaense* Rouch.	——	——	——	
26	*Puzosia* aff. *belus* d'Orb.	– –	– –	– –	
27	*Phyllopachyceras baborense* Coq.	——	——	——	——
28	*Ammonitoceras transcaspium* Sinz.		——		
29	*Epicheloniceras subnodosocostatum* Sinz.		——		
30	*E. tschernyschewi schernyschewi* Sinz.		——		
31	*E. tschernyschewi laticostatum* Sinz.		——		
32	*E. pusillum* Sinz.		——		
33	*E. intermedium* Kas		——		
34	*E. martini orientalis* Jac.		——		
35	*E. martini occidentalis* Jac.		——		
36	*E. elissoae* Scharik.		——		
37	*E.* cf. *waageni* Anth.		——		
38	*Colombiceras caucasicum* Lupp.		——		
39	*C. sinzowi* Kas.		——		
40	*C. subtobleri* Kas.		——		
41	*C. crassicostatum* d'Orb.		——		
42	*Euphylloceras velledae georgica* Erist.		——	——	
43	*E. anthulai* Kas.		——	——	
44	*Hypophylloceras guettardi* Rasp.		——	——	
45	*H. hofmanni* Sim., Bač., Sor.		——	——	
46	*H.* aff. *ernesti* Uhl.		——	——	
47	*Cicatrites abichi* Anth.		——	——	
48	*C. godoganense* Kakab.		——	——	
49	*Desmoceras* aff. *inornatum* d'Orb.		——	——	
50	*D.* aff. *quinquecostatum* Math.		– –	– –	
51	*D. akuschaensis* Anth.		——	——	
52	*Zuercherella zuercheri* Jac. et Tobl.		——	——	
53	*Puzosia falcistriata* Anth.		——	——	
54	*P. emerici* Rasp.		——	——	
55	*Pseudoaustralicears* cf. *pavlowi* Wass.		——	——	
56	*P. ramososeptatum* Anth.		——	——	
57	*Ammonitoceras colchicum* Kakab.		——	——	

Table 16. (Contd.)

No.	Ammonite species	Lower Aptian	Middle Aptian		Upper Aptian
		Dufrenoyia furcata Zone	*Epicheloniceras subnodosocostatum* Zone	*Colombiceras tobleri* Zone	*Acanthohoplites nolani* Zone
58	*Tonohamites* cf. *limbatus* Casey		—	—	
59	*Hamiticeras aliensis* Lobj.		—	—	
60	*Parachelониceras guenoti* Collign.		—	—	
61	*Epicheloniceras kasanskyi* Erist.		—	—	
62	*E. rouchadzei* Erist.		—	—	
63	*Colombiceras discoidalis* Sinz.		—	—	
64	*C. elissoae* Kvant.		—	—	
65	*C. subpeltoceroides* Sinz.		—	—	
66	*C. tobleri* Jac. et Tobl.		—	—	
67	*Euphylloceras velledae velledae* Mich.		—	—	
68	*Argonauticeras kudrjavzevi* Drushits		—	—	
69	*Tetragonites duvalianus* d'Orb.		—	—	—
70	*Melchiorites saltense* Sayn		- - -	- - -	- - -
71	*M. angladei* Sayn		—	—	—
72	*Hamiticeras pilsbryi* Ander.		- - -	- - -	- - -
73	*Callizoniceras* ex gr. *hoyeri* Koen.		- - -	- - -	- - -
74	*Australiceras* (*A.*) *tenuicostatum* Kakab.		- - -	- - -	- - -
75	*Toxoceratoides* cf. *rochi* Casey		—	—	—
76	*Tonohamites* ex gr. *decurrens* Spath			—	
77	*Protacanthoplites abichi* Anth.			—	
78	*P. quadratus* Kas.			—	
79	*P. rectangularis* Kas.			—	
80	*P. mirus* Tovb.			—	
81	*P. monilis* Tovb.			—	
82	*P. bigoti* Seun.			—	—
83	*Acanthohoplites aschiltaensis aschiltaensis* Anth.			—	—
84	*A. bigouret bigoureti* Seun.			—	—
85	*Diadochoceras nodosocostatum* d'Orb.				—
86	*D. eristavii* Kvant.				—
87	*D. charatischvilii* Kvant.				—
88	*D. trapezoides* Kvant. et Kvern.				—
89	*Nodosohoplites margaritae margaritae* I. Mich.				—
90	*N. margaritae tenuicostata* Kvant.				—
91	*N. caucasicus* Lupp.				—
92	*Paracanthohoplites subplanatus* Eg.				—
93	*P. cubanicus* Eg.				—
94	*P. papavai* Kvant.				—
95	*Acanthohoplites nolani* Seun.				—
96	*A. crassa crassa* Sinz.				—
97	*A. crassa mangyschlakensis* Glasun.				—
98	*Paracanthohoplites multispinatus* Anth.				—
99	*Acanthohoplites migneni* Seun.				—
100	*A. bergeroni* Seun.				—
101	*A. subangulatus* Sinz.				—
102	*A. aschiltaensis rotundata* Sinz.				—
103	*A. tsagarelii* Kvant.				—
104	*A. subangulicostatus* Sinz.				—
105	*A. uhligi* Anth.				—
106	*A. trautscholdi* Sim., Bač., Sor.				—
107	*A. tamarae* Erist.				—
108	*A. andranomenensis* Besair.				—
109	*A. multisoinatoides* Rouch.				—
100	*A.* cf. *laticostatus* Sinz.				—
111	*A. bigoureti luppovi* Kvant.				—
112	*A. raretuberculatus* Lupp.				—
113	*A. subraretuberculatus* Kvant.				—
114	*Chaschupseceras abchasicum* Kvant.				—

is constituted by uncoiled ammonites of the genus *Macroscaphites* and several desmoceratid genera. It is possible that the ranges of this zone and the English *Tropaeum bowerbanki* Zone are similar, but Kotetishvili believes that the substantiation of the zone in Georgia needs further study.

The *Dufrenoyia furcata* Zone of the **central part of the northern Caucasus and Dagestan** (Tables 9 and 10) contains considerably fewer ammonites known from the above regions. The assemblage includes *Dufrenoyia furcata, D. dufrenoyi,* rare *D. lurensis,* and the local species *D. subfurcata;* in *Cheloniceras, Cheloniceras seminodosum, Ch. gottchei,* and *Ch. meyendorfi* are present. In the central part, the assemblage includes *Pseudosaynella,* while in Dagestan, the index species of the English *Tropaeum bowerbanki* Zone has been recorded. The range of the zones in this region is problematic. It is possible that here, like in France, the very basal horizons of the English *T. bowerbanki* Zone are absent.

In **Turkmenistan** (Table 11), the ammonite composition of this zone is more diverse than in the Caucasus. Apart from the known representatives of the genera *Dufrenoyia* and *Cheloniceras,* the assemblage contains phylloceratids, tetragonitids, and the Mexican genus *Burckhardtites.* The Tuarkyr sections contain *Colombiceras crassicostatum,* an early species of the Middle Aptian genus *Colombiceras. Aconeceras (A.) nisus,* characteristic of this interval in France, is absent at this level and appears only in the Middle Aptian part of the section to replace *A. (A.) nisoides* characteristic of this zone. The range of the zone in Turkmenistan is difficult to assess because of a deep erosion in its base, which is observed in most sections: the *Deshayesites deshayesi* Zone and, most likely, the lower part of the *D. furcata* Zone are missing. All the above listed ammonites were found in several sections, where these beds are present and which are likely to correlate with the middle part of the English *T. bowerbanki* Zone and French *D. furcata* Zone.

Middle Aptian. The subdivision of the Aptian into three substages was accepted by the Interdepartmental Stratigraphic Committee after the Clansayesian horizons (i.e., the *Acanthohoplites nolani* and *Hypacanthoplites jacobi* zones had been transferred from the Albian to the Aptian (*Postanovleniya ...*, 1981, p. 62). The boundary between the Lower and Middle Aptian is drawn as proposed by Renngarten (1951, p. 55), at the top of the *D. subfurcata–D. furcata* Zone (currently *D. furcata* Zone). Luppov (1956, p. 223) supported this position of the boundary. However, one of the arguments in support of this position used by Renngarten and Luppov was the co-occurrence of *Dufrenoyia* and *Dehayesites* in the same Lower Aptian beds, whereas in modern understanding, the most important for the definition of the boundary is the morphological and evolutionary affinity of the genera *Deshayesites* and *Dufrenoyia* (which have different geochronological age) within the same family (Bogdanova and Mikhailova, 1999). Several years prior to the French stratigraphers' proposal of the position of this boundary, Casey et al. (1998) analyzed the distribution of ammonite genera in the boundary Lower and Upper Aptian beds (in England, the Aptian is subdivided into two parts) and concluded that the most sudden change in the ammonite assemblage is somewhat above the upper boundary of the English Lower Aptian *Tropaeum bowerbanki* Zone (Casey et al., 1998, Fig. 6). The disagreement about the level of the most sudden change from the Early Aptian ammonite assemblage to the Late Aptian in our opinion is connected with the choice of genera used for the level definition.

The meeting of the Kilian group has decided that the existence of the ammonite subfamily Deshayesitinae (*Deshayesites* and *Dufrenoyia*) is limited by the Early Aptian (Report on the 4th ..., 2011, p. 788). We concur with this decision.

The lower part of the Middle (or Upper) Aptian was recognized in the zone, which has various names. For a long time, the scheme of the working group on the Tethyan ammonite scale of the Cretaceous, the *Epicheloniceras subnodosocostatum* Zone was recognized at the base Middle Aptian. However, in the Neuchâtel 2005 meeting of the Kilian group, based on the proposal of the French working group (Dutour, 2005, p. 273), its name was replaced by *Epicheloniceras martini,*[7] with three subzones of the English scheme: *debile, gracile,* and *buxtorfi* (Report on the 2nd ..., 2006). The ammonite distribution in the *Epicheloniceras subnodosocostatum* Zone and its equivalents is shown in Table 17.

Thus, at present in **France**, this part of the section is recognized as the *Epicheloniceras martini* Zone, which base is drawn at the level of the first appearance of this species. Dutour (2005), who proposed this zone, noted the total distribution in the zone of the ammonite genus *Epicheloniceras* and, primarily, *E. martini,* which however, is found only in the lower part of the zone (Dutour, 2005, p. 220, text-fig. 15). The whole zone from its base to the top is characterized by *Phyllopachyceras baborense* and *Zuercherella zuercheri,* which in fact have a much wider stratigraphic distribution and cannot be zonal index species. The recognition of three subzones named after various species of *Epicheloniceras* according to Dutour (2005, p. 273), reflects the evolution of this genus. Apart from *Epicheloniceras,* which can be considered as an index of this interval, the assemblage contains numerous phylloceratids, lytoceratids, tetragonitids, and desmoceratids, many of which continue from the underlying to the overlying beds. Horizons are recognized based on the occurrences of members of these groups in certain parts of the zone. For further corre-

[7] Our views on the stratigraphic position of Epicheloniceras martini are given in the systematic paleontology section.

Table 17. Ammonite distribution in the *Epicheloniceras subnodosocostatum* Zone and its equivalents

No.	Ammonite species	Southeastern France: *Epicheloniceras martini* Zone, Debile Subzone / Gracile Subzone: *Eugaudr. raspaili* Horizons	Southeastern France: *Epicheloniceras martini* Zone, Gracile Subzone / Buxtorfi Subzone: *Eugaudr. depressus* Horizons	Southeastern France: *Epicheloniceras martini* Zone, Buxtorfi Subzone: *Salf. caucasica* Horizons	England: *Cheloniceras martinioides* Zone, *Cheloniceras debile* Subzone	England: *Cheloniceras martinioides* Zone, *Cheloniceras gracile* Subzone	England: *Cheloniceras martinioides* Zone, Cheloniceras buxtorfi Subzone	Germany: *Tropaeum drewi* + *T. tenuinodosum* Zone	Germany: *Cheloniceras laticostatum* + *Ch. tschernyschewi* Zone	Germany: *Cheloniceras buxtorfi* Zone	Georgia: *Epicheloniceras subnodosocostatum* Zone	Central region of Northern Caucasus: *Colombiceras crassicostatum*–*Epicheloniceras subnodosocostatum* Zone	Dagestan: *Colombiceras crassicostatum*–*Epicheloniceras subnodosocostatum* Zone	Turkmenistan: *Epicheloniceras subnodosocostatum* Zone
1.	*Melchiorites strigosa* Fallot													
2.	*Pseudohaploceras angladei* Sayn													
3.	*Salfeldiella (Gyrophyllites) paquieri* Sayn													
4.	*Phyllopachyceras baborense* Coq.													
5.	*Zuercherella zuercheri* Jac. et Fall.													
6.	*Aconeceras nisus* d'Orb.													
7.	*Eugaudryceras (E.) numidum* Coq.													
8.	*Colombiceras crassicostatum* d'Orb.													
9.	*Dufrenoyia dufrenoyi* d'Orb.													
10.	*Phylloceras (Hypoph.) morelanum* d'Orb.													
11.	*Epicheloniceras martini* Jacob													
12.	*Epicheloniceras debile* Casey													
13.	*Epicheloniceras eotipicum* Casey													
14.	*Uhligella jacobi* Burckhardt													
15.	*Aconeceras* nov. sp. 1													
16.	*Gabbioceras lamberti* Breistr.													
17.	*Protetragonites* cf. *obliquestrangulatum* Kil.													
18.	*Phylloceras (Hypoph.) cyprus* Jac. et Fall.													
19.	*Diadochoceras (Vergun.) pretiosum* d'Orb.													
20.	*Eugaudryceras (Eotetr.) raspaili* Breistr.													
21.	*Phylloceras (Hypoph.) aptiense* Sayn													
22.	*Salfeldiella (S.) guettardi* Raspail													
23.	*Epicheloniceras tschernyschewi* Sinz.													
24.	*Epicheloniceras gracile* Casey													
25.	*Epicheloniceras nickchitchi* Dutour													
26.	*Eugaudryceras (Eotetr.) depressus* Rasp.													
27.	*Salfeldiella (Gyroph.) lateumbonatum* Perv.													
28.	*Jauberticeras coloti* Dutour													
29.	*Phylloceras fortunei Honnorat* Bestide													
30.	*Eugaudryceras (Eotetr.) duvali* d'Orb.													
31.	*Epicheloniceras buxtorfi* d'Orb.													
32.	*Phylloceras (Hypoph.) moriezense* Sayn													
33.	*Salfeldiella (S.) caucasica* Sayn													
	England													
34.	*Tropaeum (Ancylotropaeum) pondorosum* Casey													
35.	*Tropaeum (T.) pseudohillsi* Casey													
36.	*Tropaeum (T.) benstedti* Casey													
37.	*Tropaeum (Ancylotr.) baylissi* Casey													
38.	*Ammonitoceras rex* Casey													
39.	*Vectisites simplex* Casey													
40.	*Epicheloniceras subvolgense* Casey													
41.	*Tropaeum (T.) rossicum* Casey													
42.	*Ammonitoceras tovilense* Crikm.													
43.	*Ammonitoceras boughtonense* Casey													
44.	*Ammonitoceras sowerbyi* Casey													
45.	*Epicheloniceras martinioides* Casey													
46.	*Epicheloniceras cantianum* Casey													

Table 17. (Contd.)

No.	Ammonite species	Southeastern France					England			Germany			Georgia	Central region of Northern Caucasus	Dagestan	Turkmenistan
		Epicheloniceras martini Zone					*Cheloniceras martinioides* Zone									
		Debile Subzone	Gracile Subzone		Buxtorfi Subzone											
		Eugaudr. raspaili Horizons		*Eugaudr. depressus* Horizons		*Salf. caucasica* Horizons	*Cheloniceras debile* Subzone	*Cheloniceras gracile* Subzone	Cheloniceras buxtorfi Subzone	*Tropaeum drewi* + *T. tenuinodosum* Zone	*Cheloniceras laticostatum* + *Ch. tschernyschewi* Zone	*Cheloniceras buxtorfi* Zone	*Epicheloniceras subnodosocostatum* Zone	*Colombiceras crassicostatum*–*Epicheloniceras subnodosocostatum* Zone	*Colombiceras crassicostatum*–*Epicheloniceras subnodosocostatum* Zone	*Epicheloniceras subnodosocostatum* Zone
47.	*Vectisites caprotinus* Casey						—									
48.	*Caspianites vectensis* Casey						—	—								
49.	*Valpenites tardesulcatus* Casey							—								
50.	*Epicheloniceras claudi* Casey							—								
51.	*Epicheloniceras sellindgense audax* Casey							—								
52.	*Doridiscus rotulus* Casey							—								
	Germany															
53.	*Cheloniceras seminodosum* Sinz.										—					
54.	*Cheloniceras cornuelianum cornuelianum* d'Orb.										—					
55.	*Aconeceras (Sinzowia) stolleyi* Casey										—	—	—			
56.	*Tropaeum subarcticum* Casey												—			
57.	*Ammonitoceras transcaspium* Sinz.										—	—	—			
58.	*Epicheloniceras subnodosocostatum* Sinz.										—	—	—	—	—	—
59.	*Epicheloniceras laticostatum* Sinz.											—	—	—	—	
60.	*Parahoplites multicostatus* Sinz.												—			
61.	*Neohibolites inflexus* Stolley												—			
62.	*Neohibolites ewaldi* Stromb.												—			
63.	*Tropaeum drewi sinosum* Kemper												—			
64.	*Trpaeum tenuinodosum* Kemper												—			
	Georgia															
65.	*Euphylloceras aptiense* Sayn												—			
66.	*Phyllopachyceras crassum* Druz.												—			
67.	*Pseudohaploceras liptoviense* Zuerch.												—			
68.	*Desmoceras lakhepaense* Rouch.												—			
69.	*Epicheloniceras pusillum* Sinz.												—		—	—
70.	*Epicheloniceras intermedium* Kas.												—	—	—	—
71.	*Epicheloniceras martini orientalis* Jac.												—			
72.	*Epicheloniceras elissoae* Scharik.												—			
73.	*Epicheloniceras* cf. *waageni* Anth.												—		—	
74.	*Combiceras caucasicum* Lupp.												—	—		—
75.	*Colombicer sinzowi* Kas.												—	—		
76.	*Colombiceras subtobleri* Kas.												—	—	—	—
77.	*Euphylloceras velledae georgica* Erist.												—			
78.	*Epicheloniceras anthulai* Kas.												—			
79.	*Hypophylloceras hofmanni* Sim., Bač, Sor.												—			
80.	*Cicatrites abichi* Anth.												—			
81.	*Cicatrites godoganense* Kakab.												—			
82.	*Desmoceras akuschaense* Anth.												—			
83.	*Puzosia emerici* Rasp.												—			

Table 17. (Contd.)

No.	Ammonite species	Southeastern France, *Epicheloniceras martini* Zone: Debile Subzone / Gracile Subzone, *Eugaudr. raspaili* Horizons	Southeastern France, *Epicheloniceras martini* Zone: Gracile Subzone / Buxtorfi Subzone, *Eugaudr. depressus* Horizons	Southeastern France, *Epicheloniceras martini* Zone: Buxtorfi Subzone, *Salf. caucasica* Horizons	England, *Cheloniceras martinioides* Zone: *Cheloniceras debile* Subzone	England, *Cheloniceras martinioides* Zone: *Cheloniceras gracile* Subzone	England, *Cheloniceras martinioides* Zone: Cheloniceras buxtorfi Subzone	Germany: *Tropaeum drewi* + *T. tenuinodosum* Zone	Germany: *Cheloniceras laticostatum* + *Ch. tschernyschewi* Zone	Germany: *Cheloniceras buxtorfi* Zone	Georgia: *Epicheloniceras subnodosocostatum* Zone	Central region of Northern Caucasus: *Colombiceras crassicostatum*–*Epicheloniceras subnodosocostatum* Zone	Dagestan: *Colombiceras crassicostatum*–*Epicheloniceras subnodosocostatum*	Turkmenistan: *Epicheloniceras subnodosocostatum* Zone
84.	*Pseudoaustraliceras* cf. *pavlowi* Wass.										—			—
85.	*Pseudoaustraliceras ramososeptatum* Anth.										—			
86.	*Ammonitoceras colchicum* Kakab.										—			
87.	*Tonohamites* cf. *limbatus* Casey										—			
88.	*Hamiticeras aliensis* Lobj.										—			
89.	*Paracheloniceras guenoti* Collign.										—			
90.	*Epicheloniceras kasanskyi* Erist.										—			
91.	*Epicheloniceras rouchadzei* Erist.										—			
92.	*Colombiceras discoidale* Sinz.										—			
93.	*Colombiceras elissoae* Kvant.										—			
94.	*Colombiceras subpeltoceroides* Sinz.										—	—		—
95.	*Colombiceras tobleri* Jac. et Tobl.										—	—		—
96.	*Euphylloceras velledae* Mich.										—			—
97.	*Argonauticeras kudrjavzevi* Drushits										—			
98.	*Tetragonites duvalianus* d'Orb.										—			
99.	*Toxoceratoides* cf. *rochi* Casey										—			
	Central region of Northern Caucasus													
100.	*Toxoceratoides depereti* Kil.											—		
101.	*Toxoceratoides crudus* Drushits											—		
102.	*Epicheloniceras stuckenbergi* Kas.											—	—	—
103.	*Epicheloniceras orientale* Jac.											—	—	
104.	*Epicheloniceras caucasicum* Lupp.											—		—
105.	*Epicheloniceras meyendorfi* d'Orb.											—		
106.	*Colombiceras korotkovi* I. Mich.											—		
107.	*Colombiceras quadrarium* Kas.											—		
108.	*Aconeceras* (*Sinzovia*) *aptiana* Saras.											—		—
109.	*Aconeceras* (*A.*) *haugi* Saras.											—		—
110.	*Colombiceras bogdanovae* Tovb.											—		
	Dagestan													
111.	*Cymatoceras* ex gr. *neckeri* Pict. et Camp.												—	
112.	*Puzosia falcistriata* Anth.												—	
113.	*Colombiceras sinzowi* Kas.												—	—
114.	*Colombiceras* aff. *quadratum* Kas.												—	
115.	*Puzosia saltaensis* Kas.												—	
	Turkmenistan													
116.	*Juberticeras latericarinatum* Anth.													—
117.	*Caspianites wassiliewskyi* Renng.													—
118.	*Caspianites* aff. *wassiliewskyi* Renng.													—
119.	*Luppovia dostschanensis* Bogd., Kakab., I. Mich													—
120.	*Luppovia adjiderensis* Bogd., Kakab., I. Mich.													—
121.	*Epicheloniceras* ex gr. *martini* d'Orb.													—
122.	*Hypophylloceras anthulai* Kas.													—

lation of this interval, it is important to mention that the heteromorphic ammonite genera *Tropaeum, Ammonitoceras, Caspianites, Luppovia,* and others are absent from the French section.

Several years earlier, a different subdivision was proposed for the lower part of the Upper Aptian of the Vocontian Basin (Dauphin, 2002). The *Colombiceras crassicostatum* Zone was recognized above the *Dufrenoyia furcata* Zone, with the lower boundary drawn based on the disappearance of *Dufrenoyia* (rather than on the entry of *Epicheloniceras*), which coincides with a change in the coloration of the rock in the sections.

The **English** *Epicheloniceras martinioides* Zone[8] was established by Casey (1961b) with three subzones, *debile, gracile,* and *buxtorfi*. In contrast to the French index of this zone (*martini*), the species *E. martinioides* is found from the lower to upper zonal boundary. The English sections are dominated by the uncoiled ammonite genera *Tropaeum, Ammonitoceras,* and *Caspianites,* while *Colombiceras* is missing from parahoplitids, but *Vectisites* and *Walpenites* are present. It is quite possible that the ranges of the English and French zones are similar, since all the subzonal indexes are present in both regions in the same succession and at the same stratigraphic levels. Dauphin (2002) considered that the lower boundaries of the zones (*martinioides* in England and *martini* and *crassicostatum* in France) coincide, whereas the upper boundary of the *crassicostatum* Zone is approximately in the middle of the *martinioides* Zone, within the *debile* Subzone (Dauphin, 2002, p. 118, text-fig. 55, p. 21). In her opinion, this position of the boundary is suggested by the distribution of *Vectisites* and *Walpenites* species, which are found in the upper part of the *crassicostatum* Zone and also in the lower and partly in the middle parts of the *martinioides* Zone (upper *debile* Subzone and the base of the *gracile* Subzone).

In **Germany**, three "zones" are recognized in this part of the section (Kemper, 1995, p. 175, inverted commas are by E. Kemper): *Tropaeum drewi + T. tenuinodosum, Cheloniceras laticostatum + Ch. tschernyschewi,* and *Ch. buxtorfi*. Here, as in England, the assemblage contains uncoiled ammonites of the genera *Tropaeum* and *Ammonitoceras,* which may suggest close connections between the English and German basins at that time. For the lower zone, Kemper indicated *Cheloniceras seminodosum* Sinz., *Ch. cornuelianum cornuelianum* d'Orb., *Tropaeum drewi spinosum* Kemper, and *Tr. tenuinodosum* Kemper. Two *Cheloniceras* species are index species for the Lower Aptian, and are not restricted to the *Dufrenoyia furcata* Zone, but are also found below, in association with *Dehayesites*. *Tr. drewi* Casey is found in England in the upper part of the Lower Aptian, in the *meyendorfi* Subzone. However, Casey et al. (1998, p. 528) were in doubt that *Tr. drewi* in Germany is equivalent to the English *Tr. drewi*. However, in spite of that, it is possible to suggest that the *Tropaeum drewi + T. tenuinodosum* "Zone" of Germany is Lower Aptian and should more likely be correlated with a part of the *Dufrenoyia furcata* Zone of France and *Tropaeum bowerbanki* Zone of England. In the two upper "zones," there are virtually no species in common with previously discussed regions, except *Epicheloniceras subnodosocostatum,* which is the index species of this interval in other regions. The precise range of the upper two "zones" is difficult to estimate, but they are likely to correspond to the *Epicheloniceras gracile* and *E. buxtorfi* subzones of France (in the stratotype) and England.

The *Epicheloniceras subnodosocostatum* Zone in **Georgia** is characterized by a rich ammonite assemblage different from French and English assemblages (Kotetishvili, 1986). The assemblage contains numerous Caucasian species, including local Georgian species (they are currently known from other regions, but were first established based on Caucasian material). Compared to other above considered regions, parahoplitids (genus *Colombiceras*) appeared earlier. *Epicheloniceras* represents a high proportion of the assemblage characteristic of this interval of the Aptian. The assemblage contains heteromorphic ammonites of the genera *Pseudoaustraliceras, Ammonitoceras, Tonohamites,* instead of *Tropaeum* widely distributed in the northern regions. The Caucasian genus *Cicatrites* established by Anthula on the material from the northern Caucasus and characteristic of the Middle Aptian is a new element of the assemblage. Interestingly, Casey, who doubted the identity of the German representatives of *Tropaeum drewi* to the English representatives of this species, proposed a similarity between the German *Tr. drewi* and the Caucasian species *Cicatrites abichi* Anth.

The similarity of the Georgian ammonite assemblage and the assemblage of the French *martini* Zone is observed in the presence of phylloceratids and desmoceratids, which do not play such a great role in the northern Caucasus and Turkmenistan sections as in France. However, the occurrence of *Epicheloniceras martini orientale* across the entire Georgian zone (as reported by M.Z. Sharikadze), i.e., of *martini* as understood by French paleontologists, allows identification of the zones under consideration. It is noteworthy that the Georgian sections do not contain *Epicheloniceras debile* and *E. gracile,* which in England and France characterize two lower subzones. The assemblage lacks *E. buxtorfi,* the index of the upper subzones. This may result from washouts in the Early and Middle Aptian in Georgia, which involved these levels of the Early Cretaceous. However, none of the aggregated layers or conglomerates in the region studied contains these species in above district. Therefore, it can be suggested that the above species were absent here in the interval under consideration. However,

[8] In 1961, Casey considered *Epicheloniceras* as a subgenus of *Cheloniceras*. Later he considered it as a separate genus (Casey et al., 1998).

none of the above information can be considered for or against the possible correlation of the Georgian *E. subnodosocostatum* and the entire range of the English *E. martinioides* and French *E. martini* zones.

In the central regions of the northern slope of the **Caucasus** and in **Dagestan**, this interval is referred to as the *Colombiceras crassicostatum* and *Epicheloniceras subnodosocostatum* zones. The former species characterizes the upper part of the zone and the second, the entire zone. Species of the genera *Epicheloniceras* and *Colombiceras* play a leading role in the ammonite assemblages that are found immediately above the lower boundary of the zone and continue to its upper limit. *Colombiceras* continue to the next parahoplitid zone. Among representatives of *Epicheloniceras,* the species *E. subnodosocostatum* and *E. orientale* are worth mentioning. The former species was considered by Dutour (2005) as a microconch of *E. tscherny-schewi,* i.e., its synonym.[9] *E. tschernyschewi* in the northern Caucasus is found throughout the section of the zone. We consider the variety *orientalis* of species *martini* established by Jacob as a separate species. Thus, *orientale* in our interpretation is *martini* as interpreted by Dutour (2005, pp. 163, 164). Relatively rare representatives of phylloceratids, tetragonitids, and desmoceratids are common with species of the French assemblage of this interval. Large heteromorphs characteristic of the English and German sections are extremely rare. *Aconeceras (A.) nisus* d'Orb., in the Caucasus appears in the upper part of this Middle Aptian zone, unlike its distribution in French sections, where it is typical of the *D. furcata* Zone.

The Middle Aptian beds in the western part of the northern Caucasus occur to the west of the Pshekha River, along the Pshish River. Lithologically, they are mostly represented by clay, less commonly, by siltstones and sandstones. Almost all researchers who studied this region indicate the presence of septarian concretions in the clay series. According to Egoian (1986), the Middle Aptian beds are included in several formations (Shapsukho, Dol'men, and Samur formations), which replace each other laterally. The Shapsukho Formation is the thickest and includes the Middle and Upper Aptian beds (400–500 m).

The *Epicheloniceras tschernyschewi–Colombiceras crassicostatum* Zone (the lower zone of the Middle Aptian) (Egoian, 1986) or *Colombiceras crassicostatum–Epicheloniceras tschernyschewi* Zone (Egoian, 1989) contains many diverse ammonites: *Salfeldiella guettardi* Rasp., *Pseudoaustraliceras ramososeptatum* Anth., *P. pavlowi* Wass., *Aconeceras nisus* d'Orb., *Epicheloniceras subnodosocostatum* Sinz., *Ep. tschernyschewi* Sinz., *Ep. martini* d'Orb., *Ep. buxtorfi* Jac., *Ep. waageni* Anth., *Ep. intermedium* Kas., *Colombiceras crassicostatum* d'Orb., *C. subtobleri* Kas., *C. tobleri* Jac. et Tobl., *C. sinzowi* Kas., *C. caucasicum* Lupp. and the ammonite genera *Tetragonites, Ptychoceras,* and others. The taxonomic composition of ammonites is very similar to that of the Central and eastern Caucasian assemblages.

In **Turkmenistan**, this part of the section is referred to as the *Epicheloniceras subnodosocostatum* Zone. The ammonite assemblage of Turkmenistan is almost the same as in the Caucasus. It is distinct in the presence in this region, apart from *A.(A.) nisus,* of two more *Aconeceras* species, *A. aptianum* and *A. haugi.* Of heteromorphic ammonites, the genera *Caspianites* and *Luppovia* are present. Among *Epicheloniceras, E. debile* and *E. gracile,* index species of the two lower subzones in England and France, are absent, although the index species of the third, upper, *E. buxtorfi* Subzone is present. This was noted by Cecca et al. (1999), who suggested that the lower part of the European *E. martini* and *E. martinioides* zones is absent in Turkmenistan. Later, this hypothesis was supported by Dauphin (2002, p. 118, text-fig. 55) based on the erosional gap in the Lower and Middle Aptian boundary interval in the western regions of Turkmenistan, clearly observed in the *D. furcata* phase. It is possible that the basal horizons of the Aptian could also be eroded. However, it is also possible that English species were missing in Turkmenistan, as in the northern Caucasus and Georgia. The range of the *subnodosocostatum* Zone in Turkmenistan completely corresponds to the range of the Middle Aptian lower zone in England and France.

To the north of Tuarkyr (Turkmenistan), the Middle Aptian beds are present in the **Mangyshlak** Peninsula (western Kazakhstan). They are represented by a uniform series of dark, almost black clay with infrequent small and large septarian, calcareous concretions and beds of sandstones (the "septarian clay" series as designated by A.D. Natsky). According to Saveliev and Vasilenko (1963), the thickness of the clay series ranges from 69 to 140 m. Since the works of Wassiliewskyi (1908) and Natsky (1912, 1915c), these beds were subdivided into several ammonite zones, which these authors compared with synchronous beds of Western Europe. Saveliev (in Saveliev and Vasilenko, 1963, p. 272) referred to these ammonite-based units as "zones with no thickness," since the boundary and thickness of zones are extremely difficult to recognize in this uniform series. However, in the same paper by Saveliev and Vasilenko and also in the summary review of the Cretaceous stratigraphy (Luppov et al., 1986), the *Epicheloniceras subnodosocostatum* Zone was recognized as a separate zone with the following ammonite assemblage: *Epicheloniceras subnodosocostatum* Sinz., *Ep. robustum* Sinz., *Ep. laticostata* Sinz., *Ep. minuta* Sinz., *Ep.* cf. *martini* d'Orb. var. *orientalis* Jac., *Ep. waageni* Anth., *Ep. tschernyschewi* Sinz., *Ep. pusillum* Sinz., *Pseudoaustraliceras pavlowi* Wass., *Tropaeum cadoceriforme* Sinz., *C.* aff. *laguseni* Sinz., and *Luppovia dotschanensis* Bogdanova, Kakab,

[9] Our views on the taxonomy of *subnodosocostatum* and *tschernyschewi* are explained in the Systematic Paleontology section.

I. Mich. This assemblage shares many species with the assemblages of Turkmenistan and the Caucasus.

The subdivision of the higher part of the Aptian Stage (above the *Epicheloniceras subnodosocostatum* Zone) is based on the evolution of parahoplitids. This family is rooted in the stratigraphically older beds, i.e., in the *E. subnodosocostatum* Zone or in the uppermost Lower Aptian, in the *furcata* Zone (genus *Colombiceras*). However, beginning from the *P. melchioris* phase, representatives of this family become dominant among the ammonite fauna. The international "Kilian Group" accepted the *Parahoplites melchioris* Zone for this part of the Aptian (Report on the 4th ..., 2011), since that name replaced the name *Colombiceras tobleri* (Hoedemaeker and Company, 1993). The ammonite distribution in the *Parahoplites melchioris* Zone and its equivalents is shown in Table 18.

The *Parahoplites melchioris* Zone is recognized in **France**, in the stratotype Gargasian section (Dutour, 2005). However, the range and the boundaries of this zone are not precisely determined because of the absence of the index ammonite genera *Parahoplites* and *Colombiceras* in this Aptian interval. Dutour mentioned that Dauphin managed to find a single specimen of *Parahoplites* (Dauphin, 2002, pl. 4, fig. 16) in one of the sections, which constitute a part of the modern Gargasian stratotype (Baudinard section), but this single record cannot help in placing the boundaries and identifying the ranges of zones. Dauphin considered the *Colombiceras tobleri* Zone as the third zone of the French Gargasian. The lower boundary of this zone is drawn based on the appearance of species of the genera *Egoianiceras, Acanthohoplites* (*A.* gr. *aschiltaensis*), *Jauberticeras,* and *Colombiceras.* In the upper part of this zones, Dauphin indicated the first appearance of the genus *Parahoplites.* She also indicated a barren interval in the uppermost part of the zones until the appearance of the Clansayesian fauna of the *nolani* zones.

In **England**, the index ammonite group for this interval is represented by *Parahoplites,* most species of which are based on English material, i.e., *irregularis, nutfieldiensis* (zonal index), *daveyi, cunningtoni,* etc. Large *Tropaeum* shells continue into this interval and one species of this genus is known from Mangyshlak. Finally, the genus *Colombiceras* is represented by the only species *C. tobleri,* which is the index of this zone in France and Georgia. Casey (1961b), the author of the English stratigraphic scheme for this interval, accepted the species *tobleri* in the authorship of I.F. Sinzow rather than M.Sh. Jacob. However, we believe that *tobleri* sensu Sinzow is identical to the species described by Jacob (see the description of *C. tobleri* in this paper). Despite the small ammonite assemblage of this zone Casey recognized two subzones in it: *Tropaeum subarcticum* and *Parahoplites cunningtoni.* The subzones have different species composition of *Parahoplites.*

A small assemblage of the combined *Parahoplites nutfieldiensis–P. melchioris* Zone of **Germany**[10] contains species of *Parahoplites,* including *P. depressus* and *P. vectensis* and the index species, two *Aconeceras* species, large heteromorphic ammonites *Tropaeum* and *Ammonitoceras,* and belemnites. The assemblage is mixed, composed of species known from England (mostly) and several species occurring in the Caucasus and Transcaspia. It is worth mentioning that the occurrences in this region of *Acanthohoplites aschiltaensis* Anth., which for a long time in the middle of the last century was the index of the upper (third) Middle Aptian zone in the northern Caucasus. The range of the *Parahoplites nutfieldiensis–P. melchioris* Zone in Germany can tentatively be correlated with the range of the English *P. nutfieldensis* Zone.

In **Georgia**, this interval corresponds to the *Colombiceras tobleri* Zone (Kotetishvili, 1986; Atlas ..., 2005). The lower boundary of the zone is drawn based on the change in the percent content of the species of the genera *Epicheloniceras* and *Colombiceras* compared to the *E. subnodosocostatum* Zone. In this zone, in contrast to the *E. subnodosocostatum* Zone, representatives of *Colombiceras* dominate over *Epicheloniceras.* The ammonite assemblage is relatively large. It contains phylloceratids and desmoceratids, of which several species are in common with the French assemblage. It includes several *Colombiceras* species, *C. tobleri, C. discoidalis, C. subpeltoceroides,* and *C. elissoae;* two local species of *Epicheloniceras, E. kasanskyi* and *E. rouchadzei.* The assemblage of this zone, firstly, contains many endemic species, secondly, almost all its species are also found in the lower Middle Aptian zone, and, thirdly, it lacks *Parahoplites* species characteristic of the uppermost Middle Aptian in many regions of Europe and Asia. Therefore, the subdivision and correlation of the Georgian sections with European and Asian (Transcaspia) beds is, in our opinion, problematic. However, Kotetishvili (1986, p. 142) considered that the *tobleri* Zone could be readily traced by the composition of the southern elements, genus *Colombiceras,* and by the composition of northern elements, i.e., the genus *Parahoplites.*

The ammonite assemblages of the *Parahoplites melchioris* Zone in the **central part of the northern Caucasus** and **Dagestan** are very similar. They are dominated by species of the genera *Parahoplites* and *Colombiceras,* and contain first representatives of the genus *Acanthohoplites.* The difference between these two regions is the fact that the same ammonite species are found in different parts of the zones of the two regions. The zonal index is found in both regions almost continuously, from the lower to upper boundary. *Acanthohoplites aschiltaensis* is particularly interesting because a separate zone (*A. aschiltaensis* Zone)

[10]Kemper (1995, p. 175, text-fig. 1) proposed to name this zone *Parahoplites nutfieldiensis* in the southern vicinity of the region and *P. melchioris* in the vicinity of Hannover.

Table 18. Stratigraphic distribution of ammonite species in the *Parahoplites melchioris* Zone and its equivalents

No.	Ammonite species	Southeastern France	England		Germany	Georgia	Centrl region of Northern Caucasus	Dagestan	Turkmenistan
		Parahoplites melchioris Zone	Parahoplites nutfieldiensis		*Parahoplites nutfieldiensis*–*P. melchioris* Zone	*Colombiceras tobleri* Zone	*Parahoplites melchioris* Zone	*Parahoplites melchioris* Zone	*Parahoplites melchioris* Zone
			Tropaeum subarcticum Subzone	*Parahoplites cunningtoni* Subzone					
1	*Phyllopachyceras baborense* Coq.	←→				←→			
2	*Zuercherella zuercheri* Jac. et Fall.	←→				←	←		—
3	*Melchiorites alpina* Kil.	←→							
4	*Eugaudriceras* (*Eotetr.*) *depressus* Rasp.	←							
5	*Jauberticeras caloti* Dutour	←→							
6	*Eugaudriceras* (*Eotetr.*) *duvali* d'Orb.	←							
7	*Salfeldielia* (*S.*) *caucasica* Sayn	←				←		—	
8	*Jauberticeras jaubertianum* d'Orb.	- - -							
9	*Melchiorites emerici* Rasp.	—							
10	*Valdedorsella akuschaensis* Anth.	- - -							
11	*Pseudohaploceras falcistriatum* Anth.	—				←			
	England								
12	*Parahoplites maximus* Sinz.		—				—	—	—
13	*Parahoplites irregularis* Casey		—		—				—
14	*Tropaeum* (*T.*) *subsimbirskense* Sinz.		—	—					
15	*Tropaeum* (*Epitropaeum*) *subarcticum* Casey		—	—					
16	*Parahoplites nutfieldensis* Casey		—	—	—				
17	*Parahoplites daveyi* Casey		—	—					
18	*Colombiceras tobleri* Sinz. (non Jacob)		—	—					
19	*Parahoplites cunningtoni* Casey			—	—				
20	*Parahoplites depressus* Casey			—					
21	*Parahoplites vectensis* Casey			—					
	Germany								
22	*Aconeceras* (*Sinzowia*) *stolleyi* Casey				← - - -				
23	*Aconeceras* (*Sinzowia*) aff. *trautscholdi* Sinz.				—				
24	*Tropaeum arcticum* Stolley				—				
25	*Ammonitoceras transcaspium* Sinz.				←				
26	*Acanthohoplites aschiltaensis* Anth.				—				

Table 18. (Contd.)

No.	Ammonite species	Southeastern France	England		Germany	Georgia	Centrl region of Northern Caucasus	Dagestan	Turkmenistan
		Parahoplites melchioris Zone	Parahoplites nutfieldiensis		*Parahoplites nutfieldiensis–P. melchioris* Zone	*Colombiceras tobleri* Zone	*Parahoplites melchioris* Zone	*Parahoplites melchioris* Zone	*Parahoplites melchioris* Zone
			Tropaeum subarcticum Subzone	*Parahoplites cunningtoni* Subzone					
27.	*Parahoplites melchioris* Anth.								
28.	*Parahoplites multicostatus* Sinz.								
29.	*Neohibolites inflexus* Stolley								
30.	*Neohibolites ewaldi* Stromb.								
	Georgia								
31.	*Euphylloceras aptiense* Sayn								
32.	*Phyllopachyceras crassum* Drushits								
33.	*Pseudohaploceras liptoviense* Zeuschn.								
34.	*Desmoceras lakhepaense* Rouch.								
35.	*Puzosia* aff. *belus* d'Orb.								
36.	*Euphylloceras velledae* Erist.								
37.	*Epicheloniceras anthulai* Kas.								
38.	*Hypophylloceras guettardi* Rasp.								
39.	*Hypophylloceras hofmanni* Sim., Bac., Sor.								
40.	*Hypophylloceras* aff. *ernesti* Uhl.								
41.	*Cicatrites abichi* Anth.								
42.	*Cicatrites* aff. *godoganense* Kakab.								
43.	*Desmoceras* aff. *inornatum* d'Orb.								
44.	*Desmoceras* aff. *quinquecostatum* Math.								
45.	*Desmoceras akuschaense* Anth.								
46.	*Pseudoaustraliceras* cf. *pavlowi* Wass.								
47.	*Pseudoaustraliceras ramososeptatum* Anth.								
48.	*Ammonitoceras colchicum* Kakab.								
49.	*Tonohamites* cf. *limbatum* Casey								
50.	*Hamiticeras aliensis* Lobj.								
51.	*Paracheloniceras quenoti* Collign.								
52.	*Epicheloniceras kasanskyi* Erist.								
53.	*Epicheloniceras rouchadzei* Erist.								
54.	*Colombiceras discoidalis* Sinz.								
55.	*Colombiceras elissoae* Kvant.								
56.	*Colombiceras subpeltoceroides* Sinz.								
57.	*Colombiceras tobleri* Jac. et Tobl.								
58.	*Argonauticeras kudrjavzevi* Druz.								

Table 18. (Contd.)

No.	Ammonite species	Southeastern France: *Parahoplites melchioris* Zone	England: Parahoplites nutfieldiensis: *Tropaeum subarcticum* Subzone	England: Parahoplites nutfieldiensis: *Parahoplites cunningtoni* Subzone	Germany: *Parahoplites nutfieldiensis*–*P. melchioris* Zone	Georgia: *Colombiceras tobleri* Zone	Centrl region of Northern Caucasus: *Parahoplites melchioris* Zone	Dagestan: *Parahoplites melchioris* Zone	Turkmenistan: *Parahoplites melchioris* Zone
	Central region of Northern Caucasus								
59.	*Aconeceras* (*Sinzowia*) *aptiana* Saras.						←		↔
60.	*Aconeceras* (*A.*) *haugi* Saras.						←		↔
61.	*Aconeceras* (A.) *nisus* d'Orb.						←		↔
62.	*Colombiceras subtobleri* Kas.						←		
63.	*Colombiceras bogdanovae* Tovb.						←		
64.	*Tetragonites duvalianus* Rasp.						—	—	
65.	*Tetragonites heterosulcatus* Anth.						—	—	—
66.	*Ptychoceras puzosiana* Jac. et Tobl.						—		
67.	*Acanthohoplites laticostatus* Sinz.						—	—	
68.	*Acanthohoplites subrectangulatus* Sinz.						—		
69.	*Parahoplites schmidti* Jac. et Tobl.						—	—	—
70.	*Parahoplites debilecostatus* I. Mich.						—	—	—
71.	*Parahoplites multicostatus* Sinz.						—		—
72.	*Parahoplites subcampischei* Sinz.						—	—	—
73.	*Parahoplites sjogreni* Anth.						—	—	—
74.	*Parahoplites maximus* Sinz.						—	—	—
	Dagestan								
75.	*Pseudohaploceras matheroni* d'Orb.							←	
76.	*Puzosia saltaensis* Kas.							←	
77.	*Phyllopachyceras moreli* d'Orb.							—	
78.	*Pseudoaustraliceras ramosum* Anth.							—	
79.	*Colombiceras planidorsatum* Kas.							—	
80.	*Parahoplites campischei* Pict. et Ren.							—	—
81.	*Parahoplites transitans* Sinz.							—	—
82.	*Parahoplites grossouvrei* Jac.							—	—
83.	*Parahoplites artschmanensis* Glasun.							—	—

Table 18. (Contd.)

No.	Ammonite species	Southeastern France	England		Germany	Georgia	Centrl region of Northern Caucasus	Dagestan	Turkmenistan
		Parahoplites melchioris Zone	Parahoplites nutfieldiensis		*Parahoplites nutfieldiensis–P. melchioris* Zone	*Colombiceras tobleri* Zone	*Parahoplites melchioris* Zone	*Parahoplites melchioris* Zone	*Parahoplites melchioris* Zone
			Tropaeum subarcticum Subzone	*Parahoplites cunningtoni* Subzone					
	Turkmenistan								
84.	*Hypophylloceras anthulai* Kas.								↔
85.	*Parahoplites* aff. *melchioris* Anth.								—
86.	*Parahoplites luppovi* Tovb.								—
87.	*Protacanthoplites mirus* Tovb.								—
88.	*Protacanthoplites submirus* Tovb.								—
89.	*Protacanthoplites monilis* Tovb.								—
90.	*Protacanthoplites* aff. *monilis* Tovb.								—
91.	*Protacanthoplites multinodosus* Tovb.								—
92.	*Protacanthoplitts allanovi* Tovb.								—
93.	*Protacanthoplites* aff. *abichi* Anth.								—
94.	*Protacanthoplites bigoti incivilis* Glasun.								—
95.	*Protacanthoplites rectangularis* Kas.								—
96.	*Protacanthoplites quadratus* Kas.								—
97.	*Protacanthoplites* aff. *bigoureti* Seun.								—
98.	*Protacanthoplites* aff. *planidorsatus* Kas.								—
99.	*Protacanthoplites bogdanovae* Tovb.								—
100.	*Protacanthoplites abichi* Anth.								→
101.	*Protacanthoplites* aff. *bigoti* Seun								→

was previously recognized based on its distribution (especially abundant in the upper part of the zone). However, this species was always accompanied by representatives of *Parahoplites,* so the lower boundary of the *A. aschiltaensis* Zone is very indistinct. It is also important that the species *A. aschiltaensis* has also been recorded in the higher (Clansayesian) beds. In Dagestan, this species is found throughout the entire section of the zone. There, the assemblage also contains *C. tobleri* continuing from the *E. subnodosocostatum* Zone, which in France and Georgia is used as the index of the Gargasian upper zone. On the whole, the assemblage of this zone in the central part of the northern Caucasus and in Dagestan, except for the geographically widespread representatives of phylloceratids, tetragonitids, and desmoceratids, is endemic to the Caucasus, but despite that, the range of this zone, most likely correlates with the range of the English *P. nutfieldiensis* Zone and German *P. nutfieldiensis* + *P. melchioris* Zone. The species compositions of *Prahoplites* in regions under consideration are different, which can be explained by their different paleogeographical affinities. The similarity of the ranges of the Caucasian and German zones is also supported by the presence of the Caucasian species *A. aschiltaensis* in Germany.

In the western regions of the northern Caucasus, the ammonite assemblage of the *Parahoplites melchioris* Zone is almost identical to the assemblage of the central and eastern regions of the Caucasus. Egoian (1989) considers that the range of the zone coincides with that of the biozone of the genus *Parahoplites,* but notes that this zone still contains *Epicheloniceras* (except for the index species *Ep. subnodosocostatun* and *Ep. tschernyschewi*).

The rich and diverse assemblage of the *P. melchioris* Zone of **Turkmenistan** is almost identical to that of the Caucasus. As in the Caucasus, the assemblage is dominated by *Parahoplites* and *Colombiceras.* As in the lower Zone of the Middle Aptian, the assemblage contains species of *Aconeceras,* including, in our opinion, *A. nisus*, which is Middle Aptian in Transcaspia and in the Caucasus. The characteristic Middle Aptian species in this region include representatives of *Caspianites* and *Pseudoaustraliceras.* The Transcaspian sections are characterized by the presence of the genus *Protacanthohoplites* recognized based on the Turkmenistan material and represented by several species (*P. monilis, P. mirus, P. submirus, P. multinodosus, P. allanovi*) and several species, previously assigned to *Acanthohoplites* or *Colombiceras* (*A. abichi,*[11] *A. bigoti,* and *A. rectangularis*). In some Kopet Dagh sections, species of this genus are mostly found in the upper part of the zone, where *Parahoplites* gradually disappears. Tovbina (1982) suggested that this part of the zone should be recognized as the *mirus* Subzone (based on the most frequent species).

The correlation of the Turkmenistan *melchioris* Zone and the French *tobleri* Zone as interpreted by Dauphin (2002) is quite interesting. According to Dauphin, the lower boundary of the *tobleri* Zone is drawn based on the first appearance of the ammonite genera *Egoianiceras, Jauberticeras, Colombiceras,* and, most importantly, *Acanthohoplites* gr. *aschiltaensis. A. aschiltaensis* in the sections of the Caucasus and Turkmenistan is found beginning from the *melchioris* Zone (its upper horizons). Hence, the lower boundary of the French *C. tobleri* Zone placed in the middle of the Turkemenistan *E. subnodosocostatum* Zone (Dauphin, 2002, p. 118, text-fig. 55) is unjustifiably lowered compared to the lower boundary of the *P. melchioris* Zone in the Caucasus and Turkmenistan. The barren interval assigned by Dauphin to the *C. tobleri* Zone (its upper part) can correspond to the part of the Turkmenistan *P. melchioris* Zone which contains species of the genus *Protacanthoplites,* relatively rarely recorded in the *C. tobleri* Zone of Georgia. This suggests that the upper limits of the *C. tobleri* Zone of France and *P. melchioris* Zone of Turkmenistan are synchronous.

In the **Mangyshlak** Peninsula, the *Parahoplites melchioris* Zone constitutes a part of the "septarian clay" series. As mentioned above, the lower boundary of the zone cannot be precisely positioned there. Ammonites of the genus *Parahoplites* entering above one of the phosphoritic beds in the clay series mark the presence of the zone. Saveliev and Vasilenko (1963) recorded there *Parahoplites melchioris* Anth., *P. multicostatus* Sinz., *P. subcampischei* Sinz., *P. schmidti* Jac., *P. maximus* Sinz., and *Acanthohoplites* sp. A later review of the Cretaceous stratigraphy (Luppov et al., 1986) also contains *Colombiceras tobleri* Jac. et Tobl. The species assemblage of the genus *Parahoplites* in this region is almost identical to those of the Caucasus and Turkmenistan.

The zonal subdivision and correlation of the beds of the Middle (or the lower part of the Upper) Aptian is shown in Table 19.

Some countries of the world have Middle Aptian sections with ammonite associations differing numerically and taxonomically. In some of them, the Middle Aptian beds are subdivided into "Beds with fauna" or zones.

Iran. This region is interesting in the fact that the northern part of the Kopet Dagh Range in Turkmenistan is only a fragment of a larger mountainous region, which is mostly located in the northeast of Iran. Therefore, the assemblages of the Middle Aptian ammonites are very similar in Turkmenistan and Iran. In a paper on parahoplitids of the central and northeastern Iran, Seyed-Emami (1980) redescribed the zonal species *Parahoplites melchioris* Anth. from the Baqer-Abad section of central Iran and noted the presence in the northeastern Iran (Kopet Dagh) of the ammonites *Parahoplites* sp., *P. grosseri, P. melchioris,* and *Colom-*

[11] Contrary to the opinion of S.Z. Tovbina, I.A. Mikhailova assigns the above species to *Acanthohoplites*.

Table 19. Zonal subdivision and correlation of Middle and Upper Aptian deposits in the main areas of their occurrence

Substage	Tethyan ammonite standard (*Report*..., 2014) Zone	Tethyan ammonite standard Subzone	Substage	Stratotype of the Gargasian (SE France) Dutour, 2005 Zone	Subzone	Horizon	France (Dauphin, 2002)	Substage	Northern Caucasus (Drushchits et al., 1986)	Turkmenistan (Bogdanova, Tovbina, 1994)	Georgia (Kotetishvili, 1986; *Atlas* ..., 2005)	Substage	South England (Casey, 1961; Casey et al., 1998) Zone	Subzone	Germany (Kemper, 1995)
Upper	*Acanthohoplites nolani*		Clansayesian	*Acanthohoplites nolani Zone*	*Diadochoceras nodoscostatum*		*Nolani* Zone	Upper	*Acanthohoplites nolani – Diadochoceras nodosocostatum* Zone	*Acanthohoplites prodromus* Zone		Upper	*Hypacanthoplites jacobi*	*Acanthohopltes nolani* (lower)	*Acanthohoplites nolani* "Zone"
	Parahoplites melchioris Zone		Gargasian	*Parahoplites melchioris* Zone			silent interval	Middle	*Parahoplites melchioris* Zone	*Parahoplites melchioris* Zone; *Protacanthoplites monile* Subzone	*Colombiceras tobleri* Zone		*Parahoplites nutfieldiensis*	*Parahoplites cunningtoni*	*Parahoplites nutfieldiensis* + *Parahoplites melchioris* "Zone"
							Tobleri Zone							*Tropaeum subarcticum*	
	Epicheloniceras martini	*E. buxtorfi*		*Epicheloniceras martini*	*E. buxtorfi*	*Caucasica* Horizon	*Crassicostatum* Zone		*Cheloniceras subnodosocostatum – Colombiceras crassicostaum* Zone	*Epicheloniceras subnodosocostatum* Zone	*Epicheloniceras subnodosocostatum* Zone		*Epicheloniceras martinioides*	*E. buxtorfi*	*Cheloniceras buxtorfi* "Zone"
		E. gracile			*E. gracile*	*Depressus* Horizon								*E. gracile*	*Cheloniceras laticostatum* "Zone"
		E. debile			*E. debile*	*Raspaili* Horizon								*E. debile*	*Tropaeum drewi* + *T. tenuinodosum* "Zone"
Lower	*Dufrenoyia furcata*	*D. dufrenoyi*		*Dufrenoyia furcata*	*D. dufrenoyi*	*Dufrenoyi* Horizon; *Praedufrenoyi* Horizon	*Furcata* Zone	Lower	*Dufrenoyia furcata* Zone		*Dufrenoyia furcata* Zone	Lower	*Tropaeum bowerbanki*	*Cheloniceras meyendorfi*	*Tropaeum bowerbanki* + *Dufrenoyia furcata* "Zone"
		D. furcata			*D. furcata*									*Dufrenoyia transitoria*	

biceras sp. (based on the umpublished paper by Afshar-Harb of 1979). Seyed-Emami, based on the studies by A.E. Glazunova on Kopet Dagh, N.P. Luppov on Transcaspia, V.V. Drushchits on the Caucasus, and E. Kemper in Germany, suggested that the *Parahoplites melchioris* Zone (=*Parahoplites nutfieldiensis* Zone) is present in the central and northeastern Iran.

In a paper on the Iranian part of the Kopet Dagh, Immel et al. (1997) redescribed the ammonites *Cheloniceras (Epicheloniceras) subnodosocostatum* Sinz., *Ch. (E.) waageni* Anth., *Ch. (E.)* cf. *aphanasievi* Egoian, *Ch. (E.)* cf. *tzankovi* Dimitrova, and *Parahoplites* sp. ex gr. *melchioris* Anth. All these taxa come from the local Sanganeh Formation, which corresponds to the Middle Aptian and its two zones, *Epicheloniceras subnodosocostatum* and *Parahoplites melchioris,* i.e., the zones which are present in the modern stratigraphic scheme of the Turmenistan Kopet Dagh. The above authors suggested that the Iranian Kopet Dagh occupied the intermediate biogeographical position between Transcaspia (Mangyshlak) and central Iran, as a northern (or boreal) part of the Tethyan Realm.

In a paper on the Iranian Kopet Dagh, Raisossadat (2006) listed Middle Aptian ammonites from the Sanganeh Formation and added records of the two *Parahoplites* forms (*Parahoplites* cf. *campichii* Pict. et Ren., *P. maximus* Sinz.) and *Colombiceras* sp. Raisossadat also considered parahoplitids of the Middle and Upper Aptian of the Iranian Kopet Dagh to be more closely similar to parahoplitids of Mangyshlak, Caucasus, and Germany than to parahoplitids of other regions of the globe, and the Aptian fauna of Kopet Dagh belongs to the Himalayan Province of the Mediterranean Realm.

Bulgaria. According to Stoykova (1983) and Nikolov (1987), the Middle Aptian is subdivided into the *Aconeceras nisum* (lower) and *Cheloniceras (Epicheloniceras) subnodosocostatum* zones. The Lower–Middle Aptian boundary is drawn based on the "...disappearance of the family Deshayesitidae... and appearance of... *Colombiceras, Gargasiceras, Cheloniceras (Epicheloniceras)* ..." (Stoykova, 1986, p. 18). The ammonite assemblage of the Middle Aptian is relatively small. For the *Aconeceras nisum* Zone, these authors listed *Aconeceras nisum, Cheloniceras (Epicheloniceras) tschernyschewi, Ch. (E.) debile, Ch. (E.) gracile martinoides, Ch. (E.) martini orientalis, Ch. (E.) claudi, Colombiceras subpeltoceroides, C. tobleri, C. subtobleri, Hamiticeras philadelphium,* and *Gargasiceras aptiense,* and also species of *Dufrenoyia, Immunitoceras, Eogaudryceras,* and *Toxoceratoides.* The *Cheloniceras (Epicheloniceras) subnodosocostatum* Zone is characterized by *Cheloniceras (Epicheloniceras) subnodosocostatum, Colombiceras tobleri discoidale, C. subpeltoceroides, C. subtobleri, C. sinzowi, Acanthohoplites laticostatus, A. subangulucostatus, Tropaeum subsimbirskense compressus, Tonohamites decurrens, T. koeneni, Pseudohaploceras liptoviense, Hamiticeras pilsbryi,* and *Parahoplites melchioris.* Stoykova correlated the Middle Aptian of Bulgaria with beds in southeastern France, northern Germany, southern England, and southern regions of the former USSR (most likely northern Caucasus and Transcaspia). In our opinion, it is difficult to correlate precisely the beds in these regions based on the Bulgarian ammonite assemblages and the ranges of zonal subdivisions are particularly difficult. The lower zone contained *Dufrenoyia,* which may suggest that the *nisum* Zone partly includes underlying beds with *Dufrenoyia.* The upper zone contains species of both the European *E. subnodosocostatum* Zone and higher *Parahoplites melchioris* Zone.

Romania. Records of Middle Aptian deposits are present in works by Avram (1970, 1974, 1980; Patrulius et al., 1982), who studied the geology and stratigraphy of the Cretaceous sedimentary rocks in the western and eastern Carpathians. Some local formations of different tectonic–facial zones, in particular, the d'Ecleja Formation of the Apuseni Mountains (western Romania) contain *Cheloniceras (Epicheloniceras)* aff. *martini* (d'Orb.), *Colombiceras* cf. *subpeltoceratoides* Sinz., *C. (C.) tobleri discoidale* Sinz., and *Ammonitoceras* ex gr. *lahuseni* Sinz. In the southeastern regions of the Eastern Carpathians, ammonites include *Colombiceras sinzowi* Kas., *C. subpeltoceratoides* Sinz., *C. (Egoianiceras)* cf. *angulatum* Egoian, *C. (Eg.) multicostatum* Avram, and *Parahoplites* sp. Avram considers that these assemblages indicate the presence of the upper part of the Gargasian Substage. No finer subdivisions of the Middle Aptian have been recognized.

Hungary. Publications of the end of the last century and beginning of this century contain no data on the ammonites of the Middle Aptian beds. In the sections in the Bakony Region and Geresce Mountains, the Jurassic beds (Tithonian limestones) are overlain by crinoidal limestones of the Tata Formation. Basal horizons of these limestones contain pockets of conglomerates with abundant fossils, including ammonite shells. Fülop (1976) studied the ammonite assemblage of this conglomerate and identified its Middle Aptian age (Late Aptian by Fülop), more precisely, the *Cheloniceras (Epicheloniceras) subnodosocostatum* Zone. Later, Szives (1999) studied sections of the Geresce Mountains (northeast of the city of Tata) and discovered in the ammonite association from the basal horizons of the formation species typical of the Lower, Middle, and Upper Aptian and Lower Albian. The age of this conglomerate, in her opinion (Szives, 1999, p. 407), cannot be younger than the Early Albian. Finally, in a recent monograph on the geology of Hungary, Szives (2007, p. 43), in the conclusion of the chapter on the Aptian and ammonites of this region wrote that, in the Bakony and Geresce mountains, the conglomerate and pockets at the base of the Tata Formation exposed in various sections contain "isochronous ammonite assemblages, mostly of the Middle and Late Aptian age".

Austria. In western Austria, in the zone of Helvetic nappes, the Garschella Formation of Aptian and Albian age contains the phosphorite-bearing Luitere beds, with ammonites suggesting the Aptian zones from *D. deshayesi* to *P. melchioris* (Föllmi, 1989). Föllmi recognized the *furcata, crassicostatus–subnodosocostatus,* and *melchioris* zones in the Luitere Beds above the *deshayesi* Zone. The Lower Aptian is terminated by the *furcata* Zone, but table 1 (Föllmi, 1989, p. 111) shows that *D. furcata* continues to the *crassicostatus–subnodosocostatus* Zone, whereas the typical Late Aptian species *Cheloniceras tschernyschewi* (generic affinity after Föllmi) occurs in the *furcata* Zone and continues to the *melchioris* Zone. In general, the *crassicostatus–subnodosocostatus* Zone (judging from Föllmi, 1989, table 1) contains *Colombiceras tobleri, C. caucasicum, Cheloniceras tschernyschewi, Ch. subnodosocostatum* (the only species limited to this particular zone), *Ch. buxtorfi,* and three *Puzosia* species of wide stratigraphic ranges. The *melchioris* Zone contains both of the above species of *Colombiceras* and (as mentioned above) *Cheloniceras tschernyschewi* and also *Ch. buxtorfi,* which continues into the higher beds of the *nolani–nodosocostatum* Zone. Only *Parahoplites melchioris* is restricted to this zone. Föllmi noted a large similarity of the Austrian ammonite assemblage with the eastern European one, emphasizing its cosmopolitan, Tethyan aspect. It is possible that the author borrowed the names of the Middle Aptian Caucasian ammonite zones in his zonal ammonite scheme.

Italy. According to Wiedmann and Dieni (1968), small exposures of the Upper Valanginian to Lower Albian found over a large area of the Tithonian–Berriasian rocks on Sardinia, to the northwest of Orosei contain Gargasian Beds with ammonites, including *Colombiceras tobleri* and *C. caucasicum tyrrehenicum* Wiedmann et Dieni. The same block contains beds with *D. deshayesi* (most likely below the Gargasian) and beds with acanthohoplites, including *A. nolani* (above Gargasian). The precise relationships of these beds remain unstudied.

Spain. The Middle Aptian (or Gargasian) beds are known in northeastern and southeastern Spain. Castro et al. (2001) studied sections and benthic foraminifers near the town of Alicante (southeastern Spain) and assigned them to the Middle Aptian, the upper part of the Almadich Formation and the lower part of the Seguili Formation, which replace each other laterally. Along with foraminifers, this part of the section contains ammonites, *Epicheloniceras tschernyschewi, Colombiceras tobleri,* and *Parahoplites* cf. *melchioris* (Castro et al., 2001, p. 150, text-fig. 3). Castro et al. correlated these beds with the *Parahoplites melchioris* Zone, although the occurrence of the former species is characteristic of a lower zone of the European Gargasian.

The study of the Aptian ammonites from sections in the Garraf Massif near Barcelona in northeastern Spain (Garcia et al., 2006–2007) showed that their species composition suggests the presence of all Aptian substages. The Middle Aptian beds are characterized by such species as *Parahoplites melchioris, Colombiceras crassicostatus, Epicheloniceras martini,* and *Aconeceras nisum.* The ammonites are extremely poorly preserved and, if specimens figured in plate 2 do not cast doubt on their affinity to the genera *Epicheloniceras* (pl. 2, fig. 5) and *Colombiceras* (pl. 2, fig. 7), the specimen of *"Parahoplites melchioris"* (pl. 2, figs. 8, 9) has a narrower cross section than is usually found in *Parahoplites* and several ribs different from those in *Parahoplites.* No biostratigraphic units were mentioned by Garcia et al.

Moreno-Bedmar et al. (2009) recognized in this region the *Dufrenoyia furcata* Zone with the upper *Cheloniceras meyendorffi* Subzone (Lower Aptian) and a zone with the ammonites *E. martini* (d'Orb.), *Colombiceras crassicostatum* (d'Orb.), and *Tonohamites aequicingulatus* (Koen.) (Middle Aptian, lower substage).

Africa. In Africa, fossil-bearing Middle Aptian beds are known in three countries: Morocco, Tunisia, and Madagascar.

Morocco. Brief data on the Gargasian beds of Morocco are contained in a report by Ambroggi and Breistroffer (1959) at the International Geological Congress in Mexico. The High Atlas section in southern Morocco contains the Gargasian beds composed of grayish blue marly limestones 25 m thick with the following ammonite assemblage: *Parahoplites* (?) gr. *marocanus* Roch, *Ch.* gr. *cornuelianum* d'Orb., *Cheloniceras* gr. *martini* d'Orb., *Ch.* gr. *buxtorfi* Jac. et Tobl., *Ch. volgense* Wassil., *Aconeceras (Sanmartinoceras)* gr. *trautscholdi* Sinz., *A. (=Adolphia)* gr. *nisus* d'Orb., *Acanthohoplites* gr. *bigoureti* Seun., *Colombiceras* gr. *discoidale* Sinz., *C.* gr. *gargasense* d'Orb., and others (Ambroggi and Breistroffer, 1959, p. 36). Almost all species in the above list are identified in open nomenclature, but, despite that, most of the species in classical working areas of Europe are characteristic of the Middle Aptian lower zone (as accepted in this work), although several species, e.g., *Ch. cornuelianum* and *A. (S.) trautscholdi* occur in the Lower Aptian beds.

The co-occurrence of the Lower and Middle Aptian species was explained by Bergner et al. (1982), who studied the Aptian and Albian beds in this region and recognized the two levels of condensed beds: Lower–Early Aptian and Upper–Late Aptian. The upper condensed bed contained *Ch. (Epicheloniceras) subnodosocostatum, Ch. (Ep.) buxtorfi, Ch. (Ep.) martinoides, Parahoplites nutfieldiensis, P. cunningtoni, P. depressus, Nolaniceras nolani,* and *Hypacanthoplites jacobi.* This assemblage contains species of all Upper Aptian zones of England. In some sections, this assemblage is supplemented by the Early Aptian species *Cheloniceras (Ch.) cornuelianum,* which is explained by the merging of the lower and upper condensed beds in some sections of the High Atlas (Bergner et al., 1982, p. 105).

Tunisia. Lehmann et al. (2009) described a section of Aptian deposits of the northern part of central Tunisia. The Aptian Stage is accepted as composed of two substages. The Upper Aptian includes the upper part of the Hamada Formation and the Serdj Formation. The latter contained *Parahoplites laticostatus* Sinz., *P.* cf. *nutfieldiensis* J. Sow., Cheloniceratidae indet. (in the lower part), and *Parahoplites maximus* Sinz., *Riedelites* sp. (in the upper part). Those authors did not recognize any ammonite zones. The species composition of ammonites from the Serdj Formation suggests that the formation could be dated as the *Parahoplites melchioris* Zone. The authors of the above paper noted that the taxonomic composition of ammonites from the Aptian of Tunisia is similar to that of the Aptian beds in the western and central Tethyan Realm, while the presence in the assemblage of the genus *Riedelites* suggests similarity to the Aptian of its Caribbean Province.

Madagascar. Information on the Aptian beds of Madagascar can be found in several papers by Collignon. In an early study (Collignon, 1937) on the Aptian pyritized ammonites of Antanatanamirafi, two *Parahoplites* species, *P.* aff. *grossouvrei* Jac. and *P. hourcqi* sp. nov. were indicated. However, later, *Parahoplites* species have not been included in the ammonite lists.

In a report at the International Geological Congress in Mexico in 1956 (Bessairie and Collignon, 1959), the Aptian beds of Madagascar were subdivided into three ammonite zones (Bessairie and Collignon, 1959, table 3): (most likely from bottom to top), the *Tropaeum jacki* Zone (with *Acanthoplites* cf. *bigoureti* Seun., *A.* cf. *feraudi* d'Orb. *Australiceras hirtzi* Coll.), *Aconeceras nisus* and *Eotetragonites duvali* Zone (with *Salfeldiella guettardi* Rasp., *Phyllopachyceras baborense* Coq., *Aconeceras nisoides* Saras., *Valdedorsella getulina* Perv., *V. haurcqi* Coll., *Melchiorites melchioris* Tietze, *Phylloceras haurcqi* Coll.), *Acanthoplites* cf. *subpeltoceroides,* and *A. nolani* Zone (ammonites: *Acanthoplites* cf. *bergeroni* Seun., *A. seminodosum* Sinz., *Cheloniceras subnodosocostatum* Sinz., *Hypacanthoplites malgachensis* Breistr., *H. besairiei* Breistr.). We are hesitant about the above stratigraphic succession of zones, because the ammonites listed are arranged in somewhat different succession compared to that of Europe, the Caucasus, and Asia. For example, the lower (?) *Tropaeum jacki* Zone was correlated in that paper almost with the Clansayesian, whereas the *Acanthoplites* cf. *subpeltoceroides* and *A. nolani* Zone, containing the Clansayesian genus *Hypacanthoplites,* is correlated by Bessairie and Colligno with the Gargasian.

Three years later, Collignon (1962) in an atlas on the ammonites of Republic of Madagascar (Malgache) recognized two zones in the lower half of the Upper Aptian, corresponding to the Gargasian: the lower, *Aconeceras nisus* + *Melchiorites melchioris,* and the upper, *Epicheloniceras tschernyschewi*. The species composition of ammonites from the lower Zone most likely corresponds to the *Dufrenoyia furcata* Zone (lower Gargasian of France). This zone contains mostly representatives of phylloceratids, tetragonitids, and desmoceratids. This zone also contains *Cheloniceras cornuelianum,* which in most regions is characteristic of the Lower Aptian and accompanies representatives of *Dufrenoyia*. The *Epicheloniceras tschernyschewi* Zone is characterized by *E. tschernyschewi* Sinz., *E. quadrituberculatum* Collign., *E. (Paracheloniceras) wrighti* Collign., and infrequent *Tropeaum.* This part of the Aptian could be correlated with the *Epicheloniceras tschernyschewi* Zone of the more northern regions. Collignon (1966) recognized the subgenus *Paracheloniceras* as a separate genus and described in addition to *P. wrighti* from the Upper Aptian Ambanjabe and Bemorary localities two more species, *P. guenoti* and *P. rerati,* indicating that all these species come from the *Aconeceras nisus* + *Melchiorites melchioris* Zone.

United States. Several studies published in the 20th century recorded the presence of the Aptian, including the Upper Aptian and, in particular, Gargasian ammonite assemblages in California (Khiami and Murphy, 1988), California and Oregon (Anderson, 1938), New Mexico, Texas, Arkansas, and Louisiana (Scott, 1939; Young, 1974). Anderson gave descriptions of several new species of *Parahoplites* and *Acanthohoplites* from the middle part of the Horsetown Group, in which he recognized the Gargasian part of the Aptian and beds with *nolani*, which he considered to be Albian. In a paper on ammonites of Columbia, Sharicadze et al. (2004) identified from the Middle Aptian (Gargasian) beds in that region *Epicheloniceras stoliczkanum* Gabb and *Parahoplites macfarlandi* Anders., cited by Anderson, thereby supporting Anderson's conclusion of the presence of the Gargasian beds in California. Khiami and Murphy (1988) studied the ontogeny of phylloceratins (partly from Anderson's collection), which in their opinion also come from the Middle Aptian.

Scott (1939) recognized two zones, *Dufrenoyia justina* (lower) and *Sonneratia trinitensis* (upper) in New Mexico, Texas, Arkansas, and Louisiana in the Triniti Group. The *Dufrenoyia justinae* Zone was correlated with the Pean Formation and the *Sonneratia trinitensis* Zone, with the Cuchillo Formation. Scott suggested a gap between these zones. He limited the Aptian to the *Dufrenoyia justinae* Zone. However, all ammonites he identified, including *Parahoplites, Acanthoplites, Hypacanthoplites, Cheloniceras,* and others came from the Cuchillo Formation. The same formation also yielded *Dufrenoyia.* It appears that *Parahoplites* and *Acanthohoplites* should be indicative of higher horizons of the Aptian than the *Dufrenoyia justinae* Zone, i.e., the Gargasian part of the Aptian and Clansayesian part of the Albian. Indeed, Young (1974) described many ammonites of the genus *Hypacanthoplites* from Texas. However, considerably later, Robert et al. (2002) and Robert and Bulot (2005) reidentified a well-preserved *Parahoplites* from the Lower Cretaceous of Peru published by Scott (including *P. umbilicostatus*) and representatives of the genus *Hypacanthoplites* from Yang's paper and assigned to the genus *Neodeshayesites* Casey, 1964. This genus is currently restricted to the Lower Albian (approximately the level of the *Leymeriella tardefurcata* Zone). Thus, the Aptian of the southern United States (except for California) should be restricted to the *Dufrenoyia justinae* Zone, which can be assigned either to the Lower Aptian, the view we share, or, according to the current interpretation of French stratigraphers, to the lowermost Upper Aptian. In this case, Scott was likely to have been right by suggesting a gap above the *Dufrenoyia justinae* Zone, since the Cuchillo Formation is likely to be Albian because of the presence of *Neodeshayesites.*

Mexico. Humphrey (1949) wrote a large work on the Aptian ammonites of central Mexico. The Aptian beds in Mexico were then subdivided into two parts, upper of which corresponded to the Gargasian (Clansayesian horizon was included in the Albian). In the local scale, the Gargasian Substage corresponded to the La Peña Formation, from which all the ammonites described by Humphrey were obtained. These included species of *Dufrenoyia, Hypacanthoplites,* and *Parahoplites* (*P. mexicanus* Humphrey, *P.* cf. *multicostatus* Sinzow), *Acanthoplites* (*A. potreritensis* Humphrey, *A. adkinsi* Humphrey, *A. sandidgei* Humphrey), *Burckhardtites* (*B. nazasensis* Burckh., *B. kellumi* Humphrey, *B. gregoriensis* Humphrey, *B. imlayi* Humphrey, *B. palumbes* Humphrey, and *B. ehlersi* Humphrey), *Cheloniceras* (*Ch.* cf. *cornuelianum* d'Orb. and five local species), *Megatyloceras, Colombiceras* (*C. spathi* Humphrey), *Ammonitoceras,* and others. Two ammonite-based zones were recognized, *martini* and *subnodosocostatum*. Although the ammonite distribution in the sections was not cited in the paper, it is possible to suggest that *Dufrenoyia, Burckhardtites,* and *Cheloniceras* come from the *martini* Zone, which corresponds to the European *Dufrenoyia furcata* Zone. The *subnodosocostatum* Zone, which was most likely recognized based on the genera *Parahoplites* and *Colombiceras,* and possibly contained *Acanthohoplites,* should partly correspond to the zones of the European standard, *subnodosocostatum* and *melchioris.*

Moreno-Bedmar et al. (2013) described a section of the boundary beds in northern Mexico (Durango State). Two ammonite zones were recognized in the upper part of the Lower Aptian, *Dufrenoyia justinae* and *Gargasiceras? adkinsi;* the lower zone of the Upper Cretaceous was designated *Caseyella aguilerae.* Since Moreno-Bedmar et al. identified *Epicheloniceras* in the *Dufrenoyia justinae* Zone, they selected a different marker for defining the Lower–Upper Aptian boundary, i.e., the entry of the ammonite genus *Caseyella.* However, it should be said that the boundary between the Aptian substages coincides with its position in sections of the Tethyan Realm. The ammonite assemblage of the *Dufrenoyia justinae* Zone, except for some genera, is very similar to that of the *Dufrenoyia furcata* Zone of Turkmenistan (Tuarkyr), containing, apart from *Dufrenoyia,* representatives of *Colombiceras, Gargasiceras,* and *Burckhardtites.* Although Moreno-Bedmar et al. (2013) consider that, because of the endemic nature of the generic assemblage of Mexico, the zonal scheme of the Cretaceous interval does not correspond to the Tethyan scheme, the ranges of deposits with *Dufrenoyia* of Central Asia and Mexico could be the same.

South America. Beds with the Middle Aptian ammonites are known in Colombia, Venezuela, and Argentina. They are possibly present in Peru and Chile (see below). However, their paleontological substantiation is different in different countries.

Colombia. Riedel (1938) described many ammonites from the Upper Aptian of the Eastern Cordilleras. These include species of the genera *Deshayesites* (*D. stutzeri* Riedel, *D. stutzeri contracta* Riedel, *D. rotundus* Riedel, *D. columbianus* Riedel), *Cheloniceras* (*Ch. martini occidentalis* Jac., *Ch. subnodosocostatum* Sinz.), *Parahoplites* (*P. inconstans* n. sp., *P. obliqus* n. sp.), *Colombiceras* (*C. tobleri* Jac., *C. tobleri discoidalis* Sinz.), five species *Acanthohoplites,* including two known species: *A. bigoureti* Seun. and *A.* aff. *abichi* Anth. The stratigraphic review is absent in that work, but there is a list of species with indication of their stratigraphic position. Some European and Caucasian species indeed support the presence of the Upper Aptian (if the Aptian bifid) and the Lower Albian species (if the Clansayesian is assigned to the Albian). The presence in the Upper Aptian beds of *"Dehayesites"* represented solely by new species and, as shown below, belonging a different genus.

Considerably later, Etayo-Serna (1979), based on the study of the Villa de Leiva and Apulo sections in Eastern Colombia, developed a stratigraphic scheme, in which the Aptian combined two zones, (1) *Dufrenoyia sanctorum–Stoyanowiceras treffryanus* and (2) *Parahoplites (?) hibachi–Acanthohoplites (?) leptoceratiforme.* The scheme proposed by Etayo-Serna did not intend to be used as an archetype scheme and can be later modified (Etayo-Serna, 1979, p. 13). Etayo-Serna considered these zones as "assemblage" zones and considered the assemblage *Dufrenoyia sanctorum–Stoyanowiceras treffryanus* Zone as the Lower Aptian. That zone contained *Dufrenoyia, Cheloniceras (Epicheloniceras), Vectisites, Riedelites, Gargasiceras, Aconeceras, Colombiceras,* and other genera, which in Europe and Asia characterize the *Dufrenoyia furcata* Zone (in most regions, this zone terminates the Lower Aptian) and lower Middle–Upper Aptian *Epiche-*

loniceras subnodosocostatum (=*Colombiceras crassicostatum–Epicheloniceras subnodosocostatum*) Zone. The younger *Stoyanowiceras treffryanus* and *Parahoplites (?) hibachi* complex Zone contains the ammonite genera *Parahoplites, Acanthohoplites, Riedelites, Cortesiceras,* and *Melchiorites.* Almost all species of these genera are endemic; therefore, the correlation with the European Aptian zones is complicated. Based on the presence of the genus *Parahoplites,* the Colombian Zone can be correlated with *Melchioris* or *Nutfieldiensis*, but, *Acanthohoplites* in other regions characterize both the *Melchioris* Zone and the younger *Nolani* Zone. The *Deshayesites* species, which were determined by Riedel in the Upper Aptian beds, were shown to belong to the genus *Neodeshayesites* (Casey, 1964), distribution of which is presently limited to the Lower Albian.

In one of the most recent papers on the Colombian ammonites, Sharikadze et al. (2004) identified many (including Aptian) taxa, many of which are in common with Europe: *Epicheloniceras tschernischewi, E. buxtorfi, E. debile, E. pusillum, E. subnodosocostatum, Parahoplites maximus, P.* aff. *nutfieldiensis, Gargasiceras aptiensis, C. recticostatum, Colombiceras tobleri, C. subpeltoceroides, C. caucasicum, C.* aff. *crassicostatum, Protacanthoplites abichi.* The above ammonite species apparently suggest the presence of the equivalents of the *Epicheloniceras subnodosocostatum* (=*Colombiceras crassicostatum–Epicheloniceras subnodosocostatum*) and *Parahoplites melchioris* zones in the Aptian of Colombia.

Venezuela. Collet (1922) published a short note on the presence in Venezuela of an Aptian fauna of the Mediterranean–Alpine type. The ammonite list, in the opinion of its author, contained both Bedoulian and Gargasian species. The latter included *Acanthoplites crassicostatus* d'Orb., *Uhligella zuercheri* Jac., and possibly *Douvilleiceras martini occidentalis* Jac.

Rod and Maync (1954) revised the Lower Cretaceous stratigraphy of eastern Venezuela. These authors listed *Uhligella, Colombiceras crassicostatum, Pseudosaynella, Dufrenoyia, Deshayesites, Burckhardtites,* and *Cheloniceras martini* var. *occidentalis* from the middle and upper parts of the Borracha Formation. Based on these ammonites, they recognized the Lower and Upper Aptian, and indicated the presence of the Gargasian part in the Upper Aptian. However, we are inclined to think that these are beds corresponding to the *Dufrenoyia furcata* Zone, which in the modern French scheme is placed in the Gargasian. The most characteristic Gargasian species are missing from this list, whereas *Colombiceras* can also occur in the beds with *Dufrenoyia*.

Later, many data on the Lower Cretaceous stratigraphy and fossils of Venezuela were published by O. Renz. He described five species of the genus *Mathoceras* (family Deshayesitidae) from the Garsia Formation (*Martinioides* Zone of the Upper Aptian). They were found in association with the ammonites *Aconeceras nisus, Sanmartinoceras haugi, Zuercherella zuercheri, Colombiceras* sp., *Gargasiceras* sp., *Dufrenoyia justinae,* and others. Renz believed that the Upper Aptian contained the *subnodosocostatum* Zone, which was identified there in 1972 (Guillaume et al., 1972). In our opinion, the *Martinioides* Zone of Venezuela is the level of the beds with *Dufrenoyia,* whereas the ammonites characteristic of the *subnodosocostatum* Zone are absent in this list.

The presence of the Gargasian was substantiated by Renz in his monograph on Cretaceous ammonites of Venezuela (Renz, 1982). In eastern Venezuela, ammonites were collected from the Garsia Formation and the lower part of the Ville Grande Formation. The author lists the following species from the *Martinioides* Zone: *Aconeceras nisus, Sanmartinoceras haugi, Zuercherella zuercheri, Valdedorsella getulina, Dufrenoyia dufrenoyi, D. coddaciana, Melchiorites melchioris, Burckhardtites nazasensis, Mathoceras venezolanum, M. sucre, M. caribense,* and *M. laevi.* The stratigraphically higher assemblage includes *Cheloniceras* aff. *debile, Ch. buxtorfi, Gargasiceras* cf. *recticostatus, G. acuticostatus, G. aptiense, Colombiceras* aff. *caucasicum,* and C. *tyrrhenicum.* The association of the species of the *Martinioides* Zone of Venezuela is characteristic of the Lower Aptian, if judged by the Caucasus–Asian scheme, whereas the second group of species indicated the presence in eastern Venezuela of deposits of the Gargasian part of the Upper Aptian (*subnodosocostatum* Zone). In western Venezuela, the Tibú and Cogollo formations contain representatives of the Lower Aptian genera *Dufrenoyia* and *Roloboceras,* and the Upper Aptian Machiques Formation, according to Renz, includes Riedel's species *columbianus, nodosus, stutzer,* and *rotundus,* which he assigned to *Deshayesites,* although all of these species were assigned by Casey (1964) to his new genus *Neodeshayesites.* This genus, as noted above and will be shown below, was restricted to the Early Albian. Thus, the presence of the Gargasian portion of the Aptian is not confirmed in western Venezuela.

Peru. At the beginning of the last century, the following ammonites were described from the Cretaceous of northern Peru (Sommermeier, 1910): *Parahoplites* cf. *treffrianus* (Karst.), *P.* cf. *uhligi* Anth., *P.* cf. *aschiltaensis* Anth., *P.* n. f. ex aff. *schrammeni* Jac., *P.* cf. *steinmanni* Jac. These ammonites, both the genus *Parahoplites* and some species, should have indicated the presence of the Middle Aptian in Peru. However, all species were identified in open nomenclature and were not mentioned in later publications, and also Sommermeier did not give any age determinations based on these ammonites, and only indicated age according to the original authors of the species listed, for instance, for *P. aschiltaensis* he noted that, according to Anthula, this was an Aptian species.

Benavides-Cáceres (1956) gave a correlation table for the Cretaceous of Peru, in which the entire Aptian corresponds to the Goyllarisquisga Formation, which had no ammonites, according to that author. The overlying Inca Formation contains ammonites identified as *Parahoplites: P. nicholsoni* sp. nov., *P. quilla* sp. nov., and *P. inti* sp. nov. These were dated as Albian.

Considerably later, Robert and Bulot (2005) revised ammonites from the Inca Formation, which had been identified as *Parahoplites*. As a result of that revision, all *Parahoplites* species were reassigned to *Neodeshayesites* Casey, 1964, which geochronological range is controlled by the co-occurring Early Albian *Leymeriella* and *Douvilleiceras* in all regions of their distribution. Robert et al. (2002) proposed a biostratigraphic scheme of the Lower Albian, in which the lower zone of this substage was referred to as the *Neodeshayesites nicholsoni*. Thus, there is no evidence of the presence of the Middle Aptian ammonites in Peru.

Argentina. The Aptian deposits in Argentina are recorded in southern Patagonia, near the Chilean border. Riccardi and Rolleri (1980) recognized two subdivisions, Barremian–Aptian and Aptian. The following ammonites were recorded from the Aptian: *Aioloceras argentinum* (Bonarelli), *Silesites desmoceratoides* (Stoll.), *Pseudosaynella bonarellii* Leanza, *Ancyloceras imlayi* (Leanza), *Sanmartinoceras patagoniensis* Bonarelli, and *Lithancylus guanacoensis* Leanza.

Subsequently, Aguirre-Urreta (1985, 1986) and Aguirre-Urreta and Riccardi (1989) from the same deposits in the Rio Mayer Formation listed the following species: *Australiceras (A.) ramososeptatum* (Anth.), *A. (A.) cardielensis* Aguirre Urreta, *A. (A.) hallei* Aguirre Urreta, *Tropaeum (T.) inflatum* Aguirre Urreta, *T. (Australotropaeum) magnum* Aguirre Urreta, *Peltocrioceras deeckei* (Favre), *Helicancylus patagonicum* (Stoll.), *H. bonarrellii* (Leanza), *Toxoceratoides nagerai* (Leanza), *T.* cf. *biplex* (Koen.), *T. haughtoni* Klinger and Kennedy, and *Tonohamites aequicingulatus* (Koen.). Aguirre-Urreta (1985), based on the stratigraphic distribution of ammonites, recognized three ammonite associations: *Australiceras–Tropaeum, Peltocrioceras,* and *Ferruglioceras–Silesites.* The first association most likely corresponds to the Lower Aptian and two other, to the Upper Aptian. Aguirre-Urreta (1986) indicated that all species assemblages of the genera *Helicancylus, Toxoceratoides,* and *Tonohamites* can be correlated with assemblages of Western Europe and southeastern Africa. Aguirre-Urreta and Riccardi (1989) showed the stratigraphic position of the ammonites studied in the Upper Aptian sections and Ramos and Aguirre-Urreta (1994) recognized two biostratigraphic units (assemblage zones) for the Lower Aptian (*Australiceras–Tropaeum*) and Upper Aptian –(*Peltocrioceras deeckei.* The Upper Aptian list included *Helicancylus patagonicum, Lithancylus guanacoensis, Sanmartinoceras patagoniensis, Sinzovia piatnitzkyi, Ferruglioceras piatnitzkyi,* and *Ptychoceras* sp.

Medina and Riccardi (2005), based on the previous studies, recognized three zones and correlated them with the European ammonite scale: *Tropaeum magnum* (this zone is at the boundary of the Lower and Upper Aptian), *Australiceras (A.) hallei* (corresponds to the European *Acanthohoplites nolani* Zone) and *Peltocrioceras deeckei* (=*Hypacanthoplites jacobi* Zone).

Finally, in a recent paper by Aguirre-Urreta et al. (2007) on the Lower Cretaceous beds of two Patagonian sedimentary basins, Chañarcillo and Neuquen, proposed for the Aptian of the Chañarcillo Basin (in the second basin there are no marine deposits of Aptian age) two ammonite zones. The lower *Ancyloceras (Adouliceras)* sp. Zone (corresponds to the European Mediterranean *Deshayesites deshayesi* Zone) and the upper *Hypacanthoplites* sp. Zone (corresponds to the *Hypacanthoplites jacobi* Zone). The authors indicate that the ammonite assemblage of the Barremian–Early Albian in the sections of this basin is heterogenous and dominated by cosmopolitan taxa. However, the geological record of the Aptian contains many significant gaps, especially in the Middle Aptian (Aguirre-Urreta et al., 2007, p. 169). Thus, it remain uncertain whether the Middle Aptian (Gargasian) beds with ammonites are present in southern Patagonia and, if present, they remain undescribed.

Chile. A small note on the Aptian of the Atacama region in northern Chile (Perez et al., 1990) contains a description of *Parahoplites* gr. *nutfieldiensis* (J. Sow.), which if identified to species could have indicated the presence of the lower part of the Upper Aptian. However, in a later paper, Aguirre-Urreta et al. (2007) reidentified that ammonite and reassigned to the genus *Neodeshayesites* (Perez et al., 1990, text-fig. 9C), which is restricted to the Lower Albian.

China. The following ammonites have been described from China (South Tibet, vicinity of Gamba): *Parahoplites trautscholdi* Sim., Bač., Sor., *Colombiceras (C.) subpeltoceroides* Sinz., *Cheloniceras (Ch.)* aff. *buxtorfi* Jac., *Toxoceratoides* aff. *royerianum* d'Orb., *Tonohamites multituberculatus* Immel et Guoxiong (Immel and Guoxiong, 2002). All ammonites come from the Ganbadongshan Formation in the Gamba Group and can suggest the presence of the Gargasian part of the Aptian in this region of China. However, it should be noted that specimens of *Parahoplites* figured in the above paper in (pl. 4, figs. 9, 11, 12) more strongly resemble species of *Colombiceras,* rather than of *Parahoplites* in the strongly flattened ribs on the flanks and on the venter. However, this does not contradict the conclusion on the Gargasian age of the host rocks, as *Colombiceras* occurs throughout the Gargasian. However, none of these zones can be recognized in this part of the Aptian in China.

Japan. Obata and Matsukawa (2007) identified the presence of the Barremian–Aptian beds on Honshu Island (Group Choshi). The Lower Aptian, in the opinion of these authors, corresponds to the Inubouzaki Formation and the Upper Aptian corresponds to the Toriakeura Formation, containing *Lytoceras* sp., *Pseudohaploceras* sp., *Neosilesites hagiwarai*

Obata et Matsukawa, *Cheloniceras* cf. *proteus* Casey, *Epicheloniceras* sp., and *Dufrenoyia* sp. Obata and Matsukawa correlate these beds with the lower zone of the Upper Aptian of England, *Epicheloniceras martinioides*. This conclusion contradicts the occurrence of the *Dufrenoyia* in the same bed with *Epicheloniceras* (specimen of *Dufrenoyia* (Obata and Matsukawa, 2007, pl. 5, fig. N) represents a poorly preserved ammonite, which is difficult to identify to genus). In addition, the ammonite *Cheloniceras* cf. *proteus* (Obata and Matsukawa, 2007, pl. 15, figs. A–D) is a typical representative of the Early Aptian *Cheloniceras*. Thus, the Lower Aptian should apparently include not only the Inubouzaki Formation underlying the Toriakeura Formation, but also a portion of the latter (Obata and Matsukawa, 2007, text-fig. 2).

Australia. In the first third of the 20th century, Whitehouse (1926, 1927) described several ammonites from the Rolling Downs Formation of the Roma Group of Eastern Australia. The ammonite association is dominated by heteromorphic ammonites of the genera *Tropaeum, Australiceras,* and *Toxoceratoides;* it also includes several haploceratids and desmoceratids. The stratigraphic distribution of the species described allows the recognition in the Roma Group of three beds with ammonites: Lower –(*Australiceras-Toxoceratoides*), Middle –(*Tropaeum–Aconeceras*), and Upper—(*Sanmartinoceras–Aioloceras*). Whitehouse correlated the lower beds with the Upper Bedoulian; the middle, with the Lower Gargasian; and the upper beds, with the Upper Gargasian. Considerably later, Day (1974) listed the following ammonites from the same regions of Australia: *Tropaeum* cf. *australe* (Moore), *T. imperator* Howchin et Whitehouse, *T. undatum* Whitehouse, *T. leptum* (Etheridge), *Australiceras jacki* (Etheridge), *A. irregulare* (Tenison Woods), *A.* cf. *lamprum* (Etheridge), *Toxoceratoides* sp., *Aconeceras* sp., *Sanmartinoceras* sp., and *Aioloceras* cf. *jonesi* (Gregory, Smith). Day conducted a detailed comparison of all local species of heteromorphic *Tropaeum* and *Australiceras* with species found in North and South America, Africa, and Europe [England, France, Russia (Caucasus)] and concluded that the Australian assemblage cannot be older than the later phases of the Early Aptian and younger than the Late Aptian, i.e., its range (according to the English scheme) is from the *bowerbanki* phase to the *nutfieldiensis* phase. However, in his opinion, a precise correlation with the European zones was impossible.

6. PALEONTOLOGY

We have revised the following Middle Aptian ammonite genera and species: *Parahoplites* Anthula, 1899 (*P. melchioris* Anthula, 1899; *P. campichei* (Pictet et Renevier, 1855); *P. sjogreni* Anthula, 1899; *P. grossouvrei* Jacob, 1905; *P. schmidti* Jacob, 1906; *P. multicostatus* Sinzow, 1907; *P. transitans* Sinzow, 1907; *P. maximus* Sinzow, 1907; *P. sub-campichei* Sinzow, 1907; *P. artschmanensis* Glasunova, 1953; *P. debilicostatus* I. Michailova, 1958; *P. irregularis* Casey, 1965; *P. luppovi* Tovbina, 1982]; *Acanthohoplites* Sinzow, 1907 [*A. aschiltaensis* (Anthula, 1899); *A. laticostatus* Sinzow, 1907]; *Colombiceras* Spath, 1923 [*C. tobleri* (Jacob, 1906); *C. discoidale* (Sinzow, 1907); *C. sinzowi* (Kasansky, 1914); *C. caucasicum* (Luppov, 1949); *C. bogdanovae* Tovbina, 1982; *C. korotkovi* sp. nov.]; *Epicheloniceras* Casey, 1954 [*E. tscherntschewi* (Sinzow, 1906); *E. subnodosocostatum* (Sinzow, 1906); *E. pusillum* (Sinzow, 1906);*E. orientale* (Jacob, 1905); *E. buxtorfi* (Jacob, 1906), *E. stuckenbergi* (Kasansky, 1914), *E. intermedium* (Kasansky, 1914), *E. martinioides* Casey, 1961]; *Caspianites* Casey, 1961 [*C. wassiliewskyi* (Renngarten, 1926)]; *Luppovia* Bogdanova, Kakabadze et I. Michailova, 1978 [*L. dostshanensis* Bogdanova, Kakabadze et I. Michailova, 1978; *L. adjderensis* Bogdanova, Kakabadze et I. Michailova, 1978]; *Pseudoaustraliceras* Kakabadze, 1981[*P. pavlowi* (Wassiliewskyi, 1906)]; *Aconeceras* Hyatt, 1903) [*Aconeceras (Aconeceras) nisus*[12] (d'Orbigny, 1842); *A. (A.) haugi* (Sarasin, 1893); *Aconeceras (Sinzowia) aptianum* (Sarasin, 1893)]. To compare the evolution of the sutural outlines and shell morphogenesis, we redescribed in the family Douilleiceratidae: the Early Aptian *Cheloniceras* Hyatt, 1903 [*Ch. cornuelianum* d'Orbigny, 1841; *Ch. natarius* I. Michailova, 2010] and the Late Aptian genus *Eodouvilleiceras* Casey, 1961 [*E. clansayense* (Jacob, 1905); *E. badkhyzicum* (Urmanova, 1962); *E. trituberculatum* Sacharova, 1985].

6.1. Ammonoid Evolution

A detailed onto-phylogenetic study of the Middle Aptian ammonoids conducted for the major Aptian superfamilies Deshayesitoidea, Parahoplitoidea, and Douvilleiceratoidea has shown distinct differences between the superfamilies. For two superfamilies (Deshayesitoidea and Douvilleiceratoidea), it was established that they certainly descended from the heteromorphic Ancyloceratoidea (Mikhailova, 1983; Bogdanova and Mikhailova, 1999; Bogdanova and Mikhailova, 2004).

The superfamily Ancyloceratoidea existed in the Early Cretaceous and only members of the family Bochianitidae are known in the Late Jurassic (Fig. 24). The heteromorphic Turrilitoidea appeared somewhat later, at the Valanginian–Hauterivian boundary and reached their maximum generic and specific diversity in the Late Cretaceous (Figs. 25, 26).

The generic diversities of the superfamilies Ancyloceratoidea and Turrilitoidea are similar, as shown in the histogram (see Fig. 26), whereas the monomorphic descendants of the former superfamily are few (Mikhailova and Baraboshkin, 2009).

[12] See Casey (1961a, p. 123).

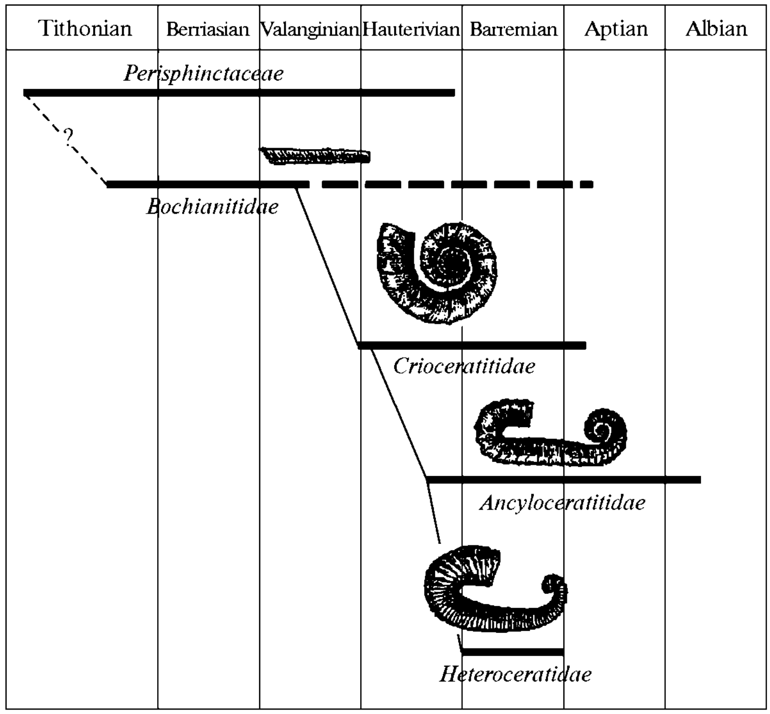


Fig. 24. Phylogenetic reconstruction of the superfamily Ancyloceratoidea (after Arkell et al., 1957, modified).

Wiedemann and Schindwolf in the 1960s proposed several different schemes of relationships of the large ammonite taxa of the Jurassic–Cretaceous. Wiedmann (1966) recognized, apart from the three suborders: Phylloceratina, Lytoceratina, and Ammonitina (Wiedmann, 1962), a new suborder Ancyloceratina (Fig. 27). He assigned to this suborder four superfamilies: heteromorphic Ancyloceratoidea (not separating Turrilitoidea) and their possible descendants Scaphytoidea, Deshayesitoidea, and Douvilleiceratoidea.

Other views are shown in a scheme proposed by Schindewolf (1968). The rank of Phylloceratina and Lytoceratina is raised to order and the Lytoceratida includes Ammonitina, Lytoceratina, Tetragonitina, and Ancyloceratina (Figs. 28, 29). Three superfamilies (Parahoplitoidea, Deshayesitoidea, and Douvilleiceratoidea) are descendants of Ancyloceratoidea. However, the superfamily Turrilitoidea is considered as a junior synonym of Ancyloceratoidea. Unfortunately, this is accepted in two large paleontological treatises (Arkell et al., 1957; Wright et al., 1996).

The above superfamilies have different ancestries: Ancyloceratoidea are descendants of ammonitids, whereas Turrilitoidea are descendants of lytoceratids, which was established based on detailed morphogenetic studies of the suture (Figs. 30, 31). N.V. Beznossov and one of us considered that the superfamily Turrilitoidea derived from lutoceratids, but is distinguished from the monomorphic lytoceratid ancestors (Fig. 32). We raised the rank of Turrilitoidea to suborder and consider the order Lytoceratida including two suborders, Lytoceratina and Turrilitina (Beznossov and Mikhailova, 1983, 1991).

The early shell morphogenesis in the representatives of the suborder Ancyloceratina is shown in Fig. 30. The superfamily Ancyloceratoidea has a varying shell shape, but the protoconch and the first whorl (embryonic shell) are uniform. The primary suture is five-lobed (VUU^1ID), but the fifth lobe soon disappears. This resulted from the heteromorphic shape of the Ancyloceratoidea acquiring in the postembryonic period a different cross section (circular, oval, etc.), which is reflected on the structure and fluting of the septum and disappearance of the fifth lobe.

The characters of the superfamily Ancyloceratoidea are distinctly traced in the heteromorphic genera *Caspianites* Casey and *Luppovia* Kakabadze, Bogdanova et I. Michailova. In these genera, the four-lobed primary suture typical of heteromorphs is absent. The primary suture observed in *Caspianites wassiliewskyi* (Renng.) is composed of five (!) lobes (Fig. 33), i.e., is not distinguished from that in Phylloceratida, monomorphic Lytoceratida, and the majority of monomorphic Ammonitida (see Fig. 33j). This outline is also observed in the third suture; the lobe (U^1) is divided by the seam. Later in ontogeny, this lobe disappears, while the sixth suture consists of four lobes. This outline remains until the 31st suture, which corresponds to the termination of the second perforated whorl, when the whorls come into contact again (see Fig. 33g). Almost immediately the wide umbilical lobe becomes trifid, and the saddles become bifid; at

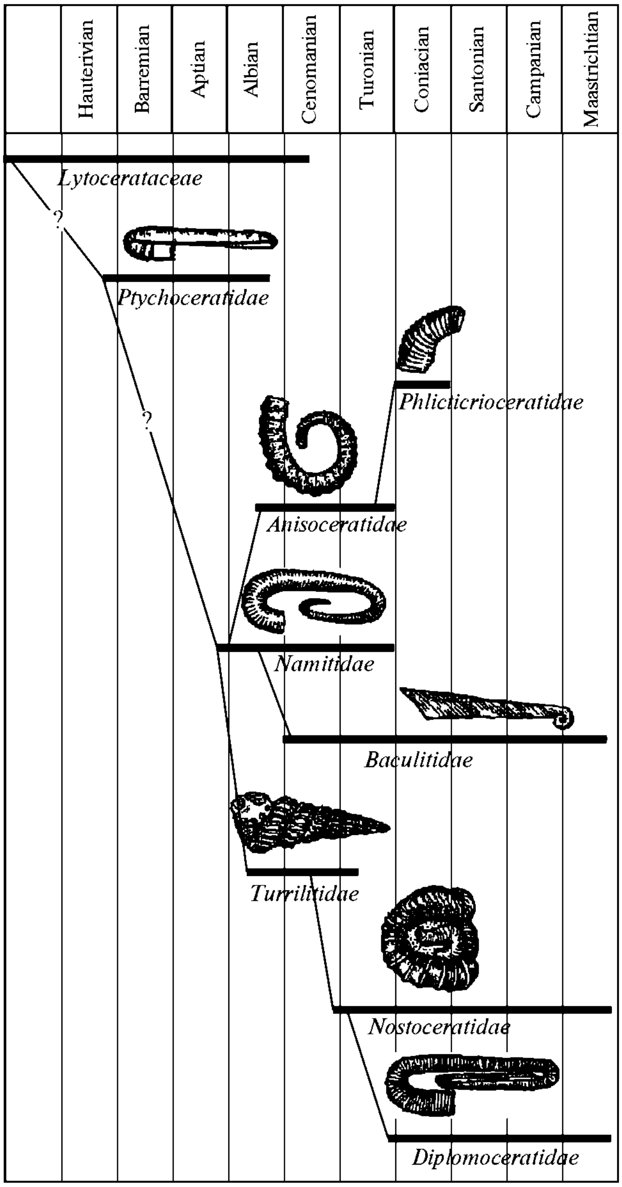


Fig. 25. Phylogenetic scheme of the superfamily Turrilitoidea (after Arkell et al., 1957, modified).

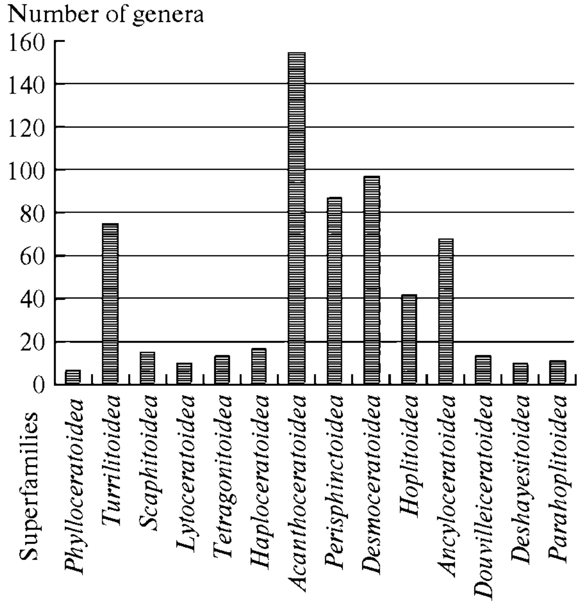


Fig. 26. Number of genera in the superfamilies of Cretaceous ammonoids (after Wright et al., 1996; Mikhailova and Baraboshkin, 2009, modified).

the same time, the dorsal lobe and inner lateras lobes become complicated. Digits on the lateral sides of the ventral lobe appear relatively late in ontogeny.

Five lobes in the primary suture are inherited from the monomorphic ancestors, whereas the reduction of the first umbilical lobe is connected with the change in the shell shape at the transition to the second perforated whorl, which is reflected in the change in the shape of the whorl cross section (see Figs. 33a–33i).

The identical morphogenesis of the suture is observed in *Luppovia dostshanensis* Bogdanova, Kakabadze et I. Michailova and *L. adjiderensis* Bogdanova, Kakabadze et I. Michailova (see species description): a bilobate prosuture, five-lobed primary suture (VUU^1ID), reduced first umbilical lobe, return to the four-lobed suture (VUID), and development of a trifid umbilical lobe.

The unstable five-lobed primary suture is inherited from the monomorphic superfamilies (Deshayesitoidea, Parahoplitoidea, and Douvilleiceratoidea). New elements in the superfamily Douvilleiceratoidea appear as a result of the subdivision of the umbilical (U) and inner lateral lobe (I), which is reflected in the formula: $VUU^1ID \rightarrow VUID \rightarrow VU_1U_2I_2I_1D$. The particularly graphic character is the subdivision of the branches of the umbilical lobe in adult Douvilleiceratoidea (Fig. 34). The superficially similar sutures of Deshayesitoidea and Parahoplitoidea are fundamentally different in the appearance of new elements in the first superfamily because of the division of the saddle I/D ($VUU^1ID \rightarrow VUID \rightarrow VU2^1D$), and in the second in the division of the saddle U/I ($VUU^1ID \rightarrow VUID \rightarrow VUU^1ID$).

Mikhailova (1976, pp. 157–158) has already explained her attitude to the orthochronic and heterochronic modes of the appearance of the suture. The same problem was discussed later in greater detail (Mikhailova, 1983): "Later some of the above statement were discussed by Tovbina (1963), Casey (1964) and confirmed by Schindewolf (1966), who studied *Dufrenoyia dufrenoyi* (Orb.) and *Prodeshayesites bodei* Koen." It appeared that the problem was solved and no new discussion was envisaged. However, Schindewolf, while accepting the four-lobed primary suture of Deshayesitidae and Parahoplitidae, surprisingly eliminated differences between them concerning the mode of appearance of new elements. He designated differently elements of the primary suture in Parahoplitidae

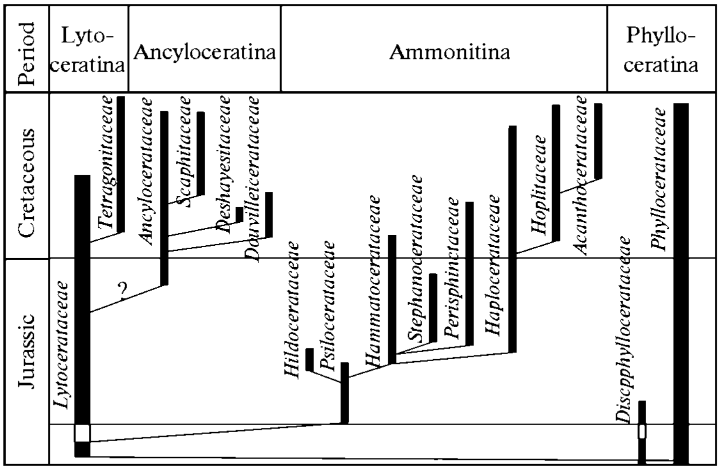


Fig. 27. Phylogenetic scheme of the Jurassic–Cretaceous ammonoids (Wiedmann, 1966).

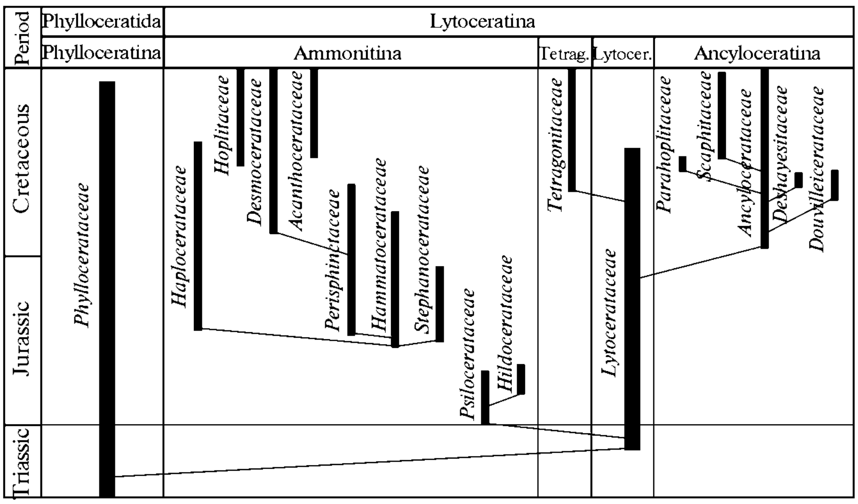


Fig. 28. Phylogenetic scheme of the Jurassic–Cretaceous ammonoids (Schindewolf, 1968).

and Deshayesitidae, considering that parahoplitids have the lobes ELU_1I and in deshayesitids have ELU_2I (Schindewolf's terminology is used in discussions of his views). The new fifth lobe, in different primary suture in these two groups, should be called differently: lobe U_2 appears in parahoplitids and lobe U_1 appears with a delay in deshayesitids. The resulting sutures look similar, EL U_1U_2I.

To justify the necessity of this indexation, Schindewolf used the concept of so-called orthochronic development of the suture in parahoplitids and heterochronic in deshayesitids. This concept was introduced quite a while ago and originally used for Jurassic ammonites (Schindewolf, 1929, 1957). In the case of orthochronic development, the new lobes appear in a usual (direct) way: the primary suture has lobe U_1, followed by lobe U_2, and so on. In the case of heterochronic development, there is a delay in the appearance of U_1 lobe and U_2 is present in the primary suture. Thus the final formula of the suture of different primary sutures because of the orthochronic development (in parahoplitids) and heterochronic development (in deshayesitids) is the same. Wiedmann (1966, 1969) provisionally supported Schindewolf's opinion. In our opinion, identical primary sutures in parahoplitids and deshayesitids do not provide any reason to designate and interpret them differently. Schindewolf emphasized that Casey and Mikhailova interpreted the evolutionary modes of deshayesitids differently (Schindewolf, 1966, text-figs. 684, 687). The subsequent study of deshayesitids allowed contest this hypothesis.

It was established that deshayesitids, like parahoplitids, have an unstable five-lobe primary suture, hence, the U^1 is present in the primary suture. We found such primary suture consisting of five lobes and

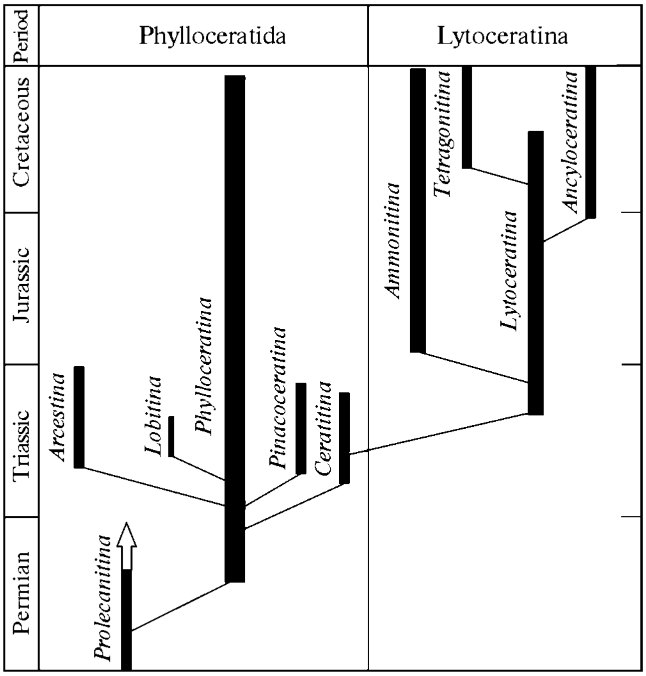


Fig. 29. Phylogenetic scheme of the Mesozoic ammonoids (Schindewolf, 1968).

the following two–three five-lobed sutures when we reexamined the TsNIGR Museum material of *Turkmeniceras* Tovbina, the genus also assigned to the family Deshayesitidae (Mikhailova, 1983, pp. 102–103).

We were able to establish that the monomorphic ammonites derived from heteromorphic ancestors, reveal relationships between the genera and sometimes species, and trace stages in the evolution of genera and species. This study was the basis of the zonal subdivision of the Aptian deposits and determination of the position of biostratigraphic boundaries of the recognized subdivisions. The composition of the superfamily Douvilleiceratoidea and its origin from the heteromorphic *Paraspiticeras* is certain (Wiedmann, 1966). The origin, evolution, and composition of the superfamily Deshayesitoidea were studied by the authors in greater detail (Bogdanova and Mikhailova, 1999, 2004). We identified the ancestral genus, and also characterized the transitional stage (*Heteroceras* → *Colchidites* → *Turkmeniceras*).

Baraboshkin and Mikhailova (2009) established the ammonite genus *Theodorites*. The succession of the two Hauterivian genera, *Theodorites* (with a perforated umbilicus) and its descendant *Lytoceras* Hyatt (lacking a perforation), shows the return from the heteromorphic shell to the monomorphic shell (Fig. 35). It has been shown that, apart from Parahoplitoidea, Douvilleiceratoidea, and Deshayesitoidea, the superfamily Theodoroceratoidea derived from Crioceratidae and existed for a short time in the Early Cretaceous.

6.2. Systematic Paleontology

Order Ammonitida

Suborder Ancyloceratina Wiedmann, 1966

D i a g n o s i s. Shell heteromorphic or monomorphic. Ornamentation variable, rarely weak. Siphuncle in ontogeny shifted ventrally. Primary suture unstable five-lobed, with early reduction of first umbilical lobe. New elements either not emerging (most heteromorphs) or usually formed by division of saddles U/I or I/O, less frequently, division of umbilical and inner lateral lobes. Umbilical and dorsal lobes trifid. Four superfamilies: Ancyloceratoidea Gill, 1871; Deshayesitoidea Stoyanow, 1949; Douvilleiceratoidea Parona et Bonarelli, 1897, and Parahoplitoidea Spath, 1924. Distinguished from other suborders of order Ammonitida by unstable five-lobed primary suture. Cretaceous (Berriasian–Coniacian).

In generic diversity, the superfamilies Ancyloceratoidea and Turrilitoidea are relatively similar, as shown in the histogram (see Fig. 26), whereas monomorphic descendants of the first superfamily are not numerous (Mikhailova and Baraboshkin, 2009).

S u p e r f a m i l y Parahoplitoidea Spath, 1922

Parahoplitaceae: Mikhailova, 1983, p. 96.

D i a g n o s i s. Shell from semi-evolute to semi-involute, medium-sized, less commonly, large. Cross section in early whorls ellipsoidal, in adults rounded square, rounded rectangular, and rounded trapezoid. Umbilicus from relatively narrow to wide.

O r n a m e n t a t i o n. The ornamentation is sometimes coarse, represented by ribs, frequently by tubercles. The ribs vary from almost straight to curved, both on the venter and on the flanks. The microscopic tubercles appear only from the second whorl; scarcely noticeable ribs appear at the end of the third whorl or the beginning of the fourth whorl. The tubercles can disappear with age, sometimes one whorl earlier than the ribs appear.

S u t u r e. The primary suture is five-lobed (VUU^1ID), with early reduction of the first umbilical lobe (U^1). New elements emerge by the division of saddle U/I, leading to the development (recurrence) of the first umbilical lobe (U^1), sometimes second umbilical lobe (U^2), and rarely, third umbilical lobe (U^3). The inner lateral lobe (I) never extends beyond the seam to the external side of the whorl. The complexity of the suture begins approximately with the middle of the third whorl, at first externally and, from the beginning of the fourth whorl, also internally part. The bifid subdivision of the ventral lobe is revealed very early: from the second–fourth sutures.

C o m p o s i t i o n. The family Parahoplitidae was originally proposed by Spath with two subfamilies Parahoplitinae and Douvilleiceratinae; a year later, he raised Douvilleiceratinae to the rank of family (Spath, 1923). In the same paper, he listed the generic compo-

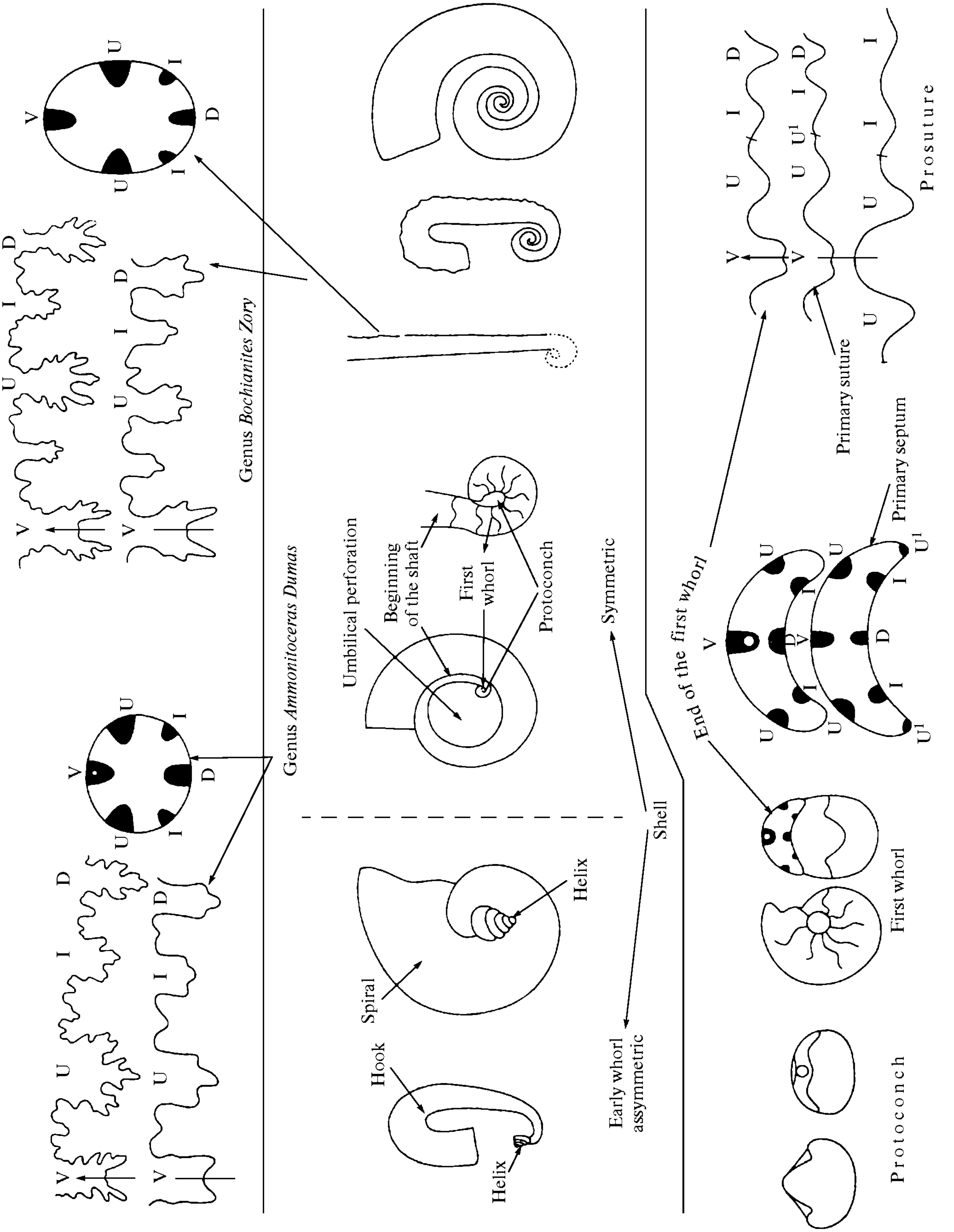


Fig. 30. Morphogenesis of the superfamily Ancyloceratoidea.

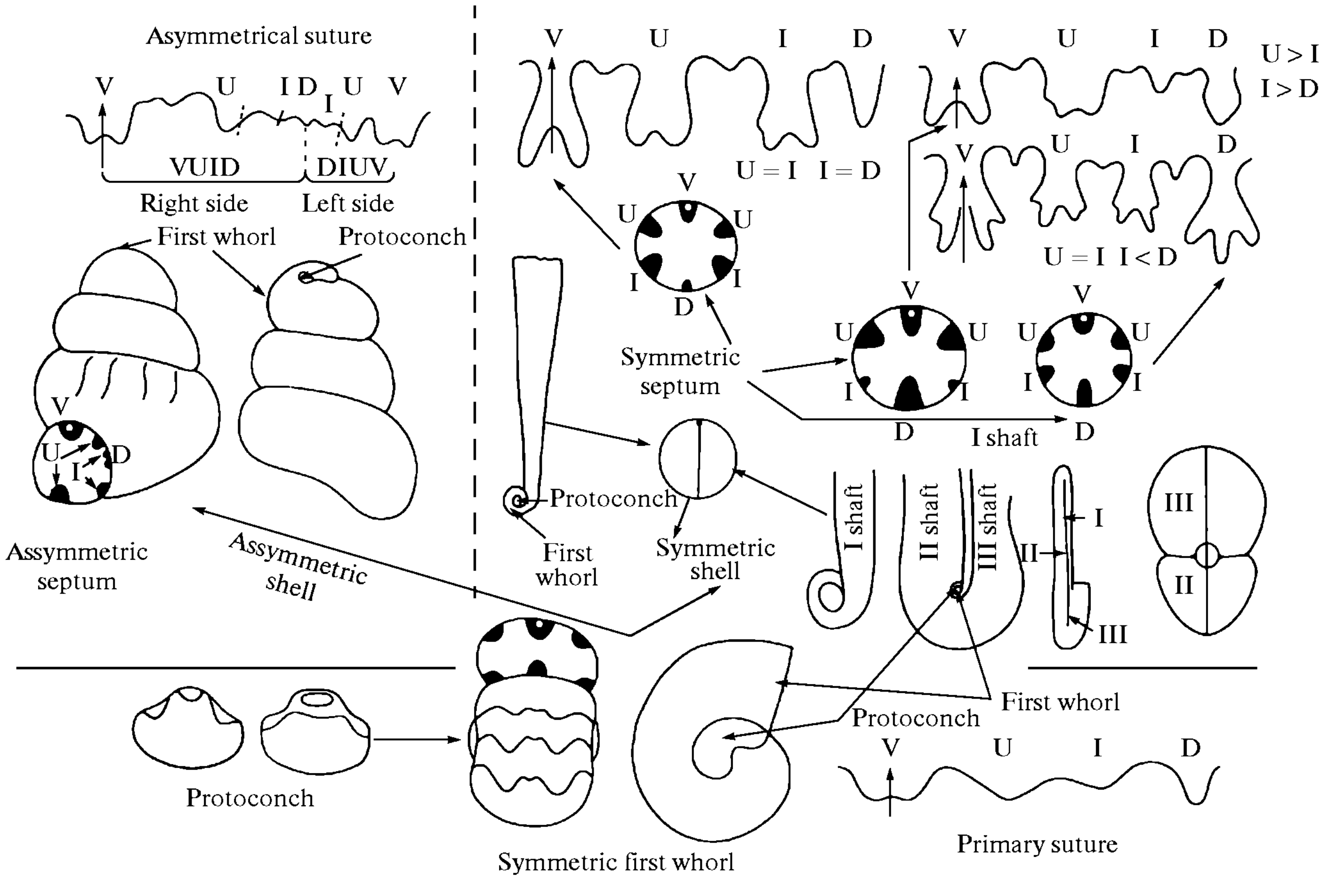


Fig. 31. Early morphogenesis of the superfamily Turrilitoidea.

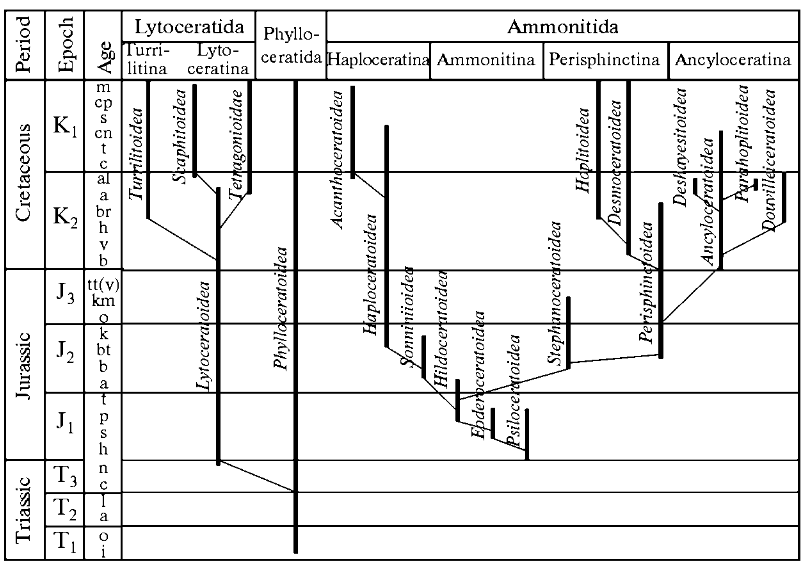


Fig. 32. Phylogenetic scheme of the Jurassic–Cretaceous ammonoids (Beznossov and Mikhailova, 1983).

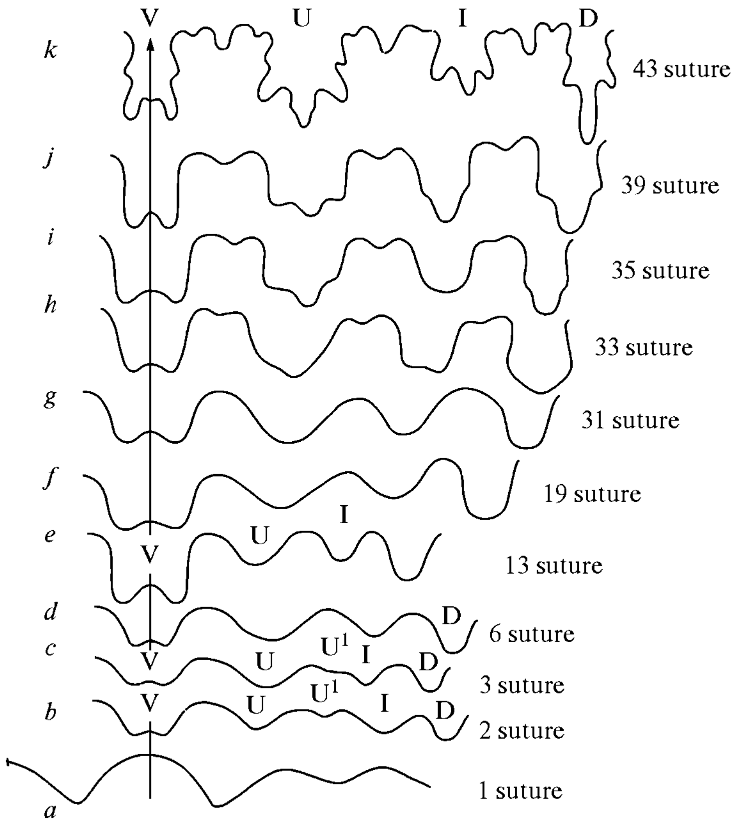


Fig. 33. Morphogenesis of the suture of *Caspianites wassiliewskyi* (Renngarten), TsNIGR Museum, no. 1/11288; Tuarkyr, Babashi well; Middle Aptian, *Epicheloniceras subnodosocostatum* Zone.

sition of parahoplitids: *Parahoplites* Anthula, 1899; *Acanthohoplites* Sinzow, 1907; *Hypacanthoplites* Spath, 1923; *Parahoplitoides* Spath, 1923 (=*Deshayesites* Kasansky, 1914); *Stenhoplites* Spath, 1923 (=*Dufrenoyia* Burckhardt, 1915). The stratigraphic distribution of Parahoplitoidea (with a small exception) is restricted to the Middle and Upper Aptian and the lower zone of the Albian. They are almost cosmopolitan and, in many regions, they are major components of zonal assemblages.

Later, the genus *Colombiceras* Spath was assigned to the family Douvilleiceratidae although some authors, following Spath, continued to include it in the family Cheloniceratidae Spath. Roman (1938, p. 319) established the new family Palaeohoplitidae, to which he assigned four subfamilies: Himalayitinae, Berriaselinae, Neocomitinae, and Parahoplitinae. By that he (Roman, 1938, pp. 346–348) lowered the rank of Parahoplitidae, and included two genera, *Parahoplites* Anthula, 1899 and *Acanthohoplites* Sinzow, 1907. According to the rules of zoological nomenclature, the family-group name Palaeohoplitidae is invalid, because the generic name *Palaeohoplites* does not exist, which is specifically mentioned by Wright et al. (1996, p. 49).

Eristavi (1955, p. 91) used the name Palaeohoplitidae, noting that this group (including the related uncoiled specimens) "is the dominant group among the Lower Cretaceous ammonites of Georgia ..." (Eristavi, 1955, p. 130). He only published descriptions of species (and in most cases, type species) and omitted diagnoses of all higher taxa.

The proposal of Stoyanow (1949, p. 95) was fundamentally different. He proposed to include three subfamilies in the family Parahoplitidae: Parahoplitinae Spath, Acanthohoplitinae Stoyanow, and Deshayesitinae Stoyanow. Stoyanow included *Parahoplites* Anthula and two new genera in the subfamily Parahoplitinae: *Kasanskyella* and *Sinzowiella*; in the second subfamily, Acanthohoplitinae, apart from *Acanthohoplites* Sinzow, *Hypacanthoplites* Spath, and *Colombiceras* Spath, he included two new genera, *Immunitoceras* and *Paracanthohoplites*. The third subfamily Deshayesitinae includes two known genera, *Dufrenoyia* Burckhardt, 1915 and *Deshayesites* Kasansky, 1914. Below we will discuss our opinion in the newly proposed genera. The third subfamily is distin-

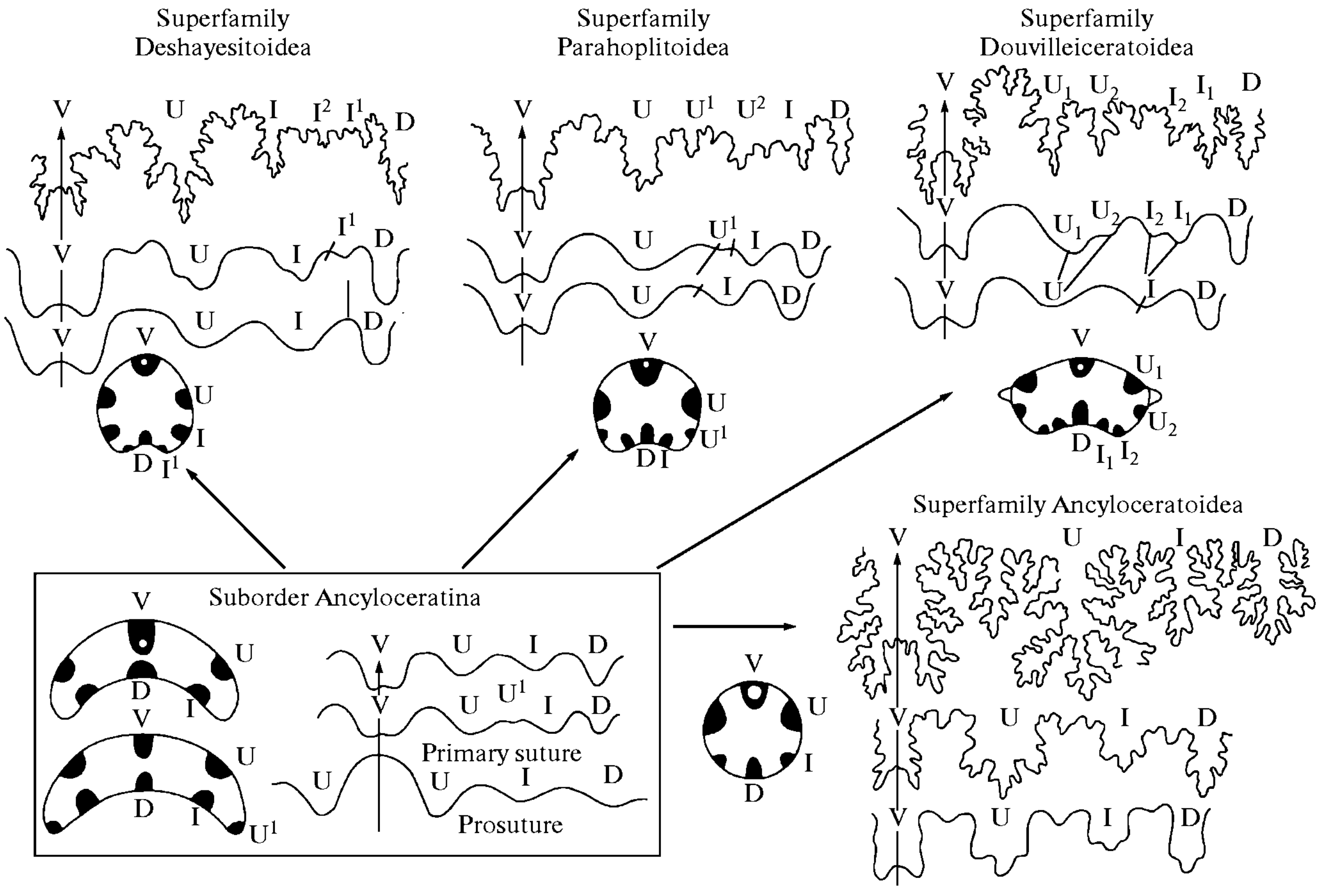


Fig. 34. Early morphogenesis of the suture and cross section in the suborder Ancyloceratina Wiedmann, 1966 (after Mikhailova, 1983, modified).

guished from other two by the mode of the appearance of new elements through the division of the saddle I/D, formation of the lobes I^1, I^2, and shifting of the inner lateral lobe (I) to the outer side of the whorl. The rank of this subfamily was shortly after raised to family (Wright, 1955; Arkell et al., 1957; Mikhailova, 1957), and later superfamily Deshayesitoidea (Bogdanova and Mikhailova, 2004).

Bogdanova and Mikhailova (2006, p. 29) argued for raising the rank of the other two subfamilies to families: Parahoplitidae Spath and Acanthohoplitidae Stoyanow, included in the superfamily Parahoplitoidea Spath. A team of authors from Georgia (Atlas ..., 2005) suggested that Parahoplitoidea and Acanthohoplitoidea should be considered as superfamilies; we do not support this view.

Family Parahoplitidae Spath, 1922

Parahoplitidae: Luppov and Drushchits, 1958, p. 102; Wright et al., 1996, part L, vol. 4, p. 274.

D i a g n o s i s. Ornamentation consisting of coarse ribs, curved forward on venter. Tubercles absent in adult whorls. However, microscopic tubercles distinctly observed on second–partly third whorls. Later in ontogeny, shell becoming smooth, while ribs only appearing on fourth whorl (Fig. 36).

Suture with trifid asymmetrical umbilical lobe and trifid (with single termination) dorsal lobe; only in two species its base slightly flattened, whereas true bifid dorsal lobe, typical of family Acanthohoplitidae, not observed.

C o m p o s i t i o n. The family Parahoplitidae includes a single genus *Parahoplites* Anthula from the Middle Aptian of Europe, Central Asia, North Africa, and North and South America. The genera *Sinzowiella* Stoyanow and *Kasanskyella* Stoyanow are most likely junior synonyms of this genus (see below).

C o m p a r i s o n. The family Parahoplitidae is distinguished from the family Acanthohoplitidae: (1) by the presence of a trifid rather than bifid dorsal lobe, (2) by the absence of tubercles at the adult stages and the presence of the stage of a smooth shell after the disappearance of the microscopic tubercles, but before

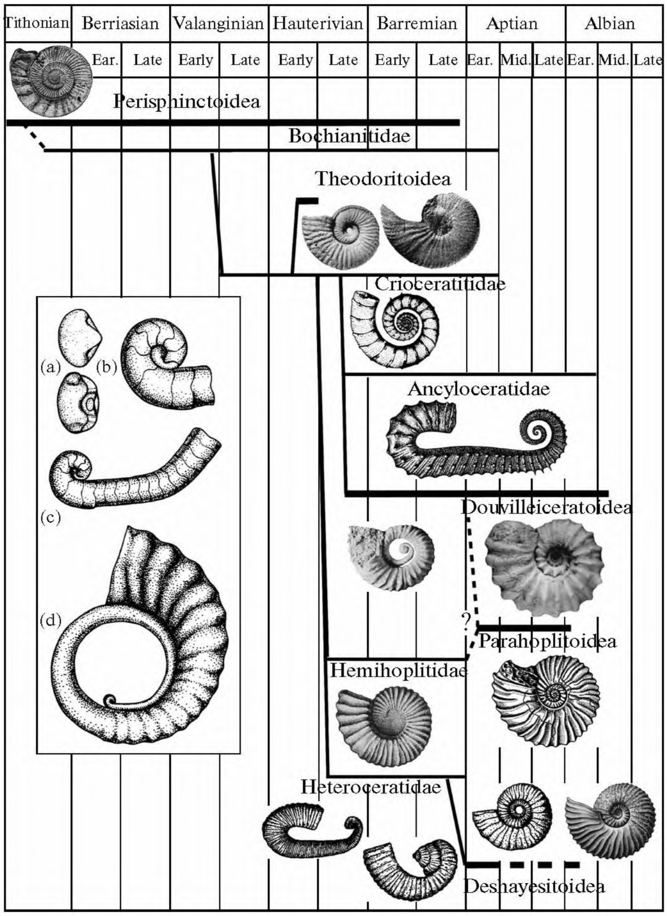


Fig. 35. Phylogeny of the superfamily Ancyloceratoidea Gill (without the families Labeceratidae Spath, 1925 and Hamulinidae Gill, 1871) and its monomorphic descendants. Inset: (a) protoconch, (b) firth whorl and beginning of straight shaft, (c) transition from straight to curved shaft, (d) transition to planispiral shell and formation of umbilical perforation in the genus *Caspionites* (Bogdanova and Mikhailova, 1975; Mikhailova and Baraboshkin, 2009).

the appearance of the ribs, and by specific ribs, which are bent ventrally.

R e m a r k s. The early reduction of the first umbilical lobe (U^1) is inherited from the heteromorphic ancestors, whereas the loss of tubercles suggests that the family Parahoplitidae evolved from the closely related family Acanthohoplitidae.

Genus *Parahoplites* Anthula, 1899

Parahoplites: Anthula, 1899, p. 109; Jacob, 1905, p. 406; 1907, p. 48; Sinzow, 1907, p. 456; Kazansky, 1914, p. 89; Danilovich, 1923, p. 3; Spath, 1930, p. 437; Rouchadze, 1938a, p. 143; Roman, 1938, p. 346; non Scott, 1940, p. 1028; Humphrey, 1949, p. 137; Stoyanow, 1949, p. 99.

Kasanskyella: Stoyanow, 1949, p. 100.

Sinzowiella: Stoyanow, 1949, p. 101.

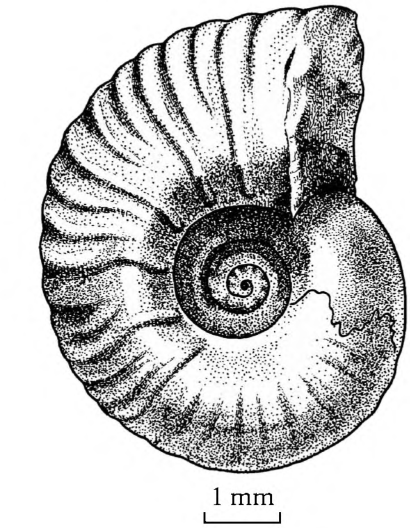


Fig. 36. Appearance and development of ornamentation in *Parahoplites melchioris* Anthula, lateral view. Dagestan, village of Akusha; Middle Aptian (after Mikhailova, 1962).

Parahoplites: Glazunova, 1953, p. 24; Arkell et al., 1957, p. L387; Mikhailova, 1957, p. 173; Luppov and Drushchits, 1958, p. 103; Kudryavtsev, 1960, p. 313; Tovbina, 1982, p. 60; Wright et al., 1996, p. 276; Sharikadze et al., 2004, p. 406; Raisossadat, 2006, p. 919.

T y p e s p e c i e s. *Parahoplites melchioris* Anthula, 1899, p. 111; Middle Aptian, *Parahoplites melchioris* Zone; Russia, Central Dagestan. Designated by the author of the genus.

S h e l l s h a p e. The shell is medium-sized or large, from semi-evolute to semi-involute. The cross section in the first three whorls is low-ellipsoidal, later in ontogeny, rounded square to rounded trapezoidal. The umbilical wall is wide and steep. The umbilicus varies from relatively narrow to relatively wide.

O r n a m e n t a t i o n. The protoconch and succeeding one or two whorls are smooth. Tubercles appear later in ontogeny and then disappear in the order of their appearance. The total number of microscopic tubercles ranges from six–eight to 15 per whorl. Sometimes, they are traced to the middle of the fourth whorl, after which the shell for some time remains smooth, and later, hardly discernible ribs appear, which are visible on the flanks and on the venter, where they are slightly bent forward (see Fig. 36).

In adult whorls, the ornamentation is represented by coarse, variously spaced primary and intercalary ribs, most commonly alternating. The alternation of the primary and intercalary ribs is often replaced by the alternation of primary ribs with so-called wedging ribs, which on one side of the whorl begin in the mid-flank, and on the other side reach the umbilicus or vice versa. Therefore, on the flank, these wedging ribs are not distinguished from the primary and intercalary ribs.

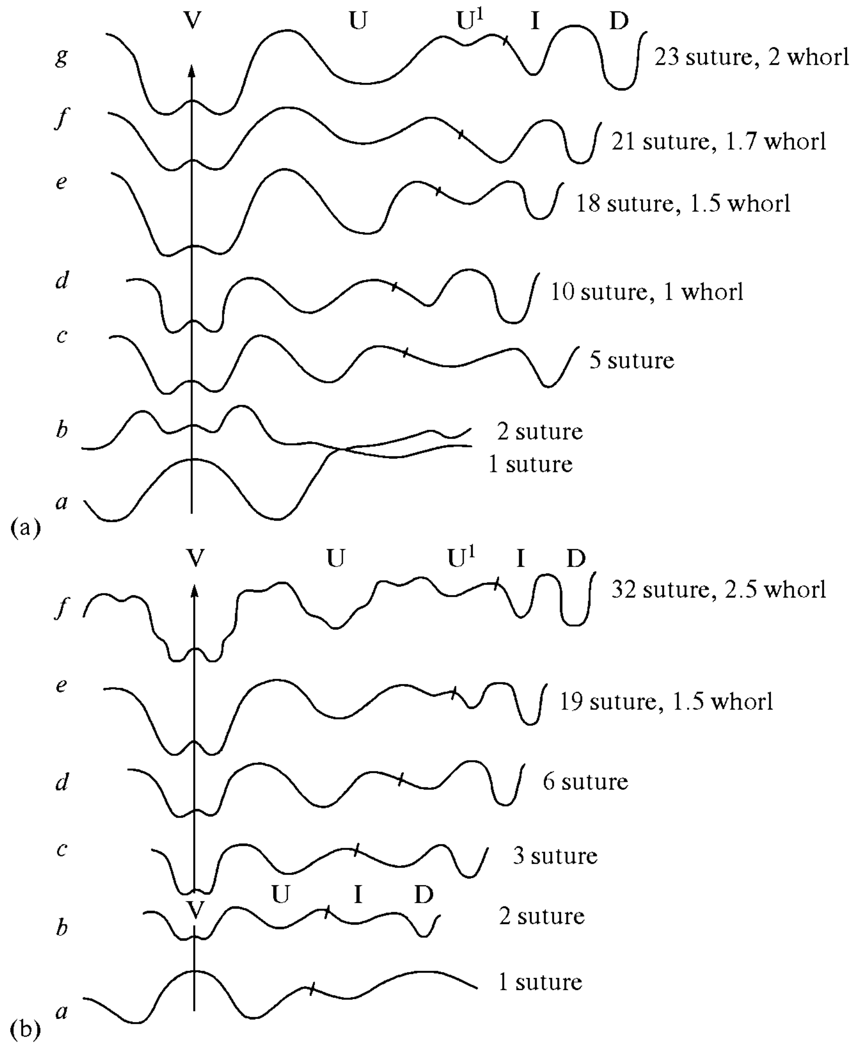


Fig. 37. Early morphogenesis of the suture in *Parahoplites melchioris* Anthula: (a) specimen PIN, no. 5265/60: (*a–d*) ×60, (*e*) ×56, (*f–g*), ×43; (b) PIN, no. 5265/61: (*a–d*), ×49, d ×34, (*e*) ×18; Dagestan, village of Akusha; Middle Aptian.

At the shell diameter above 30–40 cm in some species, ribs on the flank become weaker, but remain unchanged on the umbilical shoulder and on the venter.

S u t u r e. (Fig. 37). Figure 37a shows that the primary suture near the seam is in contact with the prosuture, with a shallow lobe U^1, but four lobes already in the fifth suture: a wide bifid ventral (V), umbilical (U), inner lateral (I), and dorsal (D) lobes.

New elements appear from the third whorl: the top or the inner slope of the saddle U/I flattens and a small depression develops on it, leading to the development of the first umbilical lobe (U^1). The existing elements become more complex from the third whorl, the process which finishes by the end of the fourth whorl. The changes primarily involve the umbilical lobe, then successively the ventral lobe, external (V/U) and umbilical (U/I) saddles; with a delay of approximately half the whorl, the entirety of the inner part of the suture is disrupted. In the fifth whorl, there are five or six lobes, apart from the first umbilical lobe, and the second umbilical (U^2) lobe appears. The bifid ventral lobe is usually the deepest. The trifid asymmetrical umbilical lobe is usually slightly smaller. The inner lateral lobe is trifid and asymmetrical. The dorsal lobe is trifid (single termination), and only in *P. multicostatus* and *P. maximus,* the base of this lobe is slightly flattened.

The changes in the suture in the shell morphogenesis are as follows: $VUU^1ID \rightarrow VUID \rightarrow VUU^1ID \rightarrow VUU^1U^2{:}ID$. For instance, in Parahoplitidae and Acanthohoplitidae, new elements appear by the division of the saddle U/I. However, the fifth lobe (U^1), which is present in the Middle–Late Aptian Acanthohoplitidae, is observed in Parahoplitidae at the contact between the prosuture and primary suture (see Fig. 37a).

S p e c i e s c o m p o s i t i o n. Apart from the type species, the genus includes more than 20 species, most of which are restricted to the beds of the upper Middle Aptian zone, which in many regions is referred to as the *Parahoplites melchioris, P. maximus* Sinzow, 1907, *P. subcampichei* (Pictet et Renevier, 1855), *P. sjogreni* Anthula, 1899, *P. grossouvrei* Jacob, 1905, *P. schmidti* Jacob et Tobler, 1906, *P. multicostatus* Sinzow, 1907, *P. transitans* Sinzow, 1907, *P. campichei* Sinzow, 1907, *P. artschmanensis* Glasunova, 1953, *P. lata* Egoian, 1957, *P. debilicostatus* I. Michailova, 1958, *P. irregularis* Casey, 1965, *P. luppovi* Tovbina, 1982, *P. robustus* Sinzow, 1907, *P. nutfieldensis* J. Sowerby, *P. cunningtoni* Casey, 1961, *P. depressus* Casey, 1961, *P. daveyi* Casey, 1961, *P. vectensis* Casey, 1961, *P. laticostatus* Sinzow, 1908, *P. mexicanus* Humphrey, 1949, *P. macfarlandi* Anderson, 1938, and *P. quilla* Benavides-Caceres, 1956. Species of the genus *Parahoplites* are found in Europe (Russia, Hungary, Germany, England, France, Switzerland, Spain), Asia (Turkmenistan, Iran, Kazakhstan (Mangyshlak)), North Africa (Tunisia, Morocco), North America (California, Mexico), and South America (Colombia, Peru, Chile).

C o m p a r i s o n. The characters distinguishing *Parahoplites* Anthula from genera of the family Acanthohoplitidae are listed above in the comparisons of families.

R e m a r k s. Anthula, when proposing the genus *Parahoplites* (Anthula, 1899), established two groups: (1) *P. melchioris* and (2) *P. aschiltaensis*, and gave species composition for each of them. Shortly later, Sinzow (1907) restricted the genus *Parahoplites* to the group *P. melchioris,* whereas the *P. aschiltaensis* group and several species of *P. melchioris* were separated into the genus *Acanthohoplites.* In this understanding, the genus *Parahoplites* has been accepted by most subsequent authors.

Stoyanow (1949) established two new genera, *Kazanskyella* and *Sinzowiella,* and assigned to the former the new species *Kazanskyella daghestanica* (=*Parahoplites melchioris* as identified by P.A. Kazansky). We cannot assign specimens described by P.A. Kazansky as *P. melchioris,* to any other genus. Stoyanow reexamined the specimen described and figured by Kazansky (1914) as *Parahoplites melchioris* and assigned it to a new genus and species, *Kazanskyella daghestanica,* and additionally described *Kazanskyella arizonica.* Thus, in Arizona, the genus *Kazanskyella* is only represented by the type species *K. arizonica* Stoyanov. Of four specimens, only syntype no. 91747 (×1.1) is well preserved at the stage with a medium-sized shell. This specimen is similar to the Caucasian parahoplites. One of two small specimens (syntype no. 91111) is similar in shell ornamentation to the earlier whorls of *Parahoplites.*

The genus *Sinzowiella* is similar to *Parahoplites.* It is represented by four small molds of the type species *S. spathi,* with the diameter from one to two centimeters, and also two fragments.

Thus, two other species established by Stoyanow (*Kazanskyella arizonica* and *Sinzowiella spathi*), in our opinion do not show characters sufficient for recognition them as separate genera.

Parahoplites melchioris Anthula, 1899

Plate 1, figs. 1–8; Plate 2, figs. 1–5; Plate 13, fig. 5; Plate 38, fig. 2

Parahoplites melchioris: Anthula, 1899, p. 112, pl. 8, figs. 4a–4c, 5a–5c; Sinzow, 1907, p. 458, pl. 2, fig. 2 (non pl. 2, figs. 1, 4 and pl. 3, fig. 3); Kazansky, 1914, p. 90, pl. 5, figs. 76 and 77, non fig. 78; Danilovich, 1923, p. 18; Rouchadze, 1938a, pp. 143, 170; Luppov in Luppov et al., 1949, p. 228, pl. 66, fig. 3, text-fig. 56; Glazunova, 1953, p. 25, pl. 2, figs. 1 and 2; Mikhailova, 1958, pp. 101–108; 1962, p. 132; Sazonova, 1958, p. 125, pl. 7, figs. 1 and 1a; Kudryavtsev, 1960, p. 314, pl. 2, figs. 1 and 2, pl. 3, fig. 1; Eristavi, 1961, p. 53, pl. 2, fig. 3; Kemper, 1971, p. 367, pl. 26, fig. 5.

L e c t o t y p e. Specimen figured by Anthula (1899, pl. 8, fig. 5); Aptian, *Parahoplites melchioris* Zone; Russia, Dagestan, village of Akusha; designated here.

S h e l l s h a p e. The shell usually consists of five–seven whorls. The protoconch is elongated (Dm = 0.53 mm, W = 0.66 mm) (Figs. 38a–38c). The primary constriction is visible at the end of the first whorl, on the tenth chamber (Figs. 38d, 38e).

The protoconch of specimen PIN, no. 5265/54 shows not just a caecum, but also a prosiphon, distinctly visible in the transmissive light (Fig. 3f). It represents a thin film, which by one side is attached to the caecum, slightly embracing it, and by another, opposite side, attached to the inner surface of the protoconch. The prosiphon resembles a depressed, slightly truncated cone, the trace of which on the wall of the protoconch resembles an ellipse. The caecum is ovate; after the first septum, it narrows, becoming a siphuncle, wider in the first two–three chambers than in the subsequent chambers. The siphuncle crosses the first septa in the mid-whorl and, at the end of the whorl, is shifted gradually ventrally.

The shell cross section is rounded subquadrate (Fig. 39). The venter is rounded, the flanks are weakly convex, the umbilical wall is steep. The umbilicus is relatively wide (26–33%). The maximum width of the whorl is located somewhat lower the mid-flank.

In the first three whorls, the cross section is elliptical. The shell overlap degree increases with age and, at shell diameter over 30–40 mm, the whorls overlap each other for approximately half their height. Later, the whorl height increases more rapidly than the width and the cross section changes to rounded rectangular.

Dimensions in mm and ratios:

Specimen no.	Dm	WH	WW	UW	WH/ Dm	WW/ Dm	UW/ Dm
PIN 5265/54	5.3	2.2	3.0	1.8	0.41	0.56	0.34
PIN 5265/54*	7.0	3.0	3.5	2.2	0.43	0.50	0.31
PIN 5265/54	8.3	3.5	4.0	2.4	0.42	0.48	0.29
PIN 5265/54	10.2	4.4	4.5	3.0	0.43	0.44	0.29
PIN 5265/54	11.5	4.8	4,9	3.2	0.42	0.43	0.28
PIN 5265/54	13.0	5.6	5.7	3.7	0.43	0.43	0.28
PIN 5265/54	17.0	7.2	7.0	5.0	0.43	0.41	0.29
PIN 5265/2	18.2	8.3	8.2	5.1	0.45	0.45	0.27
PIN 5265/1	19.4	9.1	10.0	6.5	0.46	0.51	0.33
PIN 5265/54	24.5	10.0	9.7	7.0	0.42	0.39	0.28
PIN 5265/54	27.0	12.0	10.5	8.0	0.44	0.39	0.29
PIN 5265/3	31.0	14.5	13,9	8.5	0.46	0.45	0.27
PIN 5265/54	31.7	14.5	13.2	8.5	0.45	0.41	0.27
TsNIGR Museum 54/10686	32.4	15.0	15.0	9.5	0.46	0.46	0.26
TsNIGR Museum 2/10686	34.4	16.5	14.7	9.1	0.47	0.42	0.26
PIN 5265/218	34.6	13.9	–	8.6	0.40	–	0.25
PIN 5265/4	35.5	16.7	14.2	9.4	0.47	0.40	0.26
PIN 5265/150	36.1	16.1	16.0	9.8	0.45	0.44	0.27
PIN 5265/159	37.0	16.7	14.8	9.0	0.45	0.40	0.24
TsNIGR Museum 3/10686	37.1	17.8	16.8	9.6	0.48	0.45	0.26
PIN 5265/54	37.5	17.0	14.7	10.0	0.46	0.39	0.29
PIN 5265/5	40.5	18.0	16.5	11.1	0.44	0.41	0.25
PIN 5265/54	42.2	19.2	17.0	11.5	0.45	0.40	0.27
PIN 5265/6	43.0	19.3	18.4	11.5	0.46	0.43	0.27
PIN 5265/187	45.2	21.8	20.1	11.7	0.48	0.44	0.26
PIN 5265/7	48.0	21.7	21.7	12.5	0.45	0.45	0.26
PIN 5265/131	49.0	23.0	23.0	13.2	0.46	0.46	0.20
PIN 5265/8	52.3	22.5	22.8	14.8	0.43	0.44	0.28
PIN 5265/54	54.0	25.0	21.0	14.2	0.45	0.39	0.26
TsNIGR Museum 61/10686	57.6	24.5	23.8	16.7	0.42	0.41	0.29
TsNIGR Museum 1/10686	58.7	26.7	25.2	15.2	0.45	0.43	0.26
PIN 5265/9	60.7	28.4	24.5		0.45	0.40	
PIN 5265/10	64.5	28.4	28.6	16.8	0.44	0.44	0.25
PIN 5265/11	78.0	36.0	33.0	21.0	0.46	0.42	0.27
PIN 5265/122	82.5	36.6	34.8	22.0	0.44	0.42	0.26
PIN 5265/12	97.0	41.0	38.0	29.0	0.42	0.39	0.29

* The specimen is uncoiled.

Ornamentation. The typical "*melchioris*-like" ornamentation is observed at the diameter more than 35–40 mm. It is represented by coarse primary and intercalary ribs (33–35 in the last whorl). Primary ribs begin on the umbilical wall, continue to the flank with a weak forward curvature and form a wide tongue-shaped ventral sinus. The intermediate (intercalary) ribs, usually one between two primaries, begin approximately at mid-flank and follow the course of the primaries on the ventrolateral shoulder.

Less commonly the alternation of the primary and intercalary ribs is replaced by the alternation of the "wedged" ribs, beginning like the intercalary ribs at mid-flank, but terminating on the other side of the shell on the umbilical shoulder, like the primaries. In the largest specimen studied, the number of ribs on the half of the last whorl reaches 20, but their course remains unchanged.

Ornamentation morphogenesis (Fig. 36). The protoconch and the first 1.5–2 whorls are smooth, at the end of the first whorl with a weak constriction, at the end of the second or beginning of the third whorl in mid-flank appear distinct microscopic tubercles. Their number does not exceed eight–ten; from the middle of the fourth whorl, the tubercles disappear, and the shell is smooth on the entire whorl and, after that, ribs appear at the diameter over 10 mm. At the diameter of 20 mm, the ribs on the venter are bent slightly forward. The primary ribs begin on the umbilical shoulder, with one or two intercalary ribs appearing at mid-flank between the primaries.

Suture. (Fig. 40). The suture at the end of the sixth whorl is complexly subdivided, and the total number of lobes is six: (V_1V_1) $(U_2U_1U_2)$ U^1U^2:ID. The bifid ventral lobe is considerably shorter than the trifid sharply asymmetrical umbilical lobe; the inner lateral and dorsal lobes are feather-like in outline.

The morphogenesis of the suture (see Fig. 40). The prosuture is angustisellate with a high narrow median saddle. After the early reduction of the first umbilical lobe (U^1), the suture consists of four lobes: a wide ventral lobe, umbilical lobe, inner lateral and dorsal lobes. The ventral lobe soon becomes bifid, whereas the appearance of new elements begins in the third whorl; at the diameter of 2.5 mm and whorl width 0.77 mm, the saddle U/I becomes slightly flattened; later, a small depression appears on its top, resulting in the restoration of the first umbilical lobe (U^1). From the end of the third whorl, the primary elements rapidly become more complex, terminating mainly by the end of the fourth whorl.

At the middle of the fourth whorl, the suture is composed of six lobes and five saddles. The ventral lobe is bifid, with almost parallel sides. The asymmetrical trifid umbilical lobe is with a lower inner and higher external branches. The inner lateral lobe is trifid and the dorsal lobe is with the entire termination and with two lateral digits. The bifid wide and high saddle shows bifid division of each branch. The primary saddle U/I is subdivided by the first and second umbilical lobes into three separate, also bifid saddles with additional division of some branches. Thus, the morphogenesis of the suture reflects the disappearance and secondary appearance of the first umbilical

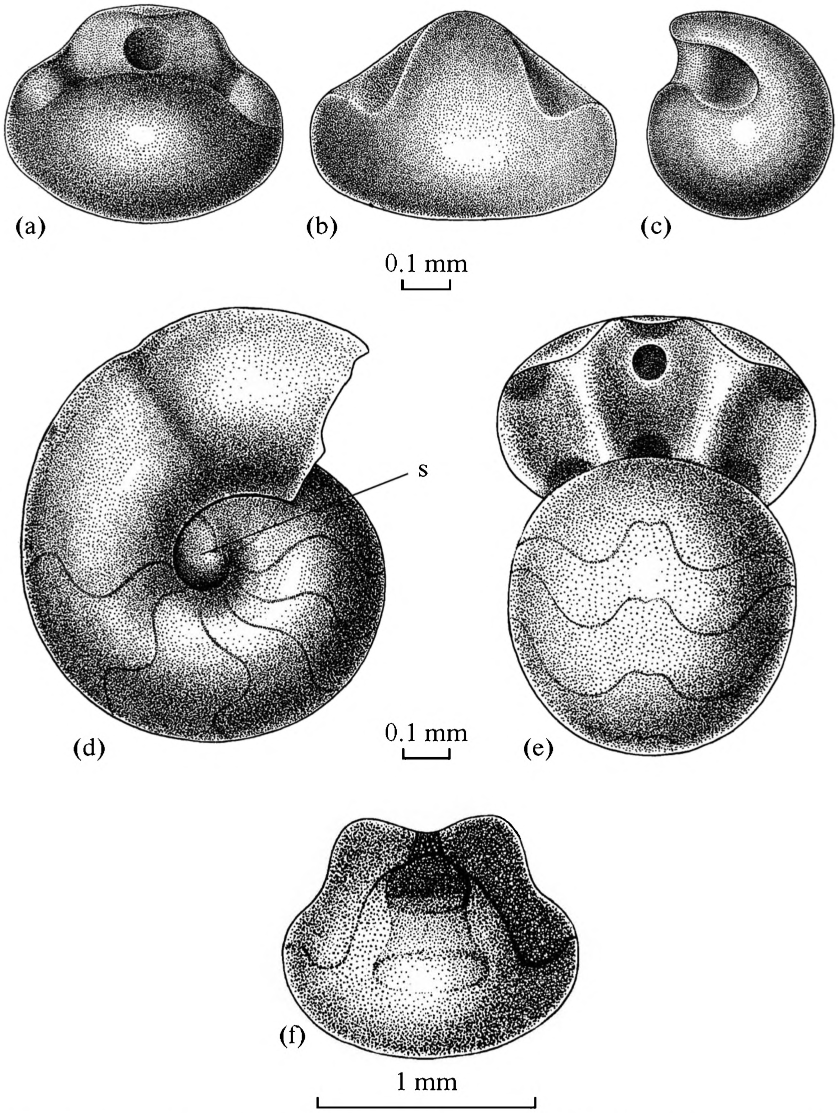


Fig. 38. Protoconch of *Parahoplites melchioris* Anthula; specimen PIN, no. 5265/63: (a) proseptum view, (b) upper view, (c) lateral view; (d, e) first whorl: (d) lateral view, (e) septal view; (f) protoconch of *Parahoplites melchioris* Anthula under an optical micrscope; specimen PIN, no. 5265/54; Dagestan, village of Akusha; Middle Aptian, *Parahoplites melchioris* Zone.

lobe and, sometimes, appearance of the second umbilical lobe: $VUU^1ID \rightarrow VUID \rightarrow VUU^1U^2{:}ID$.

At the end of the fourth whorl, the ventral and umbilical lobe have an almost similar depth; the inner lateral lobe is slightly shorter and the first and second umbilical lobes are very small. The further increased fluting of the septum and especially its periphery does not lead to any essential changes in the characters of the suture. The dissection of all elements increases with age.

V a r i a b i l i t y. Specimens studied include a small group of shells, in which the whorl width equals its height, whereas in all the remaining representatives, the whorl height exceeds its width (not including threee first whorls).

In specimen PIN, no. 5265/4 from a section near the village of Akusha, two and, in two cases, even three intercalary ribs appear between two primary ribs, and the total number of ribs reaches 39 on the last whorl. However, other characters are the same as in the typical representatives of this species, resulting from the projection of the outline of the adjacent sutures onto the ornamented shell.

C o m p a r i s o n a n d r e m a r k s. *Parahoplites melchioris* Anthula is similar to many species of the genus *Parahoplites*. The species is distinguished from *P. grossouvrei* Jacob, *P. maximus* Sinzow, and *P. subcampichei* Sinzow by the circular rather than rounded trapezoid shell cross section and by the last whorl retaining strong ribbing; from *P. multicostatus* Sinzow and *P. transitans* Sinzow, by the more widely spaced ribbing; from *P. schmidti* Jacob by the narrower whorls (height is always greater than width) and the denser and weaker ornamentation.

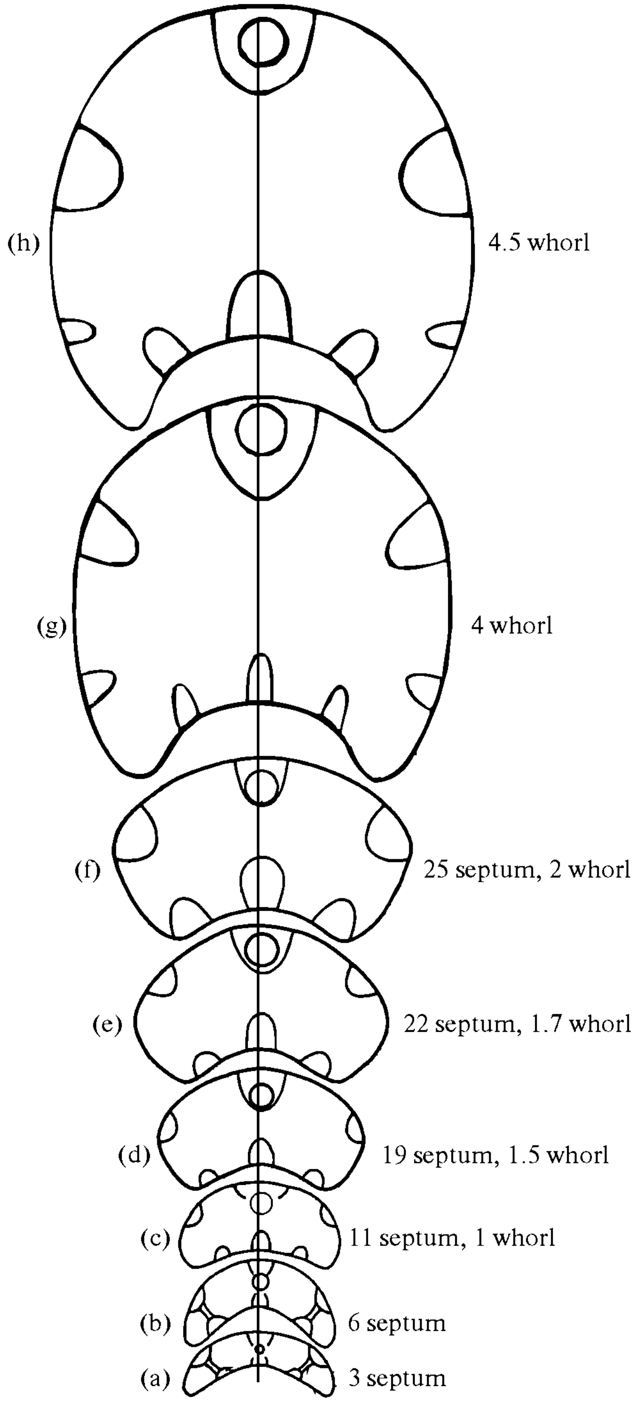


Fig. 39. Morphogenesis of the cross section of *Parahoplites melchioris* Anthula; specimen PIN, no. 5265/60: (a–f); ×43; (g, h) specimen no. PIN, no. 5265/63: (g) ×16; (h) ×11; Dagestan, village of Akusha; Middle Aptian.

Young specimens of *P. melchioris* are similar to young specimens of *Kazanskyella arizonica* Stoyanow from southeastern Arizona (Stoyanow, 1949, pl. 17, figs. 7, 8), whereas the adult specimens of this species is similar to *P. transitans* Sinzow. The American species *Kazanskyella arizonica* Stoyanow is morphologically similar to *P. melchioris* Anthula. *Sinzowiella spathi* Stoyanow also resembles *P. melchioris* and related species in general appearance.

The species *Parahoplites melchioris* established by Anthula from Dagestan and named after Melchior Neumayr has been repeatedly redescribed. Unfortunately, it is not possible to agree with some authors who assign to this species specimens very different from the type material. Specimen TsNIGR Museum, no. 1/11068, figured by Sinzow (1907, pl. 2, fig. 1), has thin ribs without noticeable curvature; their number reaches 44, which is considerably greater than in the specimens of *P. melchioris* Anthula from Dagestan. Three other specimens (TsNIGR Museum, no. 2/11608, pl. 2, fig. 2; no. 3/11068, pl. 3, fig. 3; no. 4/11068, pl. 2, fig. 4) were assigned to *Parahoplites melchioris* (Sinzow, 1907). In fact only specimen no. 2/11608, represented by an incomplete shell, corresponds to this species. Specimens nos. 3 and 4 are almost complete molds, but are distinguished from *P. melchioris* by the narrower whorl cross section.

Glazunova (1953) redescribed *P. melchioris* from the Aptian of Kopet Dagh. However, specimens figured in her pl. 2, figs. 1a–1c (TsNIGR Museum, no. 6/6426) and fig. 2 (TsNIGR Museum, no. 7/6426) have ribs coarser than in the typical *P. melchioris;* therefore, they are more similar to the species *P. multicostatus* and *P. transitans.* Sazonova (1958, p. 125) indicated *Parahoplites melchioris* Anthula (TsNIGR Museum, no. 16/11805) from Middle Aptian silty clay near the village of Guselki (Middle Volga Region to the north from Saratov). The figured specimens are similar to the Caucasian representatives of this species.

The above authors did not focus on the ornamentation of juvenile whorls; apparently, that is why they emphasize the tubercles in *P. melchioris* and other species of the genus *Parahoplites.*

The species name *melchioris* was independently used to species of two different genera of Aptian ammonites. This unfortunately caused confusion. Tietze (1872) established the species *Ammonites melchioris,* which was later designated as the type species of the genus *Melchiorites* Spath, 1923 (Superfamily Desmoceratoidea). Anthula (1899) assigned *melchioris* to the new genus *Parahoplites* (p. 112). The later use of this species name in the combination *Parahoplites (Melchiorites) melchioris* (Ropolo and Moullade, 2002, p. 4) is inexplicable, because it is not clear which species is meant. In addition, the author's species in their note is not mentioned.

O c c u r r e n c e. Russia (northern Caucasus, Dagestan), Kazakhstan (Mangyshlak), Turkmenistan (Kopet Dagh, Tuarkyr, Great Balkhan); Middle Aptian, *P. melchioris* Zone; northern Germany; Middle Aptian, *Parahoplites nutfieldensis–P. melchioris* Zone.

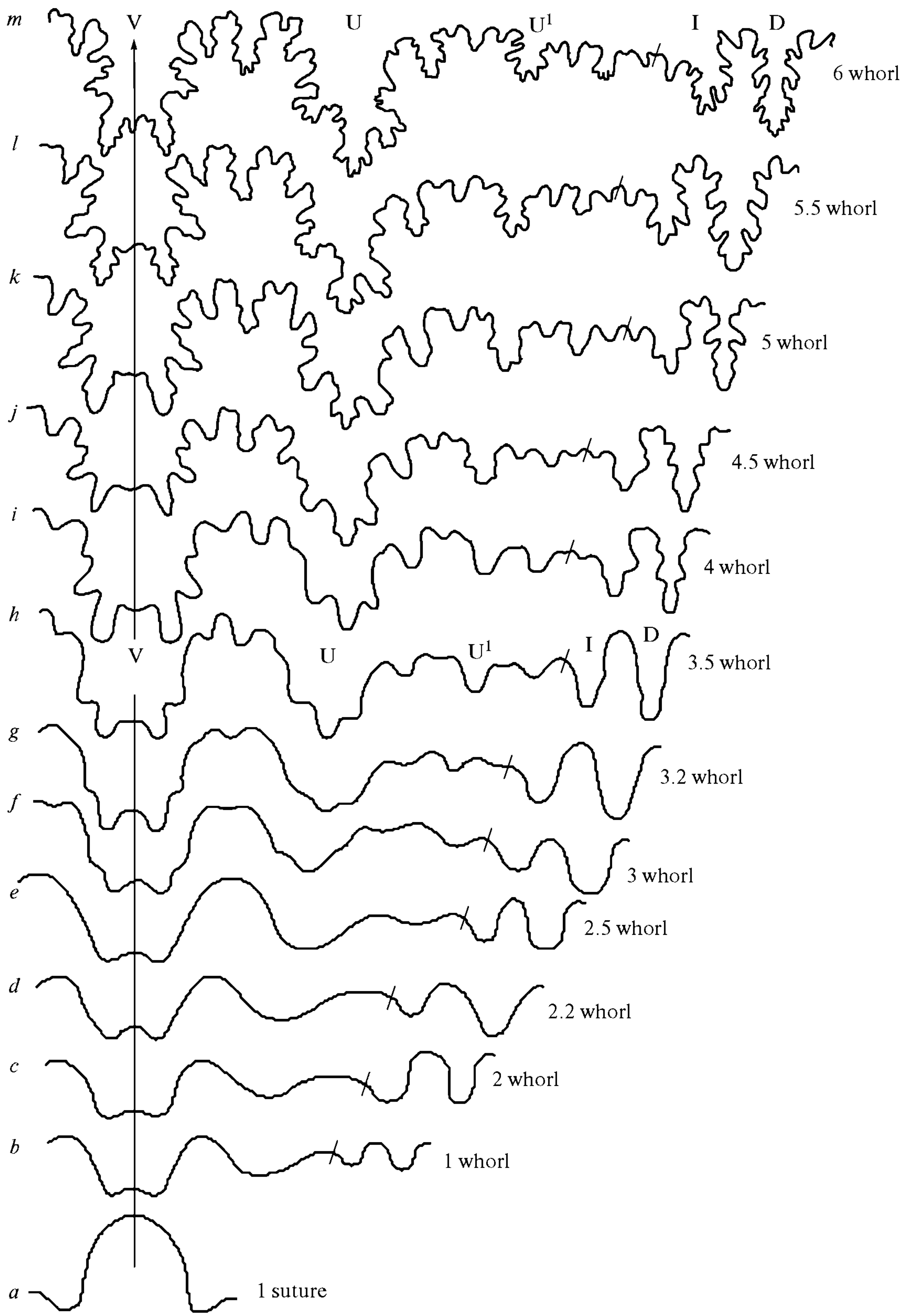
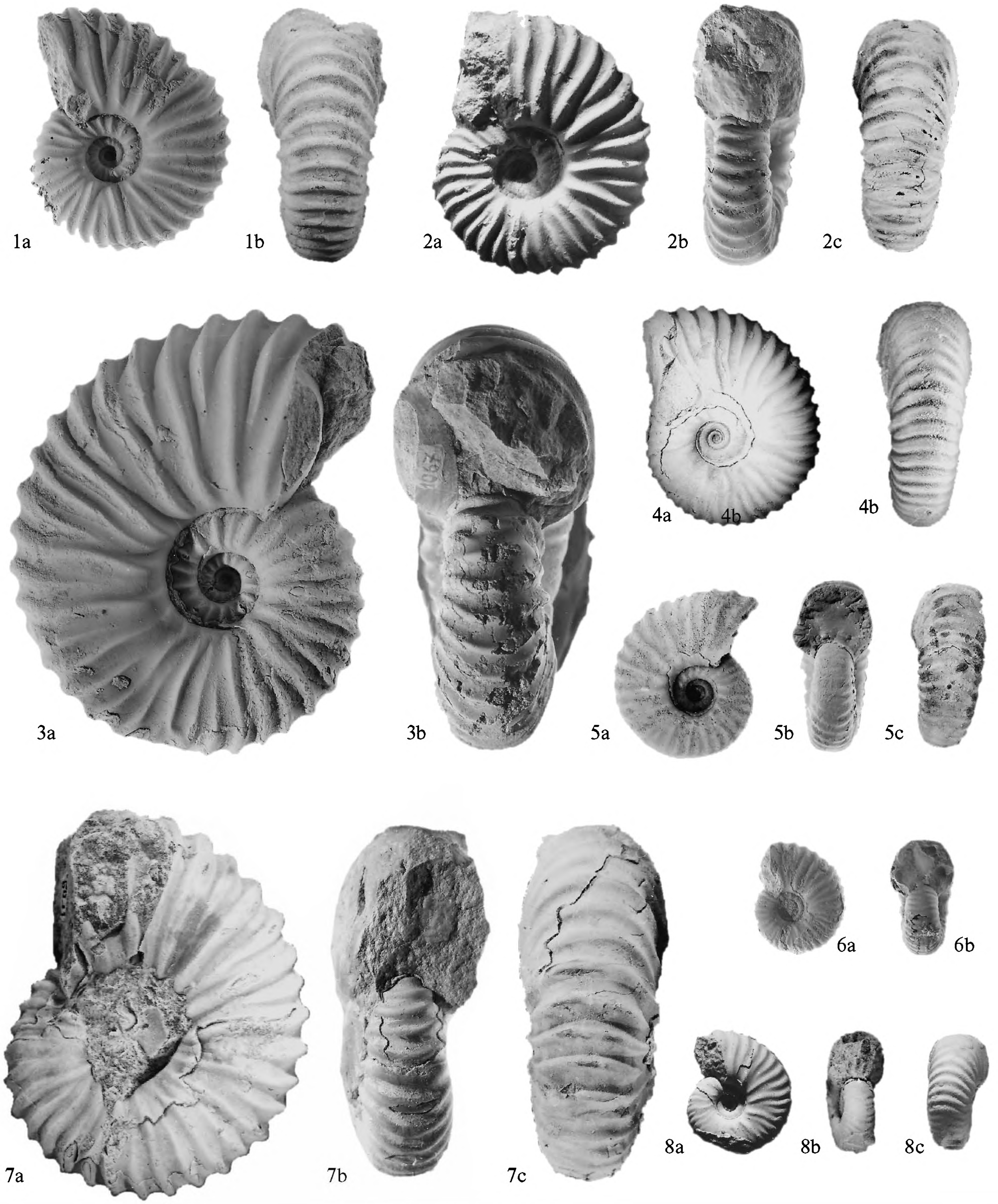


Fig. 40. Morphogenesis of the suture in *Parahoplites melchioris* Anthula, specimen PIN, no. 5265/54: (*a*, *b*) ×23; (*c*) ×19; (*d*); ×17; (*e*–*g*) ×14; (*h*, *i*) ×11; (*j*) ×8; (*k*) ×6; (*l*) ×5; (*m*) ×4; Dagestan, village of Akusha; Upper Aptian.

Plate 1



Explanation of Plate 1

Hereinafter, all sizes are natural, except specially indicated

Figs. 1–8. *Parahoplites melchioris* Anthula, 1899; specimens: (1) PIN, no. 5265/6; (2) PIN, no. 5265/5; Dagestan, village of Aya-Makhi, Middle Aptian, *Parahoplites melchioris* Zone; (3) PIN, no. 5265/11; (4) PIN, no. 5265/4; Dagestan, village of Akusha, the same age; (5) PIN, no. 5265/3; Dagestan, village of Dagva, the same age; (6) PIN, no. 5265/1; northern Caucasus, Malyi Zelenchuk River; the same age; (7) PIN, no. 5265/9; Dagestan, village of Tsudakhar, the same age; (8) PIN, no. 5265/2; Dagestan, village of Akusha, the same age.

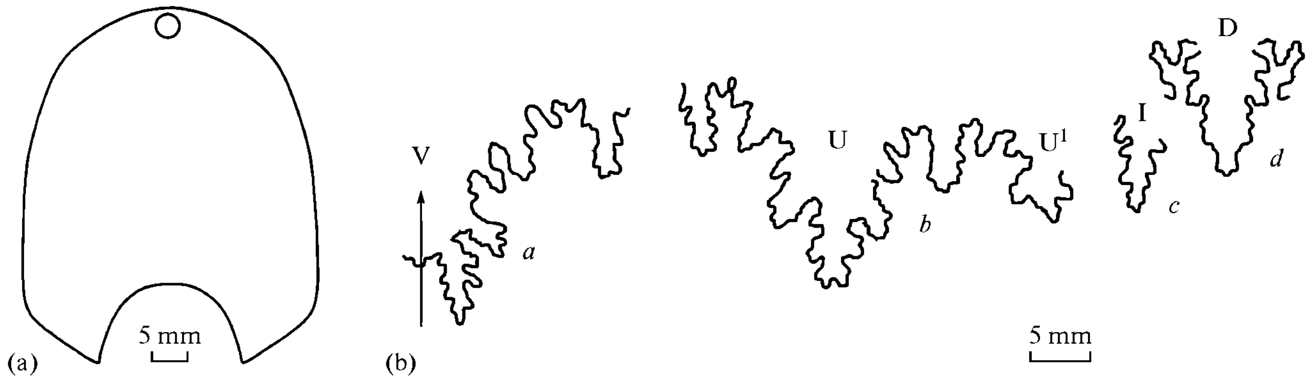


Fig. 41. (a) whorl cross section in *Parahoplites campichei* (Pictet et Renevier) at WW = 36.0 mm; specimen PIN, no. 5265/38; (b) fragments of the suture of *Parahoplites campichei* (Pictet et Renevier). (*a*) at WH = 43.0 mm and WW = 35.0 mm, (*b*) at WH = 41.5 mm and WW = 33.0 mm, (*c*) at WH= 41.5 mm and WW = 33.0 mm and (*d*) at WW = 47.5 mm; the same specimen; Dagestan, village of Dagva; Middle Aptian.

Material. Over 25 well-preserved specimens and many fragments. The body chamber is more than half of the last whorl, sometime reaching three-fourths of the last whorl. Northern Caucasus: Malyi Zelenchuk River (PIN, no. 5265/1), Baksan River (PIN, nos. 5265/201, 5265/224), Kheu River (PIN, no. 5265/223), Kuma River (PIN, no. 5265/186-188), Gundelen River (PIN, nos. 5265/194, 5265/202), Nalchik River (PIN, no. 5265/218); Dagestan: village of Akusha (PIN, nos. 5265/2, 5265/4, 5265/7, 5265/11, 5265/54, 5265/122, 5265/131, 5265/157, 5265/191–193, 5265/200, 5265/203-211), village of Aya-Makhi (PIN, nos. 5265/5, 5265/6), village of Dagva (PIN, nos. 5265/3, 5265/12, 5265/159, 5265/185, 5265/190, 5265/199), village of Tsudakhar (PIN, no. 5265/9), village of Ashilta (PIN, no. 5265/10); Mangyshlak, Tushchibek well (PIN, no. 5265/158); Kopet Dagh, village of Ushak (PIN, no. 5265/177); Tuarkyr, Babashi well (PIN, nos. 5265/8, 5265/150, 5265/195–197), Doungra (PIN, no. 5265/198, TsNIGR Museum, nos. 1/10686, 3/10686, 6/10686); Great Balkhan, Utuludzha well (TsNIGR Museum, nos. 2/10686, 5/10686); Middle Aptian, *Parahoplites melchioris* Zone.

Parahoplites campichei (Pictet et Renevier, 1855)

Plate 3, fig. 1

Ammonites campichei: Pictet and Renevier, 1854–1858, p. 25, pl. 2, fig. 2; Pictet and Campiche, 1858–1860, p. 258, pl. 37, figs. 1a–1c.

Parahoplites campichei: Sinzow, 1907, p. 460, pl. 1. figs. 4–7; Kazansky, 1914, p. 91.

Lectotype. Specimen, figured by Pictet and Renevier (1854–1858, pl. 2, fig. 2); Aptian; Switzerland, vicinity of the village of Le Ron; designated here.

Shell shape. The shell is semi-involute, whorls overlap each other for more than half of the whorl height. The cross section (Fig. 41a) is high, rounded venter gradually joins the flattened flanks, at the boundary of which with a steep umbilical wall there is a sharp shoulder.

Dimensions in mm and ratios:

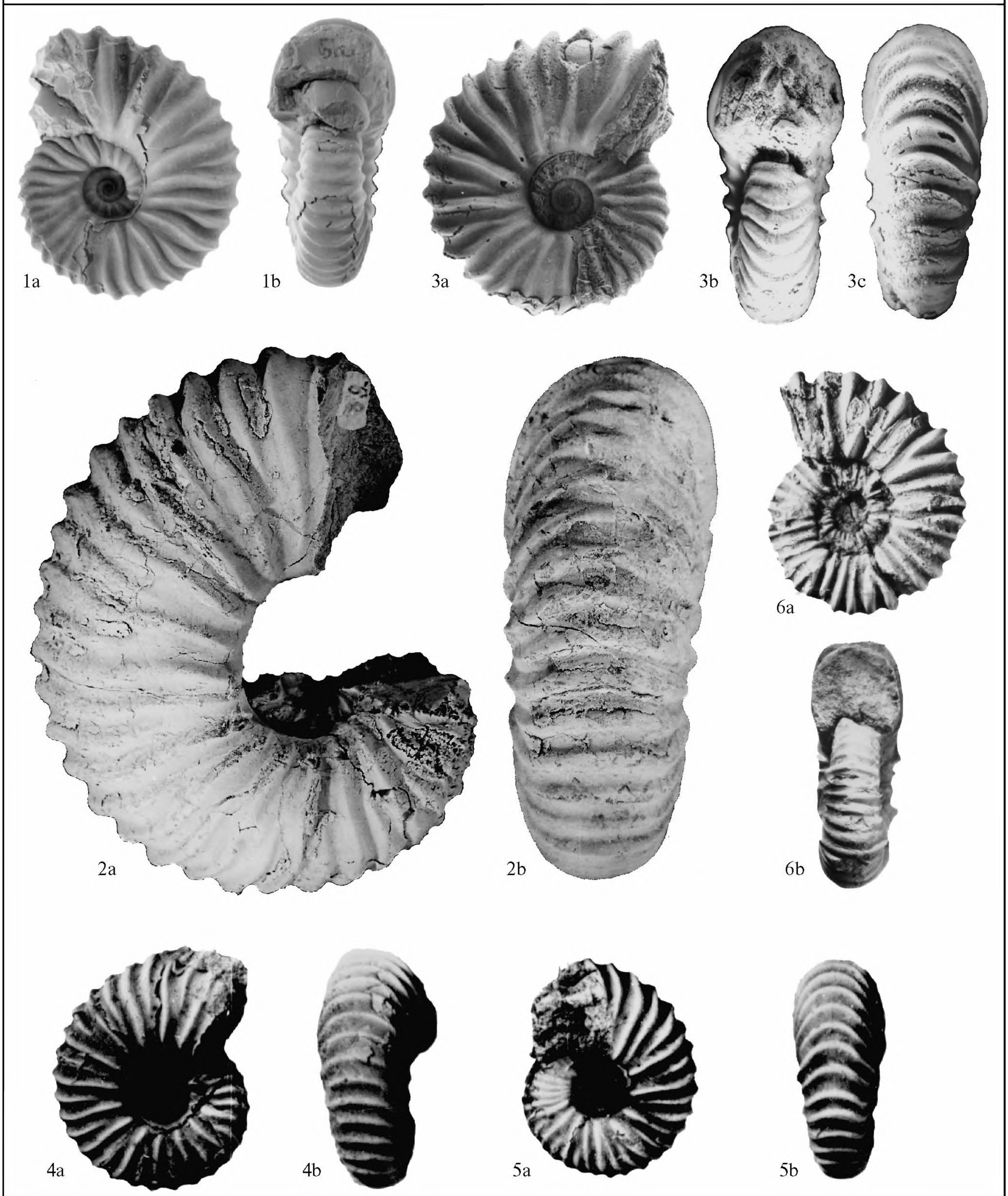
Specimen PIN, no.	Dm	WH	WW	UW	WH/Dm	WW/Dm	UW/Dm
5265/38	121.0	58.1	46.0	28.3	0.47	0.38	0.23

Ornamentation. The shell possesses ribs, 32 per half the last whorl at diameter of 121 mm. The primary ribs begin on the umbilical shoulder, weaken on the flanks, run without a noticeable curvature and widen, becoming less distinct, and effaced on the venter, bending weakly forward. The intermediate intercalary ribs, usually three between the primaries, begin in the mid-flank, above and below and in the upper part of the flank and are identical to the primaries. All ribs are very weak, especially at mid-flank. The ornamentation of the preceding whorl is much sharper. Strong umbilical bullae are visible.

Suture. (Fig. 41b). The suture was observed incompletely. The ventral lobe is bifid, with a large median saddle. The umbilical lobe is approximately as deep, trifid, asymmetrical. The first umbilical lobe is finely serrated, asymmetrically trifid. The inner lateral lobe is narrow. The dorsal lobe is shorter than the umbilical and ventral lobes, with a wider upper part and the narrow lower part. The lobe base is trifid. The saddle V/U is high and bifid. The lower saddle U/U^1 with a deep secondary lobe. The saddle I/D is bifid, with a relatively symmetrical top.

Comparison. *P. campichei* is similar in shape and ornamentation to *P. maximus* Sinzow. It is distinguished from the latter in the higher rounded quadrangular cross section and higher number of ribs (total and intercalary). In addition, in *P. campichei,* the dorsal lobe is trifid and, in *P. maximus,* a small saddle appears at the base of this lobe.

Plate 2



R e m a r k s. *P. campichei* was described from the Aptian of Switzerland. Characters of our specimen agree well with the original description. Although authors of the species indicate the presence of tubercles, but these are apparently the umbilical inflations of the ribs. In addition, Pictet and Renevier (1854–

1858) noted that four intercalary ribs are present between the primary ribs; apparently, this is a random case. Pictet and Campiche (1858–1860) described under this name a fragment very similar to our specimen. The figured specimen shows that the primary ribs can show from one to three intercalary ribs rather than four, as indicated by Pictet and Renevier (1854–1858). This specimen is particularly similar to one figured by Sinzow (1907, pl. 1, fig. 4, TsNIGR Museum, no. 10/11068). Kulzhinskaya-Voronets (1930) described *P.* aff. *campichei* from the Lower Cretaceous of the Bukhara section (TsNIGR Museum, no. 1/3358). This specimen is represented by half of the mold of an ammonite shell approximately 50 mm in diameter. The ventral and lateral sides are flattened and the ribs cross the venter rectiradially. The ammonite most likely belongs to the genus *Acanthohoplites.*

Spath (1930) recorded *Parahoplites* aff. *campichei* (Pictet and Renevier) from England, noting its similarity to the specimens from Mangyshlak, but they are less compressed and are very similar to *P. nutfieldiensis* (J. Sow.).

Raisossadat (2006, p. 919, text-figs. 4M, 4H) described and figured *Parahoplites* cf. *campichei* (Pictet et Renevier), which is very similar to this species.

Occurrence. Russia (Dagestan), Kazakhstan (Mangyshlak); Middle Aptian, *Parahoplites melchioris* Zone; Switzerland, Middle Aptian.

Material. One incomplete specimen, with no shell matrix. Dagestan, village of Dagva (PIN, no. 5265/38); Middle Aptian, *Parahoplites melchioris* Zone.

Parahoplites sjogreni **Anthula, 1899**

Plate 4, fig. 1; Plate 5, fig. 1; Plate 31, fig. 1; Plate 36, fig. 2

Parahoplites sjogreni: Anthula, 1899, p. 116, pl. XI (X), figs. 2, 3; 3a–3c.

Sonneratia sjogreni: Sinzow, 1907, p. 467, pl. 2, figs. 12 and 13.

Parahoplites sjogreni: Rouchadze, 1938a, p. 146, 186, pl. 3, fig. 2; Kudryavtsev, 1960, p. 318, pl. 7, figs. 1a and 1b.

Lectotype. The specimen figured by Anthula (1899, pl. XI (X), fig. 2): Middle Aptian; Russia, Dagestan, village of Khodzhal-Makhi. This specimen was found by Shegren and designated here.

Shell shape. The shell is large, varying from semi-involute to semi-evolute; with whorls rapidly increasing in height, overlapping each other by half of the whorl height or slightly less. The cross section is oval. The venter is rounded, the flanks are flattened; the umbilical wall is wide and steep.

Dimensions in mm and ratios:

Specimen no.	Dm	WH	WW	UW	WH/Dm	WW/Dm	UW/Dm
PIN 5265/124	148.0	75.6	54.0	31.1	0.51	0.36	0.21

Anthula's specimen is larger: Dm = 254.0 mm, WH = 117.0 mm, WH/Dm = (0.46), WW = 102.0 mm, WW/Dm = (0.40), UW = 56, UW/Dm = (0.26).

Ornamentation. The ornamentation is represented by numerous, densely spaced primary and intercalary ribs. The primary ribs begin in the upper part of the umbilical wall as elongated bullae and run across the flanks and the venter inclining slightly forward. Intercalary ribs occur mainly in twos, less commonly in threes between the adjacent primaries, and similarly on the venter. The ornamentation weakens with age; on the flanks by the end of the last whorl, there are distinctly inflated terminations of the primary ribs on the umbilical shoulder, whereas the intercalaries resemble weak striae.

Suture. Judging from the illustration (Anthula, 1899, pl. XI(X) fig. 2), the lectotype is typical of the genus *Parahoplites.* The first umbilical lobe (U^1) is deep, trifid, and asymmetrical. The external saddle (V/U) is high and wide, asymmetrical, with three tops.

Comparison and remarks. From other species of the genus *Parahoplites,* this species is distinguished by the flattened whorls and characteristic dense ribbing, becoming weaker with age. The specimens described and figured by Kudryavtsev (1960, p. 318, pl. 6, fig. 1, pl. 7, fig. 1a, 1b) are distinguished by the fewer ribs and complete disappearance of the umbilical bullae in the last whorl.

Occurrence. Russia (Dagestan); Middle Aptian, *Parahoplites melchioris* Zone.

Material. One excellently preserved specimen, with a partly preserved body chamber. Dagestan, village of Akusha (PIN, no. 5265/124), Middle Aptian, *Parahoplites melchioris* Zone.

Parahoplites grossouvrei **Jacob, 1905**

Plate 5, fig. 2

Parahoplites grossouvrei: Jacob, 1905, p. 409, pl. 13, figs. 2a and 2b; Rouchadze, 1938a, pp. 144, 170; Kudryavtsev, 1960, p. 318, pl. 5, fig. 1.

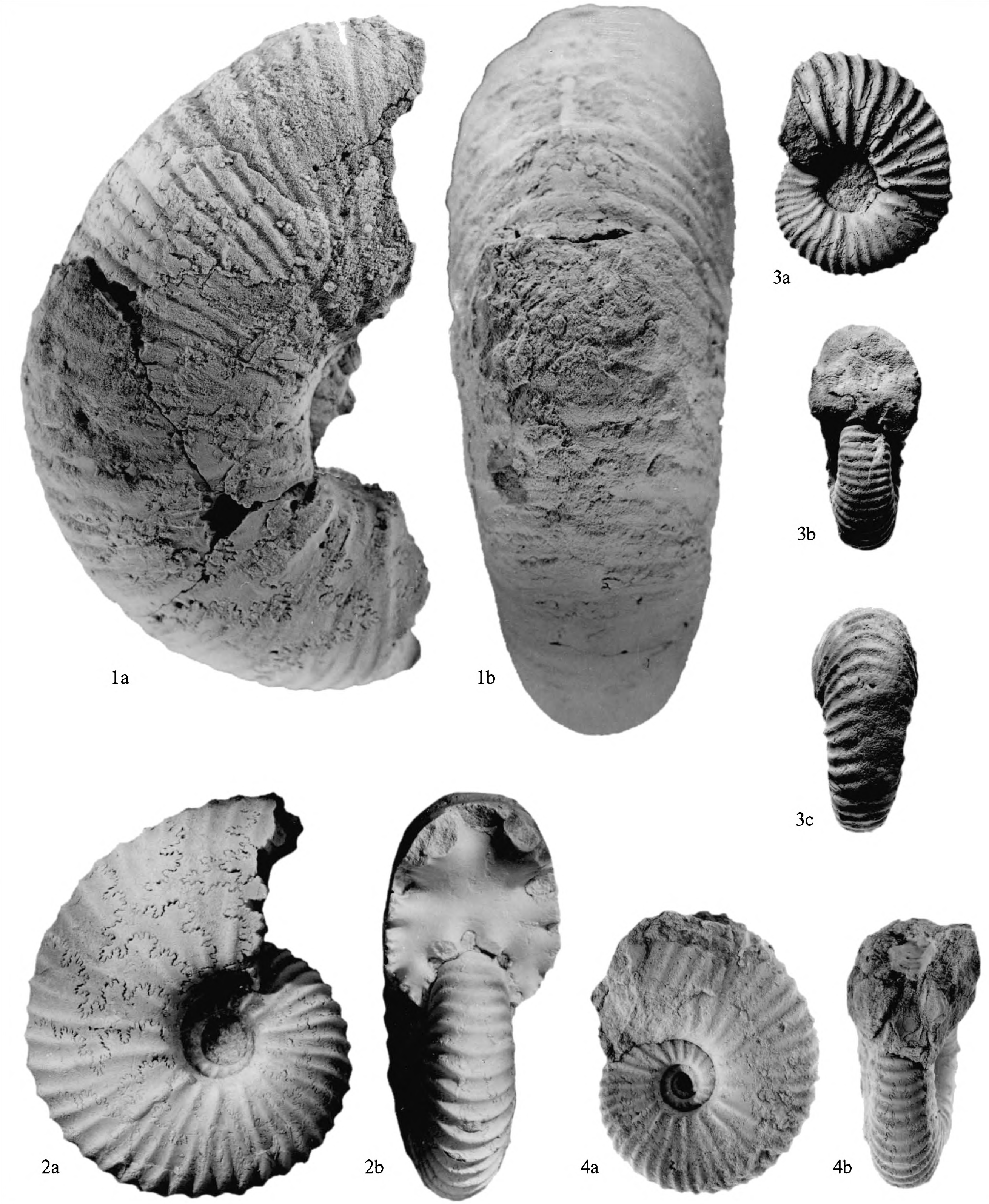
Holotype. Specimen figured by Jacob (1905, pl. 13, figs. 2a, 2b); Aptian; southeastern France, village of Clansayesian; designated here by monotype.

Explanation of Plate 2

Figs. 1–5. *Parahoplites melchioris* Anthula, 1899; specimens: (1) PIN, no. 5265/7; (2) PIN, no. 5265/12; Dagestan, village of Akusha, Middle Aptian, *Parahoplites melchioris* Zone; (3) PIN, no. 5265/8; (4) TsNIGR Museum, no. 3/10686; Tuarkyr, Babashi well, the same age; (5) TsNIGR Museum, no. 2/10686; Great Balkhan, Utuludzha well, the same age.

Fig. 6. *Colombiceras bogdanovae* Tovbina, 1982; holotype TsNIGR Museum, no. 5/11909; Kopet Dagh, village of Danata; Middle Aptian, *Parahoplites melchioris* Zone.

Plate 3



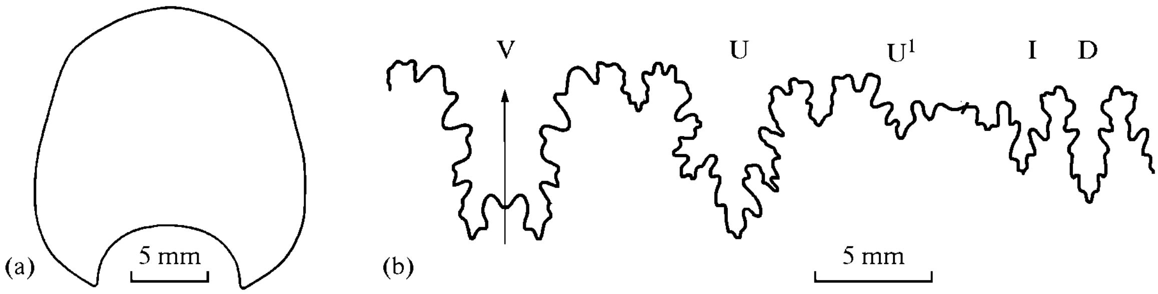


Fig. 42. *Parahoplites grossouvrei* Jacob, specimen PIN, no. 5265/40: (a) whorl cross section at WW = 18 mm; (b) suture at WW = 15 mm. Dagestan, village of Aya-Makhi; Middle Aptian.

S h e l l s h a p e. The shell is semi-involute, with whorls, overlapping one another for approximately two-thirds of the height. The whorl cross section (Fig. 42a) varies from subquadrate to rounded trapezoid. The weakly rounded venter gradually joins the flattened flanks. The umbilical wall is high and steep. The maximum whorl width is in the lower third. The umbilicus is relatively narrow and stepped.

D i m e n s i o n s i n m m a n d r a t i o s:

Specimen PIN, no.	Dm	WH	WW	UW	WH/Dm	WW/Dm	UW/Dm
5265/120	61.0	28.0	24.0	–	0.45	0.41	–
5265/40	62.5	31.0	26.7	13.0	0.49	0.42	0.42

O r n a m e n t a t i o n. The shell is covered by weak, densely spaced ribs (25 per half of the last whorl at Dm = 61 mm). Primary ribs begin in the upper part of the umbilical wall, run across the flank, curved slightly forward, and are slightly weaker at mid-flank at a diameter of 50 mm. One (and in the second half of the last whorl more commonly two) intercalary rib appears between the adjacent primary ribs, begin at mid-flank or slightly lower, independently from the primaries. Less commonly, the intercalary ribs closely approach the primaries. In most cases, these are alternating intercalary ribs. On the venter, all ribs are similarly pronounced and cross it with a small forward curvature.

S u t u r e. (Fig. 42b). The ventral lobe is with a low median saddle. The umbilical lobe is trifld, asymmetrical, and as deep as the ventral. The first umbilical lobe is shallow trifid, asymmetrical. The inner lateral lobe is symmetrical in the lower part. The dorsal lobe is monobasic. The saddle V/U and slightly lower saddle U/U^1 are bifid, with deep secondary lobes. The saddle I/D is narrowed in the middle and with an uneven dissected bifid top.

C o m p a r i s o n. *P. grossouvrei* is distinguished from *Parahoplites subcampichei* and *P. maximus* by the more distinct ornamentation with the denser ribbing and different outline of the whorl-section.

R e m a r k s. Specimens described by Sinzow (1907, p. 465, pl. 1, figs. 10, 11) as *P. grossouvrei* by the shape of their cross section and ornamentation should be assigned to *P. subcampichei*. Rouchadze (1938a) described but not figured *P. grossouvrei* and noted that the intercalary ribs are more commonly branches of the primaries than independent intercalary ribs.

O c c u r r e n c e. Russia (Dagestan), Middle Aptian, *Parahoplites melchioris* Zone; southeastern France; Middle Aptian.

M a t e r i a l. Two specimens, with a shell layer preserved on one. The incomplete body chamber occupies less than half of the last whorl. Dagestan: village of Aya-Makhi (PIN, no. 5265/40), village of Murada (PIN, no. 5265/120); Middle Aptian, *Parahoplites melchioris* Zone.

Parahoplites schmidti Jacob in Jacob, Tobler, 1906

Plate 6, figs. 1–9

Parahoplites schmidti: Jacob and Tobler, 1906, p. 12, pl. 2, figs. 7a, 7b, 8a, and 8b; Glazunova, 1953, p. 28, pl. 5, figs. 1a–1s; Kudryavtsev, 1960, p. 317, pl. 8, fig. 2; Egoian, 1969, p. 151, pl. 8, fig. 3.

Parahoplites tumidus: Egoian, 1969, p. 152, pl. 8, figs. 4 and 5; pl. 1, fig. 1.

L e c t o t y p e. Specimen figured by Jacob and Tobler (1906, pl. 11, figs. 8a, 8b); Aptian; Switzerland, village of Luter Zug; designated here.

E x p l a n a t i o n o f P l a t e 3

Fig. 1. *Parahoplites campichei* (Pictet et Renevier, 1855); specimen PIN, no. 5265/38; Dagestan, village of Dagva, Middle Aptian, *Parahoplites melchioris* Zone.

Fig. 2. *Parahoplites subcampichei* Sinzow, 1907; specimen PIN, no. 5265/35; Dagestan, village of Dagva; Middle Aptian, *Parahoplites melchioris* Zone.

Figs. 3 and 4. *Parahoplites debilicostatus* I. Michailova, 1953; (3) specimen PIN, no. 5265/147; (4) neotype PIN, no. 5265/39,; Dagestan, village of Dagva; Upper Aptian.

Plate 4

1

Explanation of Plate 4

Fig. 1. *Parahoplites sjogreni* Anthula, 1899; specimen PIN, no. 5265/124; Dagestan, village of Akusha; Middle Aptian, *Parahoplites melchioris* Zone.

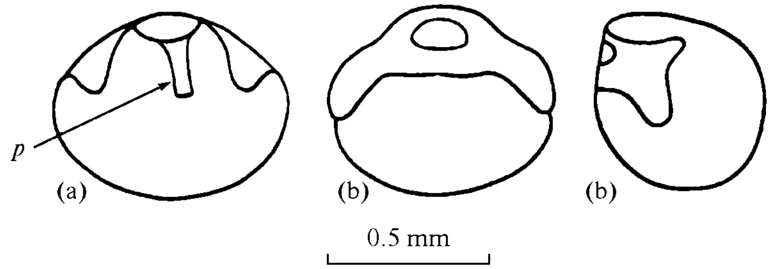


Fig. 43. Protoconch of *Parahoplites schmidti* Jacob; specimen PIN, no. 5265/19: (a) upper view, (b) proseptum view, (c) lateral view; (*p*) prosiphon; northern Caucasus, Khokodz River; Middle Aptian.

Shell shape. The protoconch is angustisellate, the caecum cross section is oval, the prosiphon is shifted (Fig. 43). The shell is relatively convex semi-involute, small, composed of 5–5.5 low, wide, half embraced whorls. The umbilicus is relatively wide and deep. The umbilical wall is steep. The cross section (Fig. 44) is rounded angular. The whorl width exceeds its height.

Dimensions in mm and ratios:

Specimen no.	Dm	WH	WW	UW	WH/Dm	WW/Dm	UW/Dm
PIN 5265/13	17.0	8.0	8.5	4.8	0.45	0.56	0.28
PIN 5265/14	17.9	8.1	9.3	6.0	0.45	0.51	0.33
PIN 5265/15	27.0	12.1	12.3	8.4	0.44	0.45	0.31
PIN 5265/49	33.8	15.5	18.5	11.9	0.45	0.54	0.35
PIN 5265/16	36.8	15.8	15.5	11.3	0.42	0.42	0.30
TsNIGR Museum 6/10686	37.4	16.3	18.6	10.0	0.44	0.50	0.28
PIN 5265/123	44.6	19.8	25.8	11.5	0.44	0.57	0.20
PIN 5265/17	44.8	22.6	25.7	12.0	0.50	0.57	0.28
TsNIGR Museum 7/10686	47.9	21.5	22.7	16.0	0.45	0.47	0.33
PIN 5265/18	49.1	23.0	24.6	13.2	0.47	0.50	0.27
PIN 5265/133	52.1	22.2	26.8	13.9	0.43	0.50	0.27

Ornamentation. The shell at the diameter of 27 mm (three quarters of the fifth whorl) is covered by 28 sharp, strongly projecting ribs. In the last whorl (Dm = 50 mm, five and a half whorls), there are 33 sharp, simple primary and intercalary ribs on the shell surface. In places, the whorls show alternation of wedging ribs. The umbilical wall is smooth and the primary ribs begin at the umbilical shoulder, curve weakly forward in the lower third of the flank and curved backward in the upper third. Intercalary ribs are located one between the primaries, begin in the mid-flank or somewhat lower and, in the upper part of the flank, are identical to the primaries.

The morphogenesis of the ornamentation was traced from the first to fifth whorl (Bogdanova and Mikhailova, 2007, text-figs. 9b, 9c). The protoconch and first whorl are smooth. A constriction is readily visible at the end of the first whorl. Tubercles appear in the middle of the second whorl; these remain almost to the end of the third whorl, which has up to 15 tubercles.

Suture. At the whorl width of 16.4 mm (Fig. 45), the suture is strongly dissected: the ventral lobe is bifid,

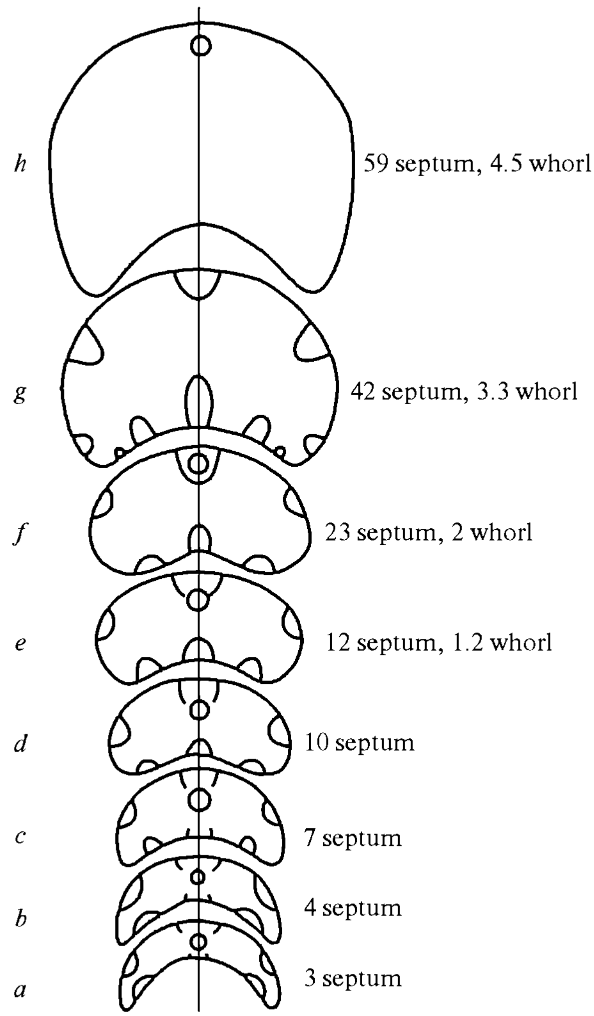


Fig. 44. Morphogenesis of the cross section in *Parahoplites schmidti* Jacob, specimen PIN, no. 5265/19: (*a–e*) ×28, (*f*); ×17, (*g*) ×8, (*h*) ×5; northern Caucasus, Khokodz River; Middle Aptian.

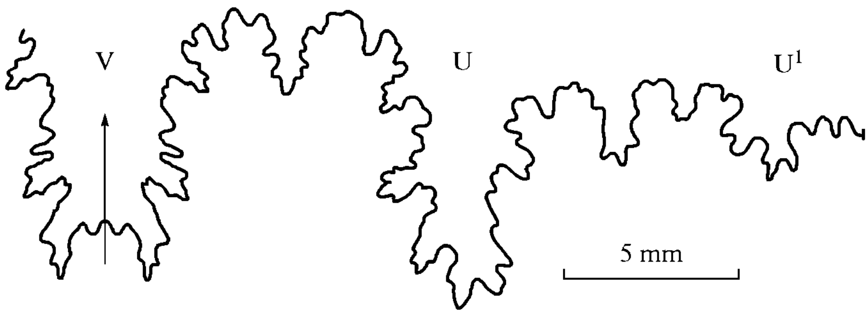


Fig. 45. Suture of *Parahoplites schmidti* Jacob, specimen PIN, no. 5265/18, Dm = 37.0 mm, WH = 16.0 mm, WW = 16.4 mm; Dagestan, village of Aya-Makhi; Middle Aptian.

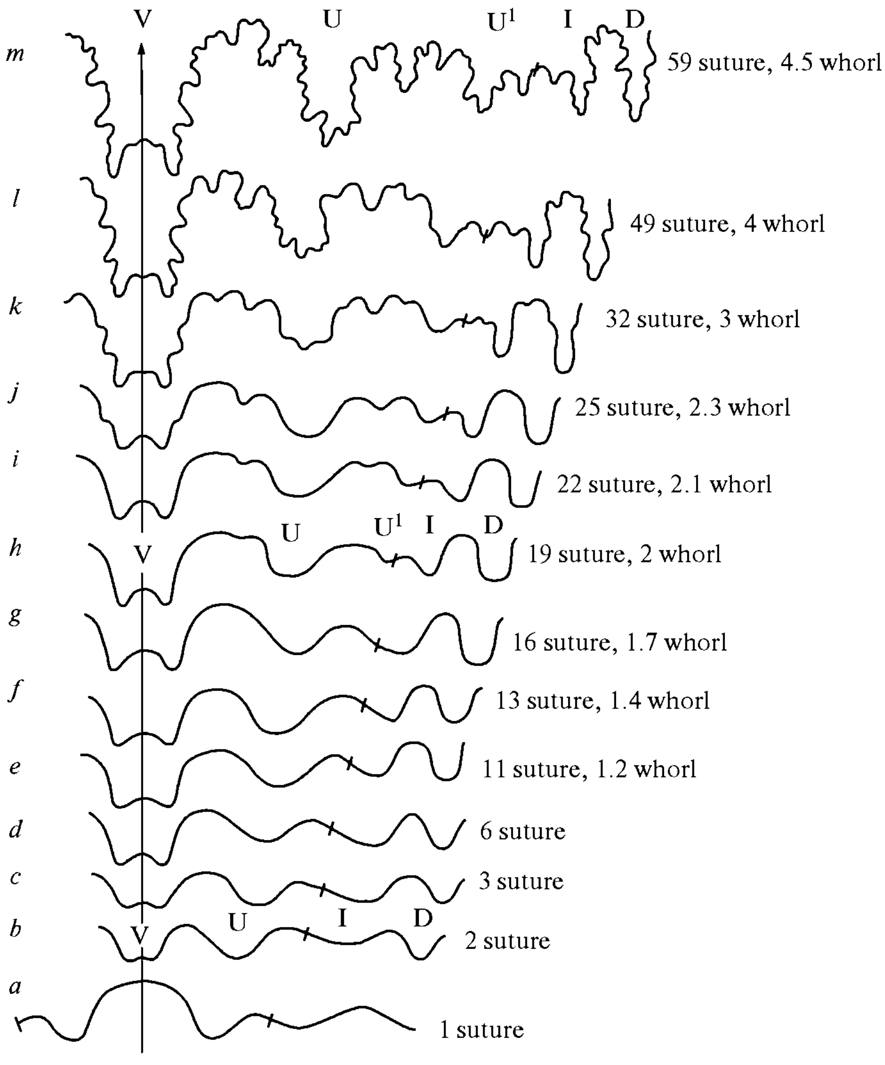
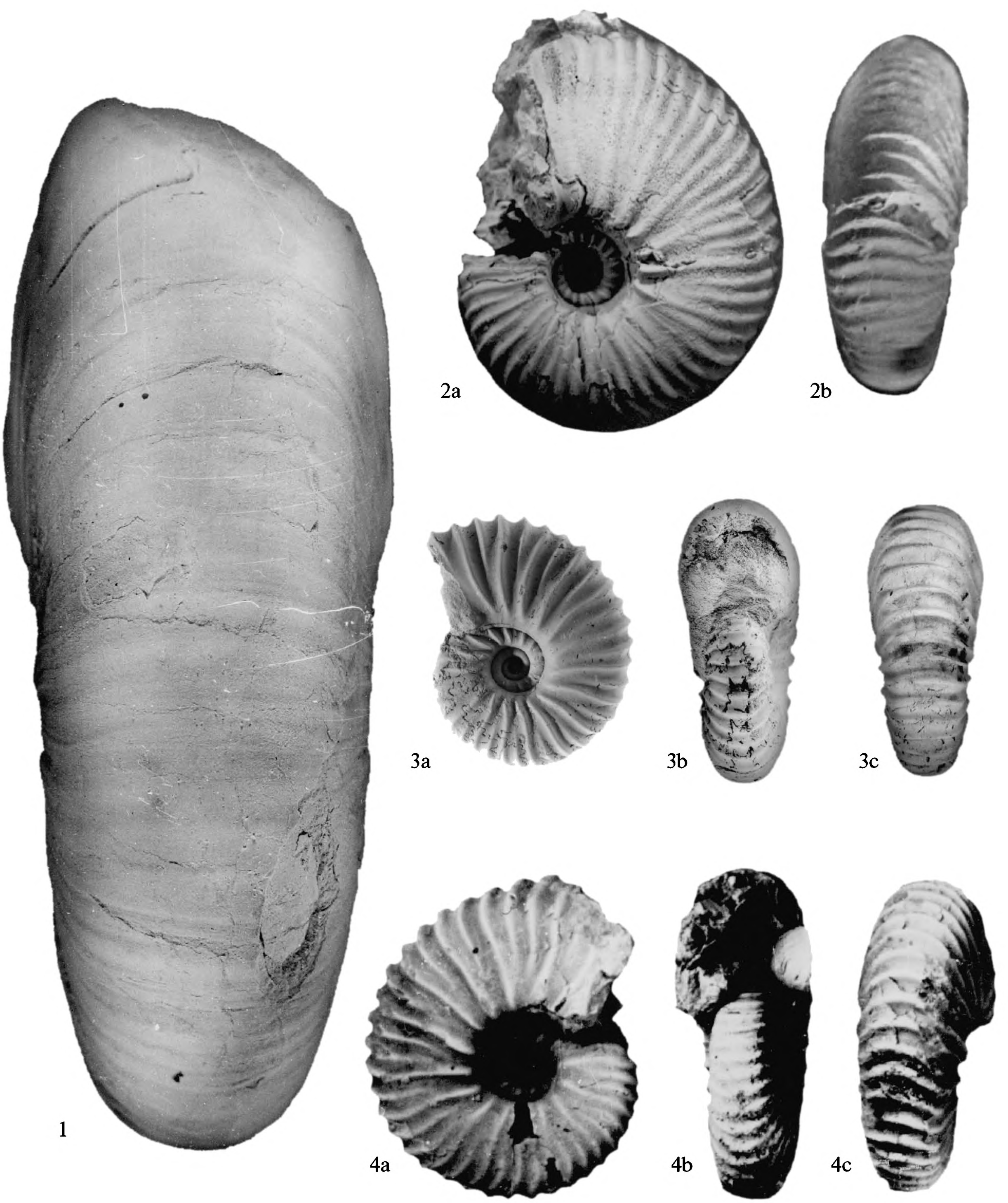


Fig. 46. Morphogenesis of the suture of *Parahoplites schmidti* Jacob, specimen PIN, no. 5265/19: (*a–e*) ×68; (f,) ×60; (*g*) 16th suture, 1.7 whorl, ×59; (*h*) ×47; (*i*) ×40; (*j*) ×36; (*k*) ×22; (*l*) ×13; (*m*) ×9; northern Caucasus, Khokodz River; Middle Aptian.

with a high median saddle; the umbilical lobe is trifid, asymmetrical; the first umbilical lobe is shallow trifid. The saddle (V/U) is considerably higher than the adjacent saddle (U/U^1).

The sutural morphogenesis (Fig. 46) was observed in specimen PIN, no. 5265/19. The prosuture is bilobed, with a high ventral and lower gently sloping dorsal saddle. The primary suture is four-lobed; the

Plate 5



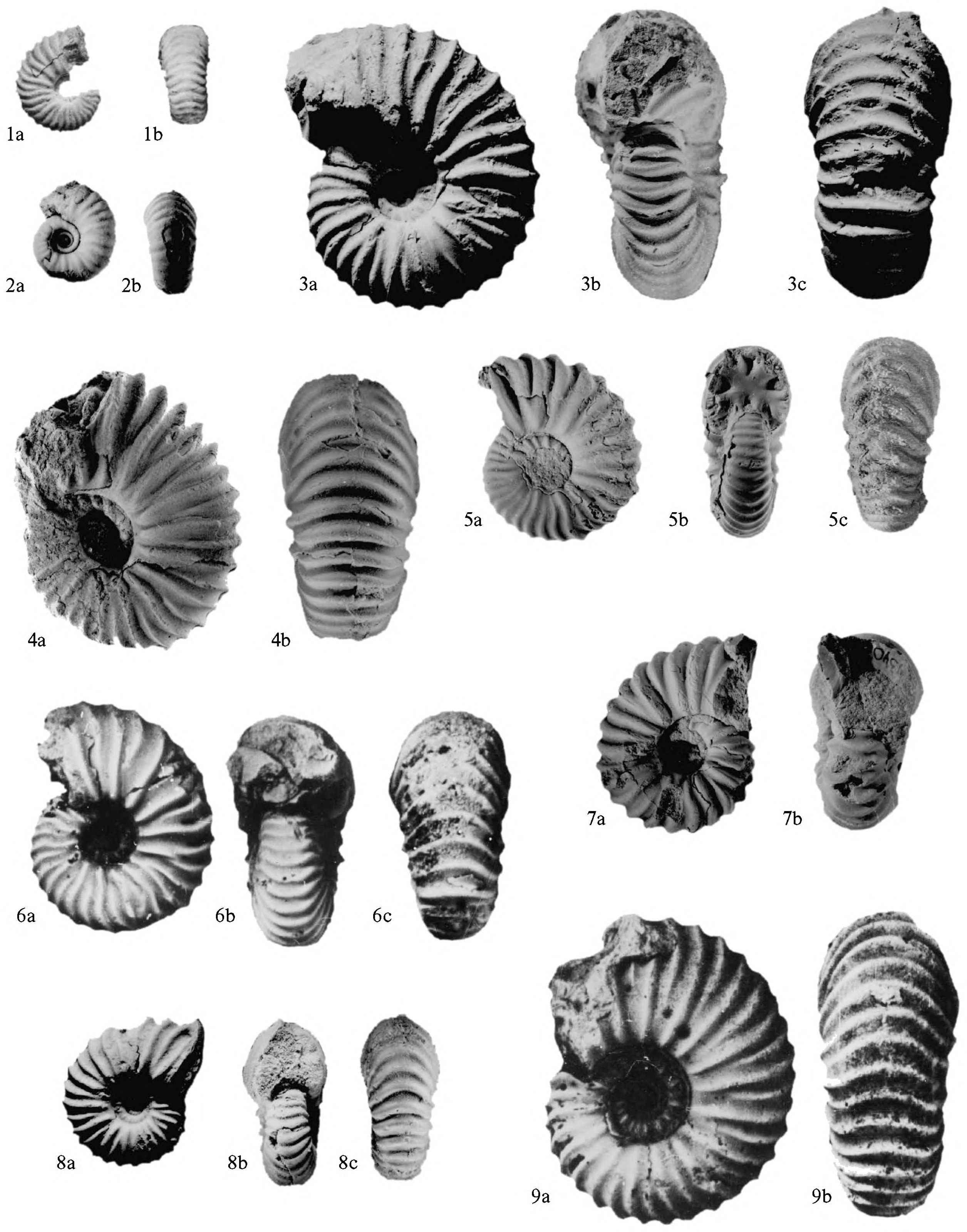
Explanation of Plate 5

Fig. 1. *Parahoplites sjogreni* Anthula, 1899; specimen PIN, no. 5265/124; Dagestan, village of Akusha; Middle Aptian, *Parahoplites melchioris* Zone.

Fig. 2. *Parahoplites grossouvrei* Jacob, 1905; specimen PIN, no. 5265/40; Dagestan, village of Aya-Makhi; Middle Aptian, *Parahoplites melchioris* Zone.

Figs. 3 and 4. *Parahoplites transitans* Sinzow, 1907, (3) specimen PIN, no. 5265/143; Dagestan, village of Akusha, Middle Aptian, *Parahoplites melchioris* Zone; (4) specimen TsNIGR Museum, no. 4/10686; Kopet Dagh, village of Danata; the same age.

Plate 6



ventral lobe is bifid and the umbilical, inner lateral, and dorsal lobes are entire. At the end of the second whorl, the fifth lobe U^1 originates in the marginal portion of the low saddle U/I and, simultaneously, the saddle V/U becomes flattened. The lateral digits of the umbilical lobe appear by the end of the third whorl. The existing elements, including the lateral digits on the ventral lobe and distinct bipartition of the saddle U/U^1 appear approximately from the middle of the third whorl.

Comparison. This species is distinguished from *P. melchioris* Anthula by the wider whorls and the more widely spaced ribbing. The similarity between *P. schmidti* Jacob and *Sonneratia dutempleana* d'Orbigny is noteworthy. M.Sh. Jacob noted this similarity, considering that *P. schmidti* was the intercalary link between the genera *Parahoplites* and *Sonneratia.*

Remarks. Fragments figured by Sinzow (1907): TsNIGR Museum, no. 17/11068, pl. 2, figs. 12, 12a and no. 18/11068, pl. 2, figs. 13, 13a should rather belong to *P. multicostatus* Sinzow rather than to *P. schmidti* Jacob. In addition, Sinzow indicated that *P. multicostatus* can have one or two intercalary ribs between the primary ribs (Sinzow, 1907, pp. 466–467).

Roman (1938, p. 349) erroneously assigned this species to the genus *Acanthohoplites,* although it has the typical *Parahoplites* ornamentation and suture.

Occurrence. Russia (northern Caucasus, Dagestan), Turkmenistan (Great and Lesser Balkhans, Kopet Dagh); Middle Aptian, *Parahoplites melchioris* Zone; Switzerland; Aptian.

Material. Seventeen specimens, two of which are distorted. The shell layer is incompletely preserved in two specimens. The body chamber is partly or completely present in most specimens. Northern Caucasus: Baksan River (PIN, no. 5265/13), Khokodz River (PIN, no. 5265/19); Dagestan: village of Aya-Makhi (PIN, nos. 5265/17,. 5265/18), village of Khuchni (PIN, nos. 5265/15, 5265/133), village of Akusha (PIN, nos. 5265/14, 5265/49, 5265/189), village of Dagva (PIN, nos. 5265/134, 5265/135, 5265/136), village of Gergebil (PIN, no. 5265/123); Tuarkyr, Babashi well (PIN, no. 5265/16); Great Balkhan, Utuludzha well (TsNIGR Museum, no. 7/10686); Lesser Balkhan, Torengly well (TsNIGR Museum, no. 6/10686); Kopet Dagh, Temen Spring (PIN, no. 5265/ 220); Middle Aptian, *Parahoplites melchioris* Zone.

Parahoplites multicostatus **Sinzow, 1907**

Plate 7, figs. 1–9

Parahoplites multicostatus: Sinzow, 1907, p. 459, pl. 2, figs. 5, 7–11 (non fig. 6 = *P transitans*); Sinzow, 1913, p. 110, pl. 6, figs. 6–6c; Luppov et al., 1949, p. 229, pl. 66, fig. 4; Kudryavtsev, 1960, p. 317; pl. 5, fig. 4; Eristavi, 1961, p. 54, pl. 2, fig. 5; Egoian, 1969, p. 150, pl. 8, fig. 2; pl. 22, fig. 24; Kemper, 1971, pl. 26, fig. 3.

Parahoplites schmidti: Sinzow, 1907, p. 466, pl. 2, figs. 12, 12a, 13, and 13a.

Lectotype. TsNIGR Museum, no. 6/11068; specimen figured by Sinzow (1907, pl. 2, figs. 7, 8); Kazakhstan, Mangyshlak, Kyzyl-Kaspak Range; Aptian, *Parahoplites melchioris* Zone; designated here.

Shell shape. (Fig. 47a). The shell is semi-involute. The cross section varies from subquadrate, rounded trapezoid to almost oval in some specimens. The umbilicus is relatively wide. The umbilical wall is steep. In the first three whorls, the shell is semi-evolute, with a low-elliptical cross section; from the end of the fourth whorl, the height of the cross section rapidly increases.

Dimensions in mm and ratios:

Specimen PIN, no.	Dm	WH	WW	UW	WH/ Dm	WW/ Dm	UW/ Dm
5265/27	21.0	9.6	9.4	6.2	0.46	0.45	0.29
5265/115	27.5	13.0	12.5	7.3	0.47	0.47	0.26
5265/28	35.5	17.0	16.5	9.8	0.48	0.47	0.28
5265/29	36.0	17.4	15.0	9.5	0.48	0.42	0.26
5265/30	40.0	19.5	19.0	9.2	0.48	0.47	0.23
5265/31	41.3	19.7	19.2	10.4	0.47	0.46	0.25
5265/113	41.5	20.9	19.8	9.3	0.50	0.47	0.22
5265/32	48.5	25.6	26.5	12.3	0.52	0.54	0.25
5265/33	62.6	29.0	26.7	16.1	0.46	0.42	0.25
5265/34	85.0	37.0	37.1	22.5	0.43	0.43	0.26

Ornamentation. The shell is covered by well-pronounced ribs, the number of which increases with age: at the shell diameter 21 mm, there are 35 primary and intercalary ribs; at the diameter 40 mm, 39 ribs; and at the diameter 75–85 mm, 43–46 ribs. Approximately six ribs are per half whorl. The primary ribs begin in the upper third of the umbilical wall and on the umbilical shoulder form longitudinal bullae; on the flank, they are curved weakly forward and, then, backward; on the venter, the primary ribs slightly widen and are slightly inclined; in some specimens, the forward inclination of the ribs is almost absent and do not expand.

Explanation of Plate 6

Figs. 1–9. *Parahoplites schmidti* Jacob, 1906; specimens: (1) PIN, no. 5265/13; northern Caucasus, Baksan River, Middle Aptian, *Parahoplites melchioris* Zone; (2) PIN, no. 5265/14; Dagestan, village of Akusha, the same age; (3) PIN, no. 5265/18; (4) PIN, no. 5265/17; Dagestan, village of Aya-Makhi, the same age; (5) PIN, no. 5265/16; Tuarkyr, Babashi well, the same age; (6) TsNIGR Museum, no. 6/10686; Lesser Balkhan, Torengly well, the same age; (7) PIN, no. 5265/49; Dagestan, village of Akusha, the same age; (8) PIN, no. 5265/15; Dagestan, village of Khuchni, the same age; (9) TsNIGR Museum, no. 7/10686; Great Balkhan, Utuludzha well, the same age.

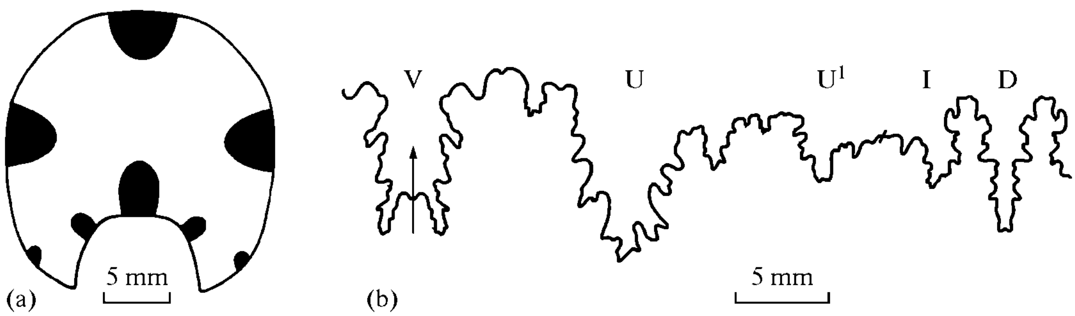


Fig. 47. *Parahoplites multicostatus* Sinzow: (a) specimen PIN, no. 5265/33, cross section, WW = 20.5 mm; (b) specimen PIN, no. 5265/31, suture, WW = 17.3 mm; Dagestan, village of Aya-Makhi; Middle Aptian.

The intercalary ribs, usually one between two primaries, begin below the mid-flank and its upper third and, on the venter, are not different from the primaries.

The wedging ribs are frequently present and, on the flanks, similar to a combination of the primary and intercalary ribs. This type of ribbing is observed in more than half specimens studied.

Ornamentation morphogenesis. The first one and a half whorls are smooth, the end of the second and third whorls possess microscopic tubercles, the number of which does not exceed ten, after which the shell again becomes smooth. On the fourth whorl, hardly noticeable ribs appear, initially visible only on the flanks.

S u t u r e. The suture is typical of the genus *Parahoplites.* At the base of the dorsal lobe, a small saddle emerges, implying its bipartition (Fig. 47b). The saddles V/U and U/U^1 are asymmetrical bifid, but the first is considerably higher than the second. The saddle U^1/I lying on the seam is low, trifid, relatively symmetrical. The saddle I/D is trifid with raised central part.

The morphogenesis of the suture is observed from 1.7 whorls (Fig. 48). The ventral lobe is bifid; the umbilical lobe is deeper, asymmetrically trifid: its inner digit approaches the central digit and, sometimes, the lobe base has a feather-like termination. The first umbilical lobe is short, weakly dissected; the inner lateral lobe is deeper. The dorsal lobe has a wider upper and narrower lower part.

V a r i a b i l i t y. Specimen PIN, no. 5265/115 is recognized by almost a quadrate whorl cross section with a flat, wide venter.

C o m p a r i s o n. The species described is distinguished from *P. transitans* Sinzow by the wider whorls and many ribs. Young specimens of *P. multicostatus* are readily distinguished from those of *P. melchioris* by the thin distinct ribs; in the second species at the same size (about 20–25 mm), ribs are indistinct and wide. The distinction of the adult specimens was indicated in the description of *P. melchioris.*

R e m a r k s. Specimens in the I.F. Sinzow collection (TsNIGR Museum: no. 6/11068, pl. 2, figs. 7, 8; no. 7/11068, pl. 2, fig. 9; no. 8/11068, pl. 2, fig. 11) have wedging ribs. Humphrey (1949) described *P. multicostatus* from the Lower Cretaceous La Pen[tilde]a Formation of Mexico. The specimen figured by him resembles the species established by Sinzow, but their identity is difficult to support, because they are geographically isolated.

Specimen *Parahoplites* aff. *multicostatus* Sinzow (Drushchits et al., 1981, p. 102, pl. 1, fig. 9) housed in the Museum of Earth Sciences of Moscow State University (MZ MGU, no. 9/79) certainly belongs to the genus *Parahoplites,* but its identification to species is difficult because of the strong distortion.

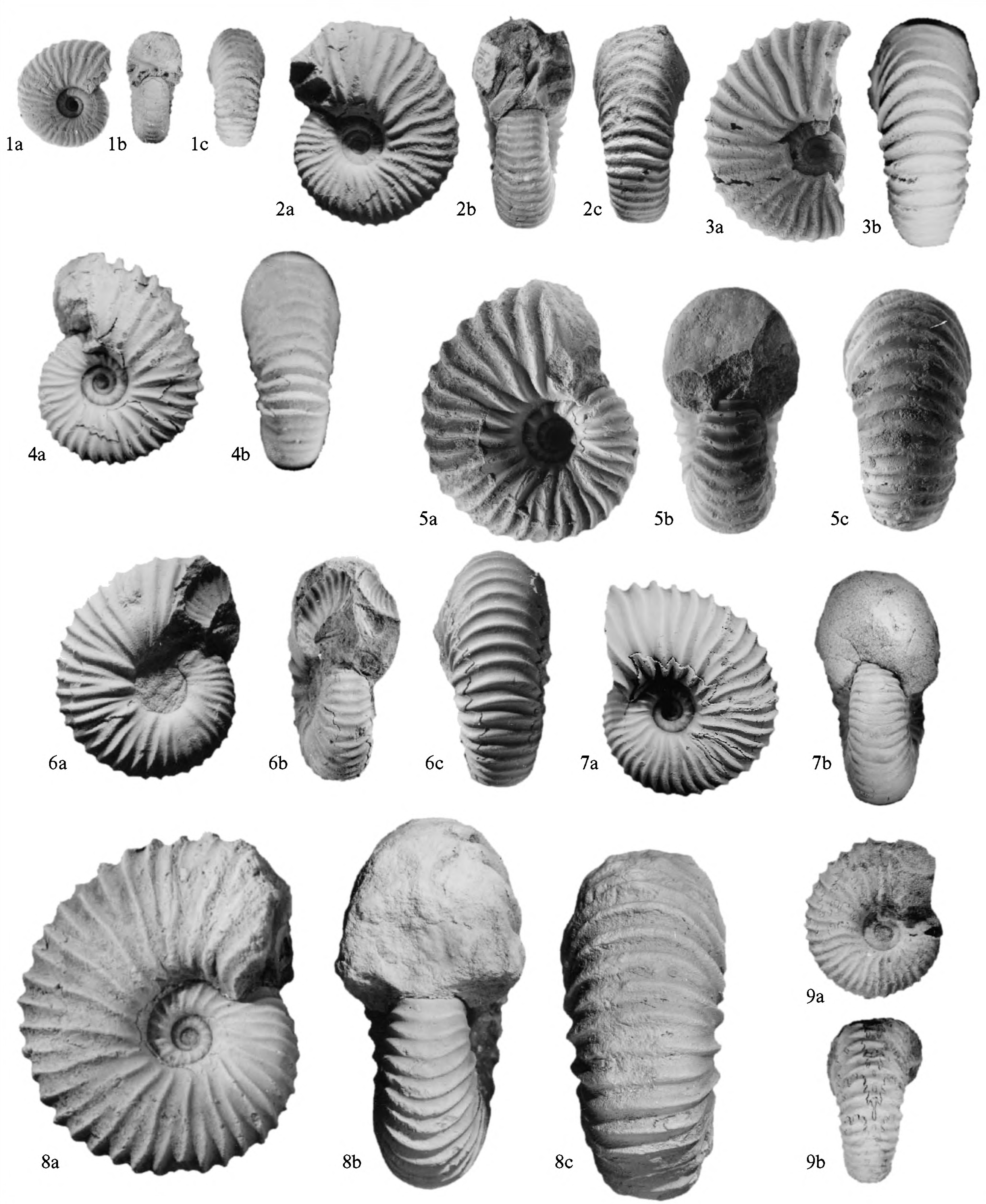
O c c u r r e n c e. Russia (northern Caucasus, Dagestan), Kazakhstan (Mangyshlak), Turkmenistan (Tuarkyr); Middle Aptian, *Parahoplites melchioris* Zone; northern Germany; Middle Aptian, *Parahoplites nutfieldiensis–Parahoplites melchioris* Zone.

M a t e r i a l. Over ten complete specimens from 21 to 85 mm in diameter and many fragments, some of them with a shell layer. The body chamber occupies half of the last whorl. Northern Caucasus: Gundelen River (PIN, nos. 5265/125, 5265/129, 5265/151), Abin River (PIN, no. 5265/32); Dagestan: village of Aya-Makhi (PIN, nos. 5265/27, 5265/28, 5265/30, 5265/31, 5265/33, 5265/34, 5265/113, 5265/127, 5265/128, 5265/176); village of Dagva (PIN, nos. 5265/29, 5265/115, 5265/126); Tuarkyr, Babashi well

Explanation of Plate 7

Figs. 1–9. *Parahoplites multicostatus* Sinzow, 1907; specimens: (1) PIN, no. 5265/27; (2) PIN, no. 5265/28; (3) PIN, no. 5265/31; Dagestan, village of Aya-Makhi, Middle Aptian, *Parahoplites melchioris* Zone; (4) PIN, no. 5265/29; Dagestan, village of Dagva, the same age; (5) PIN, no. 5265/32; northern Caucasus, Abin River, the same age; (6) PIN, no. 5265/30; (7) PIN, no. 5265/113; (8) PIN, no. 5265/33; Dagestan, village of Aya-Makhi, the same age; (9) specimen PIN, no. 5265/115; Dagestan, village of Dagva, the same age.

Plate 7



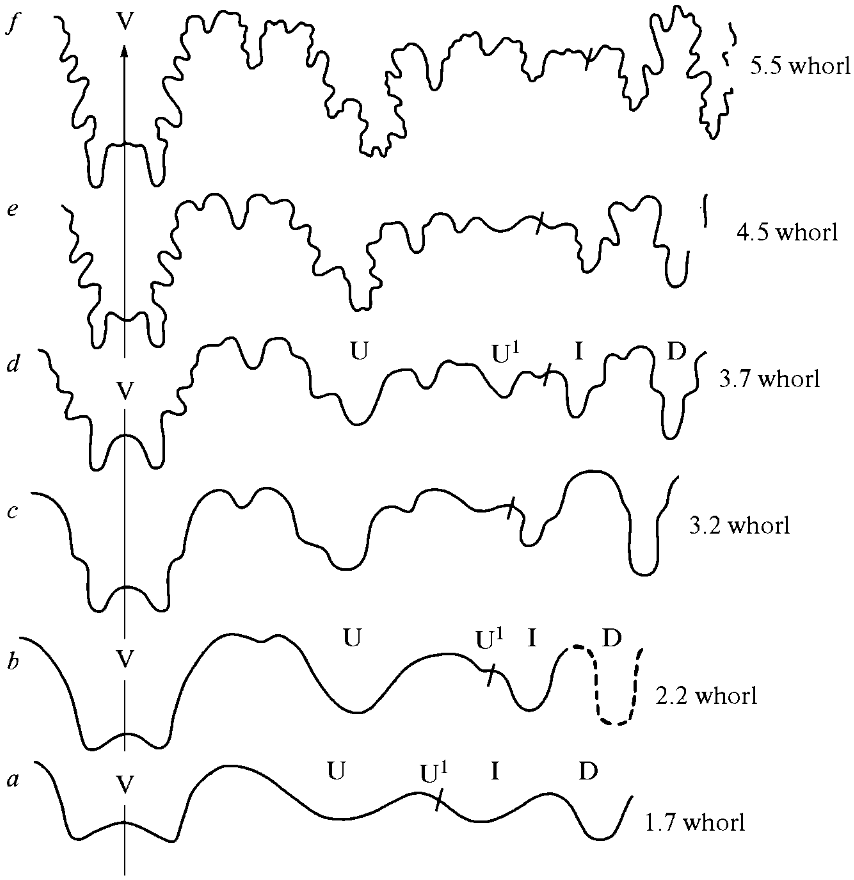


Fig. 48. Morphogenesis of the suture of *Parahoplites multicostatus* Sinzow; specimen no. 86/10013: (*a*) ×130; (*b*) ×68; (*c*) ×37; (*d*) ×26; (*e*) ×16; (*f*) ×7; Mangyshlak; Middle Aptian.

(PIN, nos. 5265/130, 5265/153, 5265/154, 5265/155); Middle Aptian, *Parahoplites melchioris* Zone.

Parahoplites transitans **Sinzow, 1907**

Plate 5, figs. 3 and 4; Plate 8, figs. 1–5

Parahoplites multicostatus var. *transitans:* Sinzow, 1907, p. 459, pl. 2, fig. 6; Glazunova, 1953, p. 26, pl. 2, figs. 3–6; Eristavi, 1961, p. 54, pl. 2, fig. 6.

Parahoplites melchioris: Sinzow, 1907, p. 458, pl. 2, fig. 1.

Parahoplites transitans: Kudryavtsev, 1960, p. 314, pl. 2, fig. 3; pl. 3, fig. 1.

Holotype. TsNIGR Museum, no. 9/11068; specimen figured by Sinzow (1907, pl. 2, fig. 6); Aptian, *Parahoplites melchioris* Zone; Kazakhstan, Mangyshlak, Karakuduk well; designated here by monotypy.

Shell shape. The shell is semi-involute, with the whorls overlapping by almost half the whorl height. The cross section is rounded rectangular, with the maximum whorl width in the umbilical edge (Fig. 49a). The flanks are weakly convex. The venter is wide and rounded. The umbilicus is relatively wide, with a steep umbilical wall.

Dimensions in mm and ratios:

Specimen no.	Dm	WH	WW	UW	WH / Dm	WW / Dm	UW / Dm
PIN 5265/22	21.7	9.3	10.0	5.9	0.43	0.46	0.27
PIN 5265/143	45.0	21.1	17.2	13.1	0.47	0.39	0.29
PIN 5265/175	45.0	20.0	19.2	12.1	0.44	0.42	0.27
PIN 5265/23	48.8	22.6	21.7	11.5	0.46	0.44	0.24
TsNIGR Museum 56/10686	50.2	20.7	19.9	14.4	0.41	0.40	0.28
TsNIGR Museum 4/10686	51.1	23.5	20.0	14.0	0.46	0.39	0.27
PIN 5265/24	52.8	24,9	21.0	13.2	0.45	0.39	0.25
PIN 5265/142	61.2	26.0	22.5	15.0	0.42	0.36	0.24
PIN 5265/25	66.2	29.0	25.5	17.5	0.44	0.39	0.26
PIN 5265/26	70.5	31.5	27.7	17.7	0.45	0.39	0.25
PIN 5265/132*	74.9	30.5	32.0	28.8	0.40	0.43	0.33

* Specimen PIN, no. 5265/132, possibly because of the deformation, has a wider umbilicus and a wider whorl, while the ornamentation remains the same.

Ornamentation. The first two and a half whorls are smooth. Only at the end of the second–

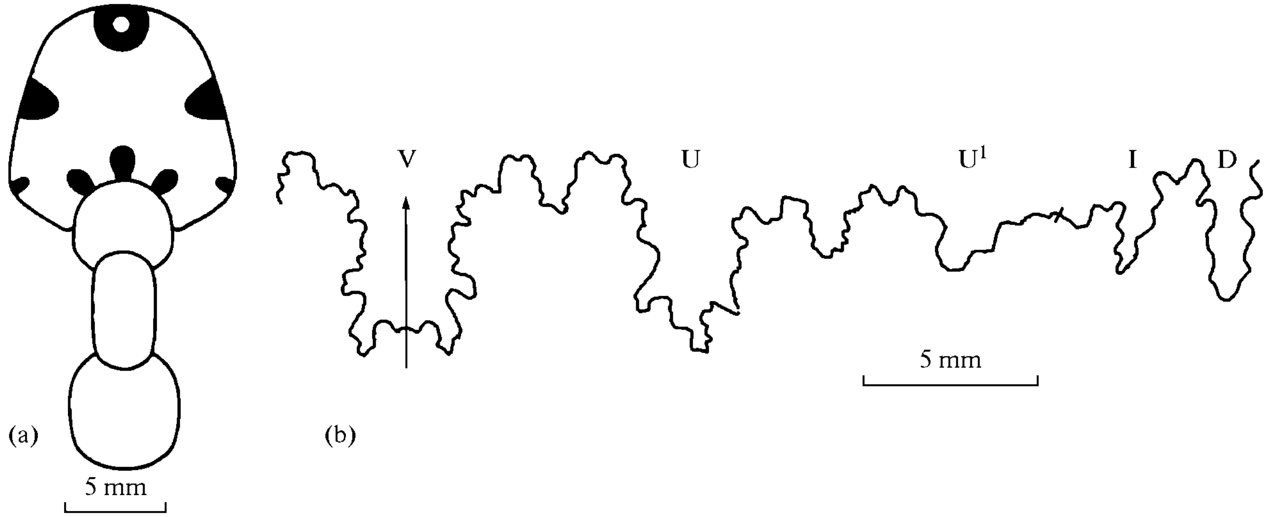


Fig. 49. *Parahoplites transitans* Sinzow, specimen PIN, no. 5265/24: (a) whorl cross section at Dm = 31 mm and WW = 11.1 mm; (b) suture at WW = 120 mm; Dagestan, village of Khuchni, Middle Aptian.

beginning of the third whorl, eight–nine microscopic tubercles are noticeable for one whorl. At diameter about 10 mm, hardly noticeable ribs appear. At the diameter from 40 to 80 mm, the shell is covered with coarse ribs directed anteriorly on the venter (from 37 to 41 ribs per whorl). Five or six ribs occupy a distance equal to the whorl height. The primary ribs begin on the umbilical shoulder, rapidly increase, on the flank, almost rectiradiate and are inclined weakly forward on the venter. The intercalary ribs, one between two primaries, begin near the mid-flank, gradually increase and on the venter become as strong as the primary ribs. Sometimes regions of wedging ribs are observed.

S u t u r e. (Fig. 49b). The ventral lobe is deep and bifid. The umbilical lobe is as deep as the ventral lobe, trifid, finely serrated, and relatively symmetrical. The first umbilical lobe is shallow, trifid, and asymmetrical. The inner lateral lobe is deeper than the first umbilical lobe and is indistinctly trifid in outline. The dorsal lobe is trifid at the base, almost as deep as the ventral lobe. The external (V/U) saddle and adjacent saddle U/U^1 are wide and bifid. The first is considerably higher than the second. The narrow bifid inner saddle (I/D) is as high as the lateral saddle. The saddle is intersected by the seam (U^1/I), has a distinctly delineated bifid inner branch.

C o m p a r i s o n a n d r e m a r k s. Sinzow (1907) figured as *P. multicostatus* var. *transitans* a specimen (TsNIGR Museum, no. 9/11068, pl. 2, fig. 6) from the Middle Aptian of Mangyshlak. In the text, he noted this variety, but did not list any typical characters. One of our specimens from Dagestan (PIN, no. 5265/24) is identical to that of Synzow. We understand this variety as species, despite its being close to *P. melchioris* and *P. multicostatus* Sinzow. This species is distinguished from *P. melchioris* by the higher number of less strongly curved ribs and from *P. multicostatus* by the fewer ribs. The specimen figured in the same Sinzow's paper in pl. 2, fig. 1 as *P. melchioris* (TsNIGR Museum, no. 1/11068) is more similar to *P. transitans* than to *P. melchioris,* hence, we included it in synonyms of the species described.

Glazunova (1953, p. 26, pl. 2, figs. 3–7) described the same variety of *transitans* as Sinzow, but assigned it to *P. melchioris* rather than *P. multicostatus.* Specimens she figured are considerably wider than our specimens of *P. transitans* and cannot be assigned to the same species.

O c c u r r e n c e. Russia (northern Caucasus, Dagestan), Kazakhstan (Mangyshlak), Turkmenistan (Tuarkyr, Kopet Dagh); Middle Aptian, *Parahoplites melchioris* Zone.

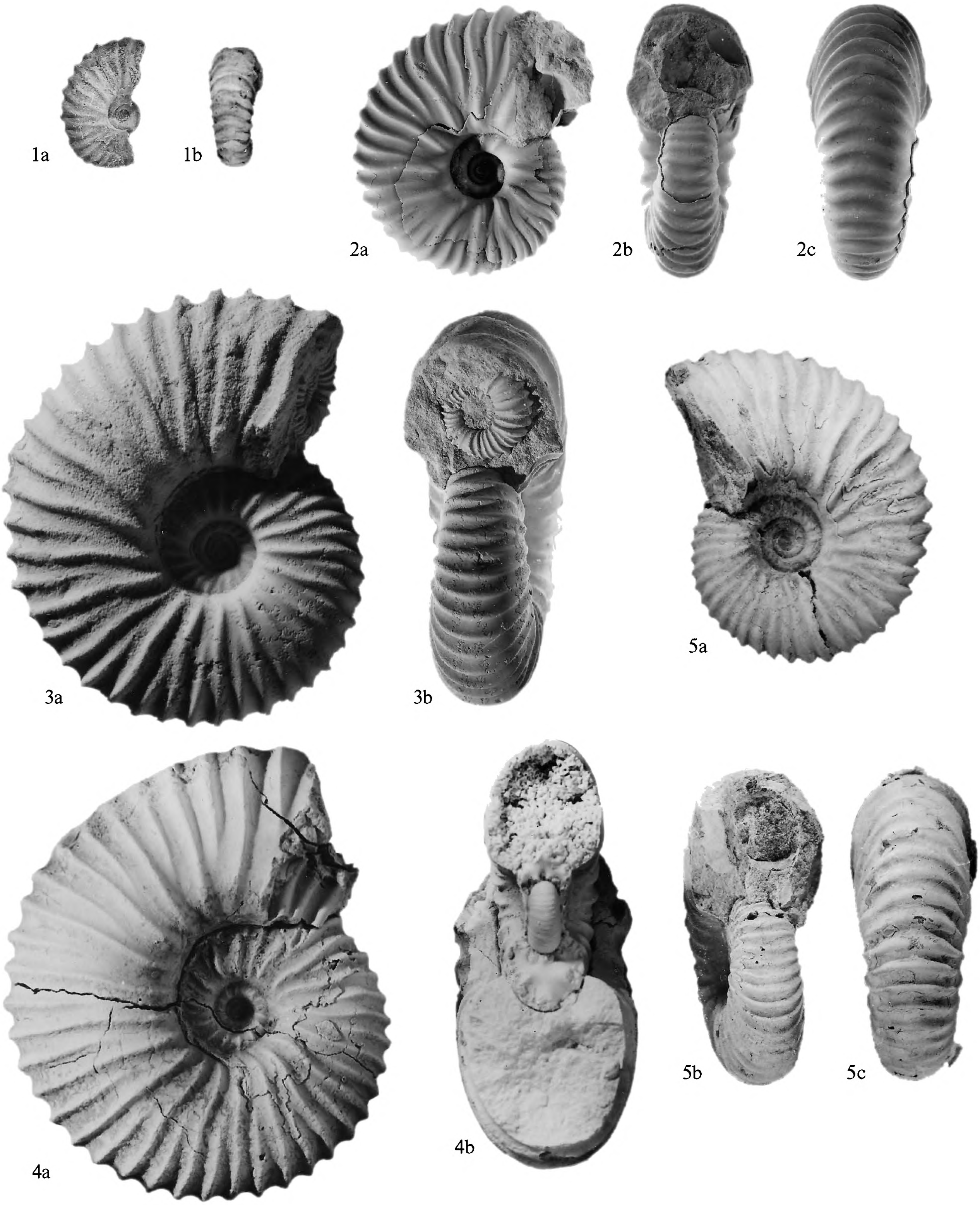
M a t e r i a l. Ten complete specimens from 19.4 to 80 mm in diameter and several fragments, shell is usually not preserved. The body chamber occupies more than half of the last whorl. Northern Caucasus, Kheu River (PIN, no. 5265/142); Dagestan: village of Dagva (PIN, nos. 5265/22, 5265/25), village of Aya-Makhi (PIN, no. 5265/26), village of Ayalakab (PIN, no. 5265/167), village of Akusha (PIN, nos. 5265/23, 5265/143), village of Kikuni (PIN, no. 5265/132), village of Khuchni (PIN, nos. 5265/24, 5265/175); Tuarkyr, Tekedzhik Range (PIN, no. 5265/141); Kopet Dagh, village of Danata (TsNIGR Museum, nos. 4/10686; 56/10686); Middle Aptian, *Parahoplites melchioris* Zone.

Parahoplites maximus Sinzow, 1907

Plate 9, fig. 1; Plate 10, fig. 1; Plate 11, figs. 1 and 2

Parahoplites maximus: Sinzow, 1907, p. 464, pl. 1. figs. 1–3; Rouchadze, 1938a, pp. 145, 201; Kudryavtsev, 1960, p. 315, pl. 3, figs. 4a and 4b; pl. 5, figs. 4a and 4b; Kemper, 1976, pl. 30, fig. 15; Sharikadze et al., 2004, p. 407, pl. 84, fig. 1; pl. 85, fig. 1; Raisossadat, 2006, text-fig. 5M.

Plate 8



Explanation of Plate 8

Figs. 1–5. *Parahoplites transitans* Sinzow, 1907; specimens: (1) PIN, no. 5265/22; Dagestan, village of Dagva; Middle Aptian, *Parahoplites melhioris* Zone; (2) PIN, no. 5265/23; Dagestan, village of Akusha; the same age; (3) PIN, no. 5265/25; (4) PIN, no. 5265/26; Dagestan, village of Dagva; the same age; (5) PIN, no. 5265/24; Dagestan, village of Khuchni; the same age.

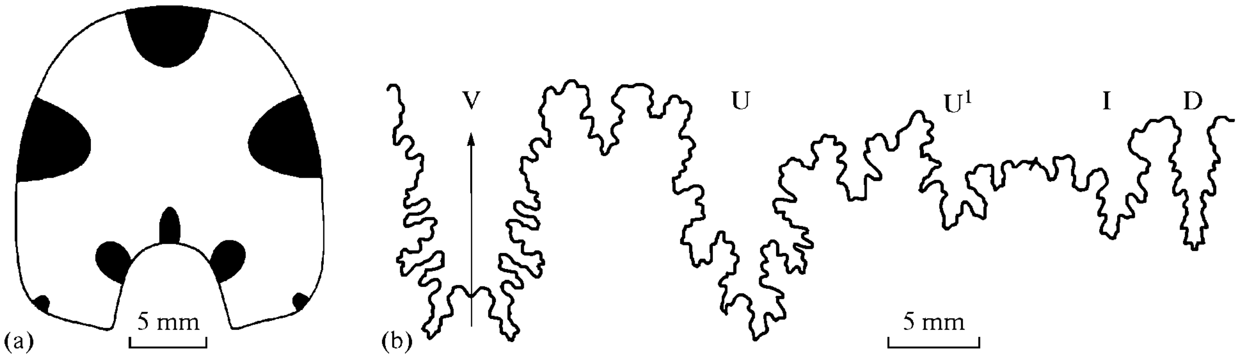


Fig. 50. *Parahoplites maximus* Sinzow, specimen PIN, no. 5265/36: (a) whorl cross section at WW = 20.5 mm; (b) suture at WW = 21.7; Dagestan, village of Dagva; Middle Aptian.

L e c t o t y p e. Specimen figured by Sinzow (1907, pl. 1, fig. 1); Aptian, *Parahoplites melchioris* Zone; Kazakhstan, Mangyshlak, Torysh spring. Designated by Casey (1965, p. 409). Unfortunately, Casey shows a specimen which is presently missing from the Sinzow collection in the TsNIGR Museum (no. 11068), whereas the incomplete specimen no. 14/11068 is present.

S h e l l s h a p e. The shell is semi-involute, the whorl overlap is more than half of the whorl height. The whorl cross section (Fig. 50a) is subtrapezoid, with the maximum width lying in the lower part of the flank. The venter is rounded, the flanks are flattened. The umbilical wall is high and steep. The umbilicus is narrow.

D i m e n s i o n s i n m m a n d r a t i o s:

Specimen PIN, no.	Dm	WH	WW	UW	WH/Dm	WW/Dm	UW/Dm
5265/36	76.2	40.0	31.5	14.7	0.52	0.41	0.19
5265/140	86.5	47.0	45.5	11.5	0.54	0.62	0.14
5265/37	90.0	47.5	31.0	18.0	0.53	0.34	0.20
5265/139	115.0	56.6	51.0	17.1	0.49	0.44	0.14
5265/152	160.0	76.6	66.9	41.5	0.47	0.41	0.25

O r n a m e n t a t i o n. The shell (Dm = 77 mm) is covered by indistinct slightly protruding ribs (25 per half of the last whorl). The primary ribs begin on the umbilical shoulder and run on the flanks almost rectiradiate up to its upper third, where they are slightly bent backwards, forming a weak forward curvature on the venter. One or two intercalary ribs are present between two primary ribs. The intercalary ribs begin in the mid-flank, slightly below or above it. At the shell diameter higher than 50 mm, ribs become weaker in mid-flank; in large shells, there are distinct ribs only on the venter and umbilical shoulder. In younger whorls, the ornamentation is sharper and resembles that of *P. multicostatus* Sinzow.

S u t u r e. (Fig. 50b). The ventral lobe has a low median saddle. The trifid umbilical lobe is as deep, and with a strongly developed central branch. The shallow first umbilical lobe is asymmetrically trifid. The inner lateral lobe is as deep as the first umbilical lobe. The dorsal lobe is shorter than the umbilical and ventral lobes and with wide upper and narrower lower part. The flattened base of the dorsal lobe has a small saddle. The saddles V/U and U/U^1 are asymmetrically bifid, with relatively deep secondary lobes. The saddle U^1/I lies on the seam, the lowest of all, very broad, quadrimodal. The saddle I/D has a wavy mushroom-shaped outline.

C o m p a r i s o n. This species at the diameter of 70–80 mm is most similar to *P. subcampichei* Sinzow and *P. grossouvrei* Jacob, and larger specimens are similar to *P. sjogreni* Anthula. It is distinguished from the first species by the trapezoid outline of the cross section and somewhat wider whorl. It differs from *P. grossouvrei* in the whorls narrower than the height and the different type of ribbing. At a shell diameter less than 45 mm, *P. maximus* Sinzow is similar to *P. multicostatus* Sinzow, like young whorls of *P. subcampichei* Sinzow resemble *P. melchioris* Anthula.

R e m a r k s. The collection of TsNIGR Museum contains specimen no. 14/11068 (Sinzow, 1907, pl. 1, fig. 3) from a section near the Kara-Kuduk well (Kazakhstan, Mangyshlak). From the vicinity of Guselki (Middle Volga Region north of Saratov), Glazunova (1973, pp. 14, 136) recorded *Parahoplites* cf. *maximus* Sinzow in association with *Epicheloniceras volgense* Wassiliewsky. Unfortunately, the specimen she described (TsNIGR Museum, no. 312/8196) is incompletely preserved and can be with certainty identified only to genus. Based on the association with *Epicheloniceras volgense* Glazunova assigned the host beds to the *Epicheloniceras tschernyschewi* Zone. In addition, Glazunova (1973, p. 14) mentioned the occurrence in the same region of *Prahoplites melchioris* Anthula, but rejected Sazonova's proposal to recognize *Parahoplites melchioris* Zone (Sazonova, 1958, p. 126). The subdivision into the zones *Epiche-*

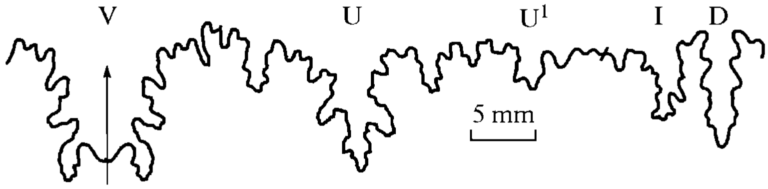


Fig. 51. Suture of *Parahoplites subcampichei* Sinzow, specimen PIN, no. 5265/35, WW = 23 mm; Dagestan, village of Dagva; Middle Aptian.

loniceras tschernyschewi and *Parahoplites melchioris* was published three years later (Sazonova, 1961).

O c c u r r e n c e. Russia (northern Caucasus, Dagestan), Kazakhstan (Mangyshlak), Turkmenistan (Tuarkyr); Middle Aptian, *Parahoplites melchioris* Zone; Iran; middle part of the Sangane Formation; northern Germany; Middle Aptian, *Parahoplites nutfieldiensis–Parahoplites melchioris* Zone; Colombia; Middle Aptian.

M a t e r i a l. Five specimens, one of which has a shell layer preserved. Dagestan: village of Aya-Makhi (PIN, nos. 5265/36; 5265/37), village of Dagva (PIN, no. 5265/152); Tuarkyr: Babashi well (PIN, nos. 5265/139, 5265/140); Middle Aptian, *Parahoplites melchioris* Zone.

Parahoplites subcampichei **Sinzow, 1907**

Plate 3, fig. 2

Parahoplites sub-Campichei: Sinzow, 1907, p. 463, pl. 1, figs. 8 and 9.

Parahoplites grossouvrei: Sinzow, 1907, p. 465, pl. 1, figs. 10 and 11.

Parahoplites sub-campichei: Rouchadze, 1938a, pp. 144, 170; Luppov et al., 1949, p. 229, pl. 66, fig. 2, text-fig. 57; Glazunova, 1953, p. 29, pl. 3, figs. 1a–1s, 2a–2c.

H o l o t y p e. TsNIGR Museum, no. 13/11068. Specimen figured by Sinzow (1907, pl. 1. figs. 8, 9); Aptian, *Parahoplites melchioris* Zone; Kazakhstan, Mangyshlak, Karakuduk well. Designated here by monotypy.

S h e l l s h a p e. The shell is semi-involute, with whorls embracing each other by two-thirds of the whorl height. The cross section is high-ellipsoidal, the maximum whorl width is slightly below its middle. The venter is rounded. The flanks are weakly convex. The umbilical wall is steep. The umbilicus is relatively narrow.

D i m e n s i o n s i n m m a n d r a t i o s:

Specimen PIN, no.	Dm	WH	WW	UW	WH/Dm	WW/Dm	UW/Dm
5265/35	70.5	34.5	26.7	15.8	0.49	0.38	0.22
5265/170	70.6	35.0	26.5	17.2	0.49	0.37	0.24
5265/169	77.2	38.0	27.2	13.5	0.49	0.37	0.24

O r n a m e n t a t i o n. The shell is covered by weak slightly curved ribs, the total number of which at Dm = 74.5 mm is 43, of these 18 are primary ribs. The primary ribs begin as bullae on the umbilical shoulder, becoming slightly weaker on the flank and running almost straight to form a small bend on the venter. The intermediate intercalary ribs (usually one, less commonly two and exceptionally rarely three, between two primaries) begin at mid-flank, sometimes traced almost to the umbilical shoulder. On the venter, primary and secondary ribs are not distinguished from one another. In shells larger than 45–50 mm in diameter, the ribs on the flank are noticeably weaken and, in large shells, are almost invisible.

S u t u r e. (Fig. 51). The ventral lobe is with a wide low bifid saddle. The asymmetrically trifid umbilical lobe is considerably narrower than the ventral lobe. The first umbilical lobe is short and asymmetrically trifid. The inner lateral lobe is narrow. The dorsal lobe is with a pointed termination. The saddles V/U and U/U^1 are asymmetrically bifid, wide, strongly dissected. The second saddle is lower than the first. The saddle U^1/I is crossed by the seam. The inner saddle (I/D) is high and bifid.

C o m p a r i s o n. *P. subcampichei* is distinguished from *P. maximus* Sinzow by the ellipsoidal rather than rounded trapezoid cross section and the wider umbilicus (0.22–0.24 instead of 0.14–0.20); it differs from *P. grossouvrei* Jacob in the narrower cross section (0.37–0.38 instead of 0.41–0.42) and narrower umbilicus (0.22–0.24 instead of 0.42). This species resembles young shells of *P. melchioris,* but in the latter spe-

E x p l a n a t i o n o f P l a t e 9

Fig. 1. *Parahoplites maximus* Sinzow, 1907; specimen PIN, no. 5265/152; Dagestan, village of Akusha; Middle Aptian, *Parahoplites melchioris* Zone.

Figs. 2 and 3. *Parahoplites artschmanensis* Glazunova, 1953; (2) specimen PIN, no. 5265/20; Dagestan, village of Dagva; Middle Aptian, *Parahoplites melchioris* Zone; (3) specimen PIN, no. 5265/21; Dagestan, village of Arakany; the same age.

Plate 9

1

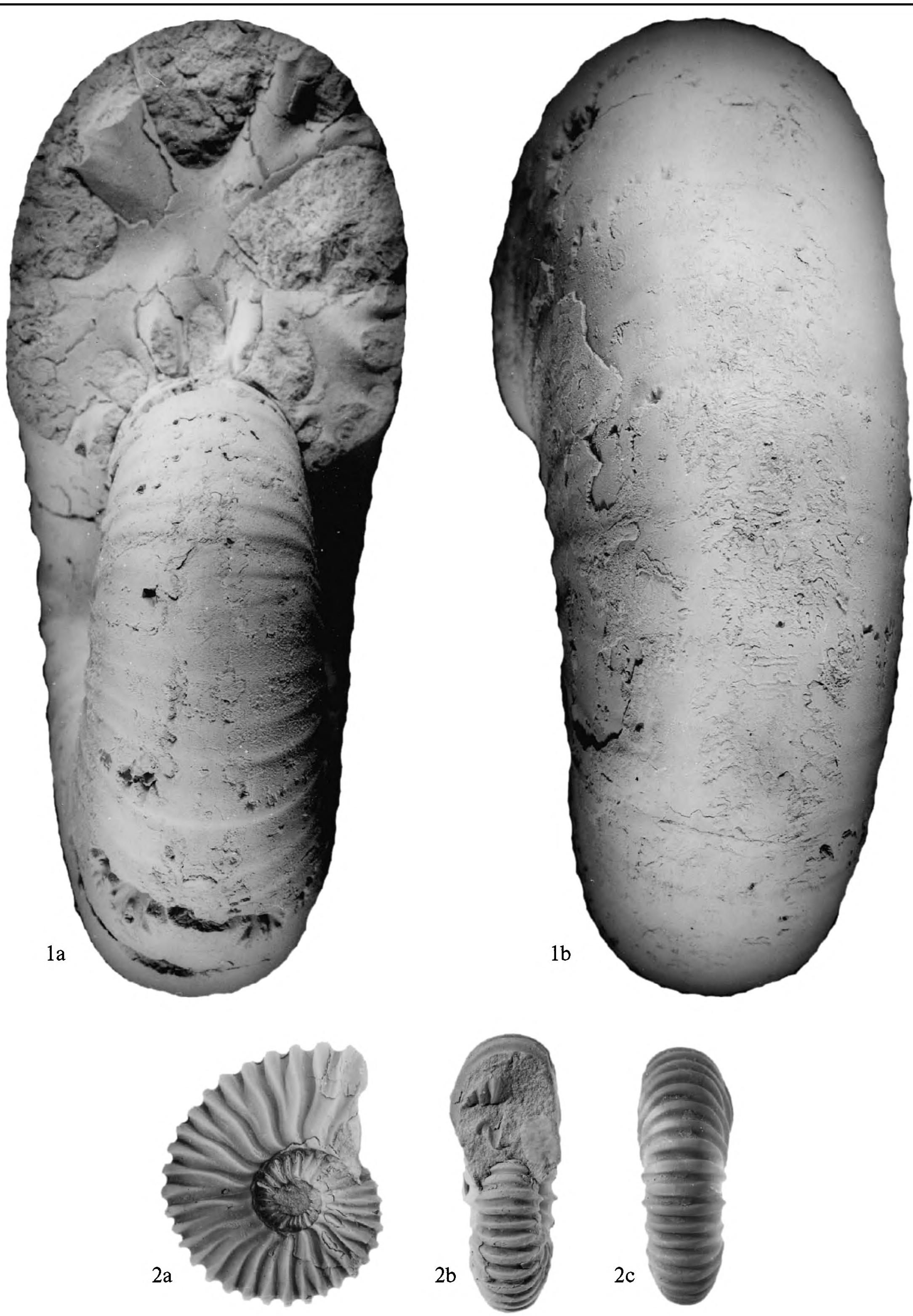
2a

2b

3a

3b

Plate 10



Explanation of Plate 10

Fig. 1. *Parahoplites maximus* Sinzow, 1907; specimen PIN, no. 5265/152; Dagestan, village of Akusha; Middle Aptian, *Parahoplites melchioris* Zone.

Fig. 2. *Colombiceras sinzowi* (Kasansky, 1914); specimen PIN, no. 5265/180; Dagestan, village of Akusha; Middle Aptian.

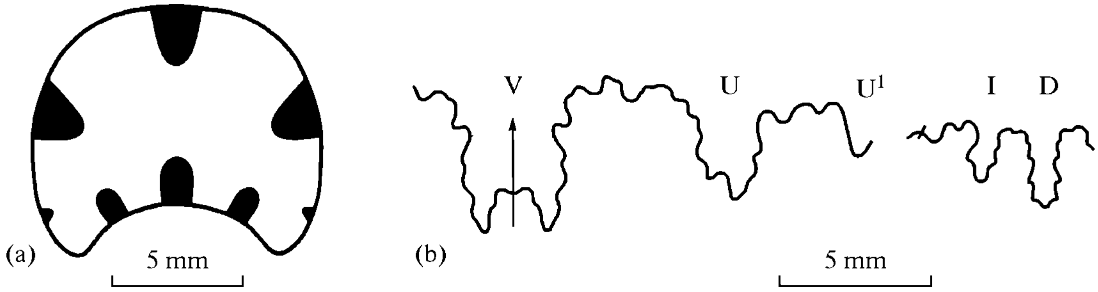


Fig. 52. *Parahoplites artschmanensis* Glasunova, specimen PIN, no. 5265/21: (a) whorl cross section; (b) suture at WW = 9.8 mm and WH = 8.7 mm; Dagestan, village of Arakany; Middle Aptian.

cies, the umbilicus is somewhat wider (up to 0.34 instead of 0.22–0.24) and ribs are inclined forward in the lower part of the flank.

R e m a r k s. Specimens indicated by Sinzow as *P. grossouvrei* (TsNIGR Museum, nos. 15/11068 and 16/11068) (Sinzow, 1907, pl. 1, figs. 10 and 11) should probably be assigned to this species. *P. subcampichei* Sinzow recorded by Rouchadze (1938a, pp. 144, 170) from the Akusha section has a wider cross section than Sinzow's specimen. This character also distinguishes *P. subcampichei* from Glazunova's collection (1953, pl. 3, fig. 1, TsNIGR Museum, no. 18/6426, pl. 3, fig. 2, TsNIGR Museum 19/6426).

Anderson (1938, p. 170) described from the Aptian of California *P. scharfi* Anderson, which he considered as a Californian equivalent of *P. subcampichei.* However, in shell morphology, *P. scharfi* more strongly resembles *P. schmidti* Jacob by both the whorl shape and ornamentation, although being much larger.

O c c u r r e n c e. Russia (Dagestan), Turkmenistan (Lesser Balkhan, Kopet Dagh), Kazakhstan (Mangyshlak); Middle Aptian, *Parahoplites melchioris* Zone.

M a t e r i a l. One complete well-preserved specimen, two incomplete specimens, and three fragments. Dagestan: village of Dagva (PIN, nos. 5265/35, 5265/169, 5265/170, 5265/171, 5265/172), village of Aya-Makhi (PIN, no. 5265/168); Middle Aptian, *P. melchioris* Zone.

Parahoplites artschmanensis Glasunova, 1953

Plate 9, figs. 2 and 3

Parahoplites schmidti Jacob var. *artschmanensis:* Glazunova, 1953, p. 29, pl. 5, figs. 2a–2r.

H o l o t y p e. TsNIGR Museum, no. 17/6426. Specimen figured by Glazunova (1953, pl. 5, figs. 2a–2c); Aptian, *Parahoplites melchioris* Zone; Turkmenistan, Kopet Dagh, Archman spring. Designated here by monotypy.

S h e l l s h a p e. The shell is relatively small and semi-involute. The cross section (Fig. 52a) is subquadrate with flattened ventral and weakly rounded flanks. The whorl width is similar to the whorl height. The umbilicus is relatively wide. The umbilical wall is steep.

D i m e n s i o n s i n m m a n d r a t i o s:

Specimen PIN, no.	Dm	WH	WW	UW	WH/Dm	WW/Dm	UW/Dm
5265/21	29.4	13.0	13.2	9.3	0.44	0.45	0.31
5265/20	33.5	15.0	15.0	9.8	0.45	0.45	0.29

O r n a m e n t a t i o n. The shell is covered by sharp, widely spaced ribs, up to 15 on the half of the last whorl. The primary ribs begin on the umbilical shoulder, rapidly increase, forming a very weak curvature forward in the lower third of the flank and back to its upper third. The intercalary ribs begin at the midflank or slightly below it, occurring one between two primaries, in rare cases absent, so that the two primary ribs are adjacent. Sometimes, the intercalary ribs are branches of the primary ribs. The ribs cross the venter without changing their strength with a wide tongue-like bend.

S u t u r e. (Fig. 52b). The ventral lobe (V) is bifid, with a low median saddle. The umbilical lobe (U) is shorter, asymmetrical, with a well-developed external branch. The first umbilical lobe (U^1) is very shallow and entire. The inner lateral lobe (I) is relatively symmetrical, with one projection on the external side and two on the inner side. The dorsal lobe (D) has a typical trifid base. The external saddle (V/U) is wide and bifid. The umbilical saddle (U/U^1) is lower, later also becoming bifid. The inner saddle (I/D) is narrow, bifid.

C o m p a r i s o n. This species is distinguished from *P. schmidti* Jacob by the narrower whorls: in *P. artschmanensis,* the WW/Dm ration is 0.45, whereas in *P. schmidti,* WW/Dm ranges from 0.46 to 0.56 and the flanks are rounded rather than flattened as in the species described.

O c c u r r e n c e. Russia (Dagestan), Turkmenistan (Kopet Dagh); Middle Aptian, *Parahoplites melchioris* Zone.

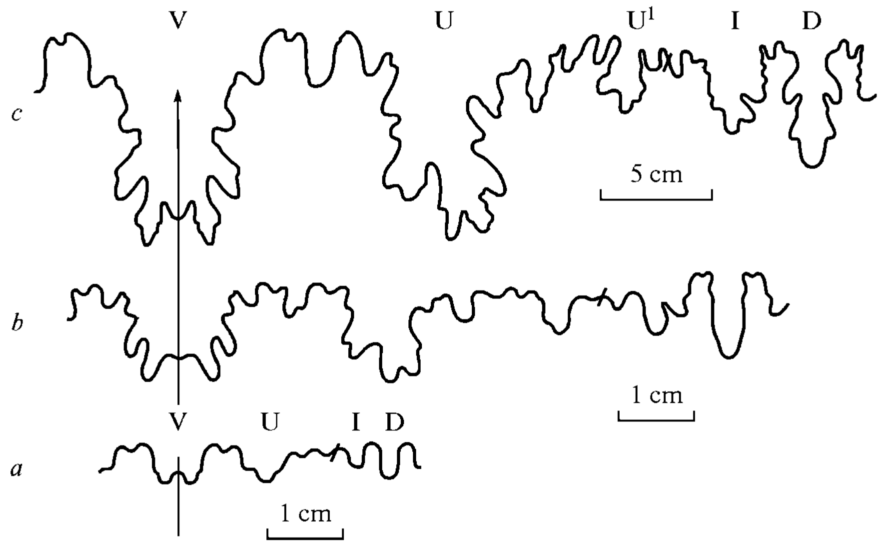


Fig. 53. Sutures of *Parahoplites debilicostatus* I. Michailova, specimen PIN, no. 5265/39: (*a*) at WW = 2.7 mm; (*b*) at WW = 5 mm; (*c*) at WW = 13.4 mm; Dagestan, village of Dagva; Middle Aptian.

M a t e r i a l. Four specimens, in places, with the shell layer preserved. Dagestan: village of Dagva (PIN, nos. 5265/20, 5265/144), village of Arakany (PIN, nos. 5265/21, 5265/145); Middle Aptian, *Parahoplites melchioris* Zone.

Parahoplites debilicostatus **I. Michailova, 1962**

Plate 3, figs. 3 and 4; Plate 13, fig. 4

Parahoplites debilicostatus: Mikhailova, 1962, pp. 137–140, text-figs. 6 and 7.

H o l o t y p e. Specimen PIN, no. 5265/146, figured by Mikhailova (1958, text-figs. 6, 7); Middle Aptian, *Parahoplites melchioris* Zone; Russia, Dagestan, village of Dagva. Mikhailova (1962) gave a collection number of the Paleontology Department: 7/35 [the number 7/85 indicated is incorrect (number of the imprint)].

P a r a t y p e s. Specimens PIN, nos. 5265/39, 5265/147, 5265/148, 5265/149.

S h e l l s h a p e. The shell is semi-involute, with the whorls embracing for more than half. At width of 2.7 mm, the cross section is ellipsoidal, later becomes rounded quadrangular, and, then, rounded trapezoid, higher than wide. The narrow rounded venter gradually joins flattened flanks. The umbilical wall is steep. The umbilicus is relatively narrow.

D i m e n s i o n s i n m m a n d r a t i o s:

Specimen no.	Dm	WH	WW	UW	WH/Dm	WW/Dm	UW/Dm
PIN 5265/39	39.3	18.8	16.8?	9.6	0.47	0.42	0.24
PIN 5265/146 holotype	40.5	19.5	17.5	10.0	0.48	0.43	0.25
TsNIGR Museum 11/10686	59.0	28.3	26.5	16.7	0.48	0.45	0.28

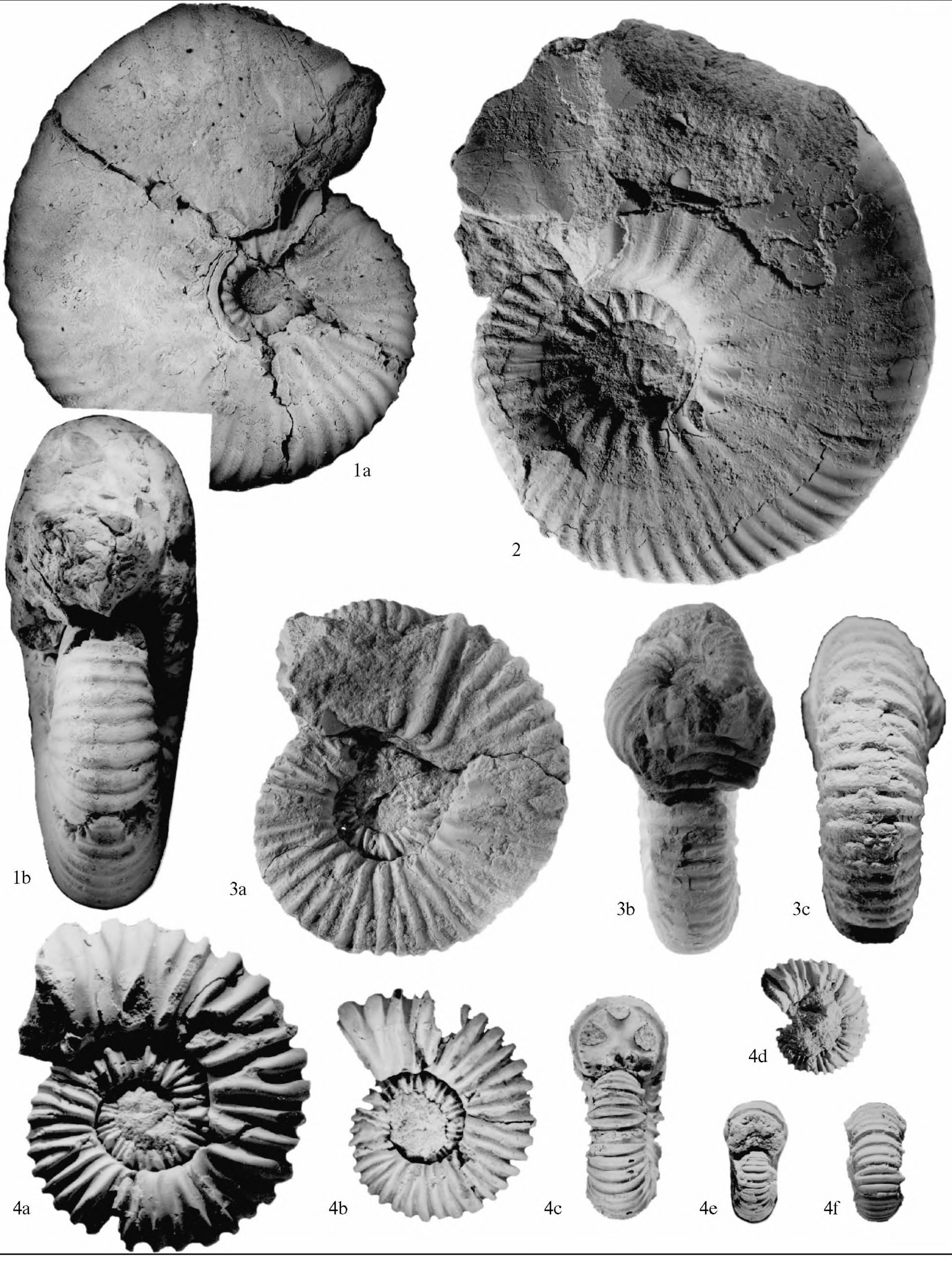
O r n a m e n t a t i o n. The ornamentation is represented by frequent fine ribs, about 40 per whorl. From six to seven ribs occur at a distance equaling the whorl height. The primary ribs begin in the upper part of the umbilical wall, increase on the umbilical shoulder, and run almost straightly on the flanks. All ribs form a small forward bend on the venter. The intercalary ribs (one and less commonly two) occur between the primary ribs, begin below the mid-flank; they are usually intercalating, rarely are branches of primary ribs. In the upper part of the flank, intercalary and primary ribs cannot be distinguished. Sometimes, the alternation of the primary and intercalary ribs is replaced by the alternation of the wedging ribs.

S u t u r e (Fig. 53). At the whorl width of 2.7 mm there are four lobes: V, U, I, D, and three saddles between the lobes. The ventral lobe is wide and bifid;

E x p l a n a t i o n o f P l a t e 1 1

Figs. 1 and 2. *Parahoplites maximus* Sinzow, 1907; (1) specimen PIN, no. 5265/36; (2) specimen PIN, no. 5265/37; Dagestan, village of Aya-Makhi; Middle Aptian, *Parahoplites melchioris* Zone.
Fig. 3. *Acanthohoplites laticostatus* Sinzow, 1907; specimen PIN, no. 5265/217; northern Caucasus, Nalchik River, Middle Aptian.
Fig. 4. *Colombiceras korotkovi* sp. nov.; specimen PIN, no. 5265/53, holotype; northern Caucasus, Kislovodsk; Middle Aptian.

Plate 11



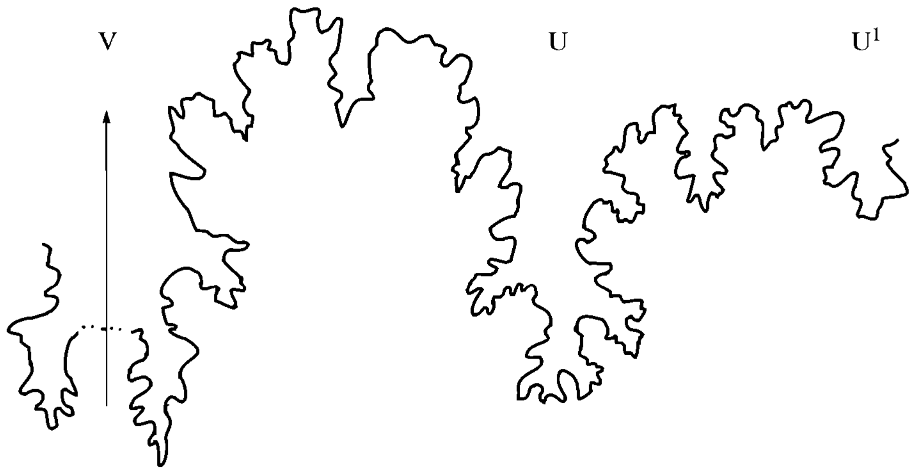


Fig. 54. Suture of *Parahoplites irregularis* Casey at WH= 25 mm; specimen TsNIGR Museum, no. 12/10686 (modified after Tovbina's manuscript, no scale indicated); Great Balkhan, Utuludzha well; Middle Aptian, *Parahoplites melchioris* Zone.

the umbilical lobe is also wide, but asymmetrically trifid. The dorsal lobe is entire, as deep as the ventral and umbilical lobes. The inner lateral lobe is undivided and shorter than the others. The saddle V/U is bifid, U/D is entire, U/I is trifid, relatively symmetrical.

As the shell grows, the first umbilical lobe (U^1) appears and, while the general plan remains unchanged, the primary elements become complicated. The ventral lobe becomes narrower; and the umbilical lobe remains asymmetrical. The first umbilical lobe is shallow, asymmetrically trifid, and somewhat deeper than the inner lateral lobe. The dorsal lobe is undivided, shorter than the ventral or umbilical lobes.

C o m p a r i s o n. *P. debilicostatus* is similar to *P. multicostatus* Sinzow in the numerous thin ribs, but is distinguished from it by the higher rounded trapezoid cross section. The weak ribs are similar to those of *P. maximus* Sinzow and *P. subcampichei* Sinzow, but in these species, the ornamentation weakens at the diameter of over 50 mm, whereas specimens of the species described do not exceed 50 mm in diameter.

O c c u r r e n c e. Russia (northern Caucasus, Dagestan), Turkmenistan (Tuarkyr); Middle Aptian, *Parahoplites melchioris* Zone.

M a t e r i a l. Six specimens and one fragment; the shell layer is not preserved. Dagestan: village of Dagva (PIN, nos. 5265/39, 5265/146, 5265/147), village of Murada (PIN, no. 5265/149), village of Aya-Makhi (PIN, no. 5265/148); Tuarkyr: Babashi well (TsNIGR Museum, no. 11/10686); Middle Aptian, *Parahoplites melchioris* Zone.

Parahoplites irregularis Casey, 1965

Plate 12, figs. 1 and 2

Parahoplites irregularis: Casey, 1965, p. 410, pl. 67, fig. 2, pl. 68, fig. 1.

(non) *Parahoplites irregularis:* Kemper, 1971, pl. 24; Kemper, 1976, pl. 23, fig. 2.

H o l o t y p e. Museum of the UK Geological Service, no. 108639; Aptian, *P. nutfieldiensis;* England. Designated by the author of the species.

S h e l l s h a p e. The shell is large, semi-involute, each succeeding whorl embraces the preceding for more than a half of the whorl height. The cross section is rounded trapezoid, the whorl is slightly higher than wide. The venter and flanks are weakly convex. The umbilicus is narrow and deep. The umbilical wall is steep. The umbilical shoulder is rounded.

D i m e n s i o n s i n m m a n d r a t i o s:

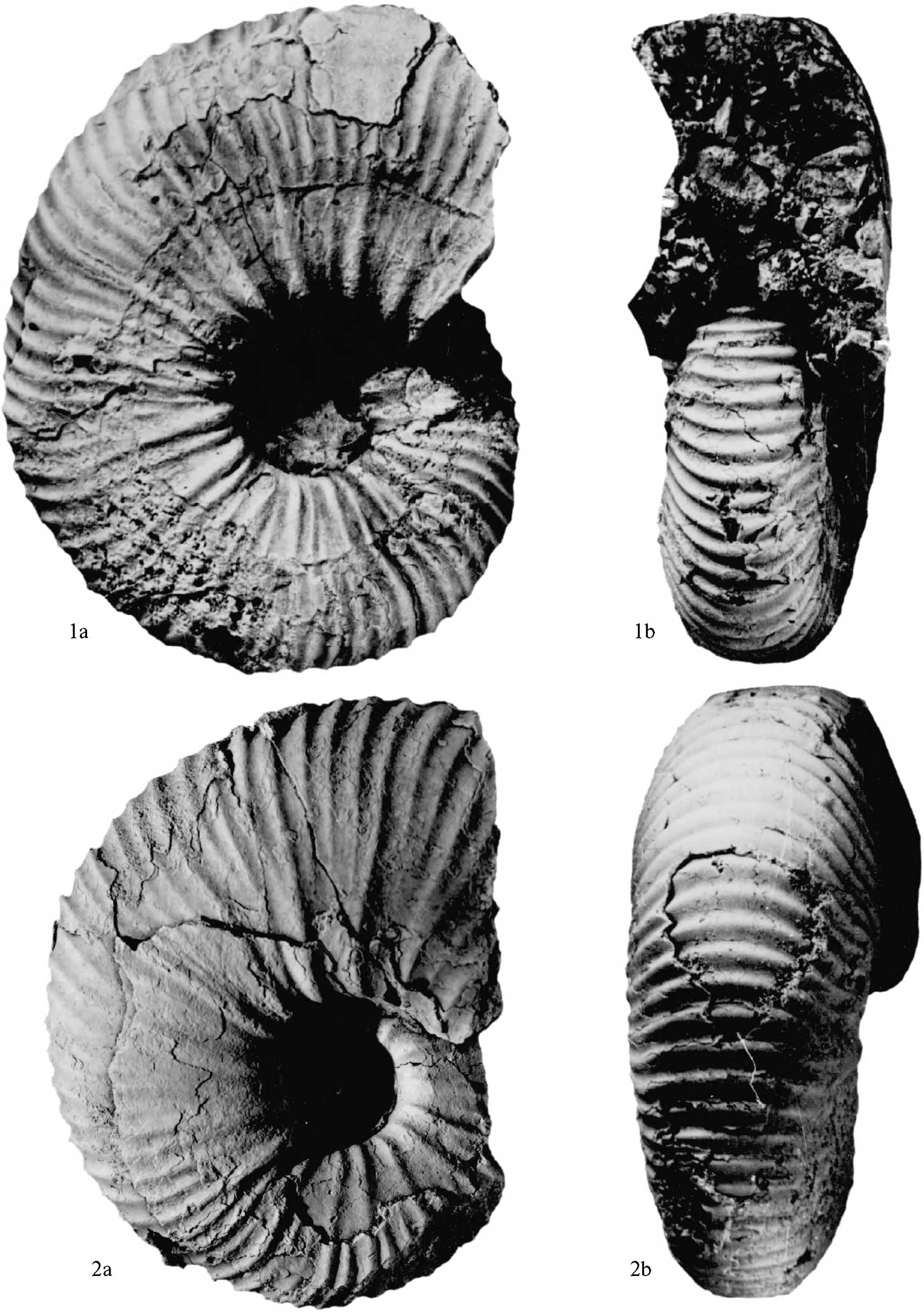
Specimen no.	Dm	WH	WW	UW	WH/Dm	WW/Dm	UW/Dm
PIN 5265/116	111.5	54.5	59.0	24.5	0.47	0.51	0.21
TsNIGR Museum 12/10686	103.1	49.0	48.3	24.4	0.48	0.47	0.23

O r n a m e n t a t i o n. The last whorl shell is covered by numerous low primary and intercalary ribs. At the beginning of the whorl, the main ribs begin on the umbilical wall or on the umbilical shoulder and, in the lower part of the flank, are slightly inflated and raised. Later in ontogeny, in the lower half of the flank, the primary ribs branch into two, one branch is initially weaker than another.

There are also singular intercalary ribs, about two—three, less commonly one. One rib begins mostly on the umbilical wall and in the lower part of the flank is distinguished from the primary rib by its heigth and wigth. One or two other intercalary ribs begin in the upper half of the flanks as weak striae. In the upper half of the flank, intercalary and primary ribs are not differentiated. On the flank, all ribs are weakly S-like curved and, on the venter, they are distinctly bent toward the aperture.

S u t u r e (Fig. 54). The narrow asymmetrical trifid umbilical lobe is shorter than the ventral lobe. The saddles are broad and asymmetrically bifid.

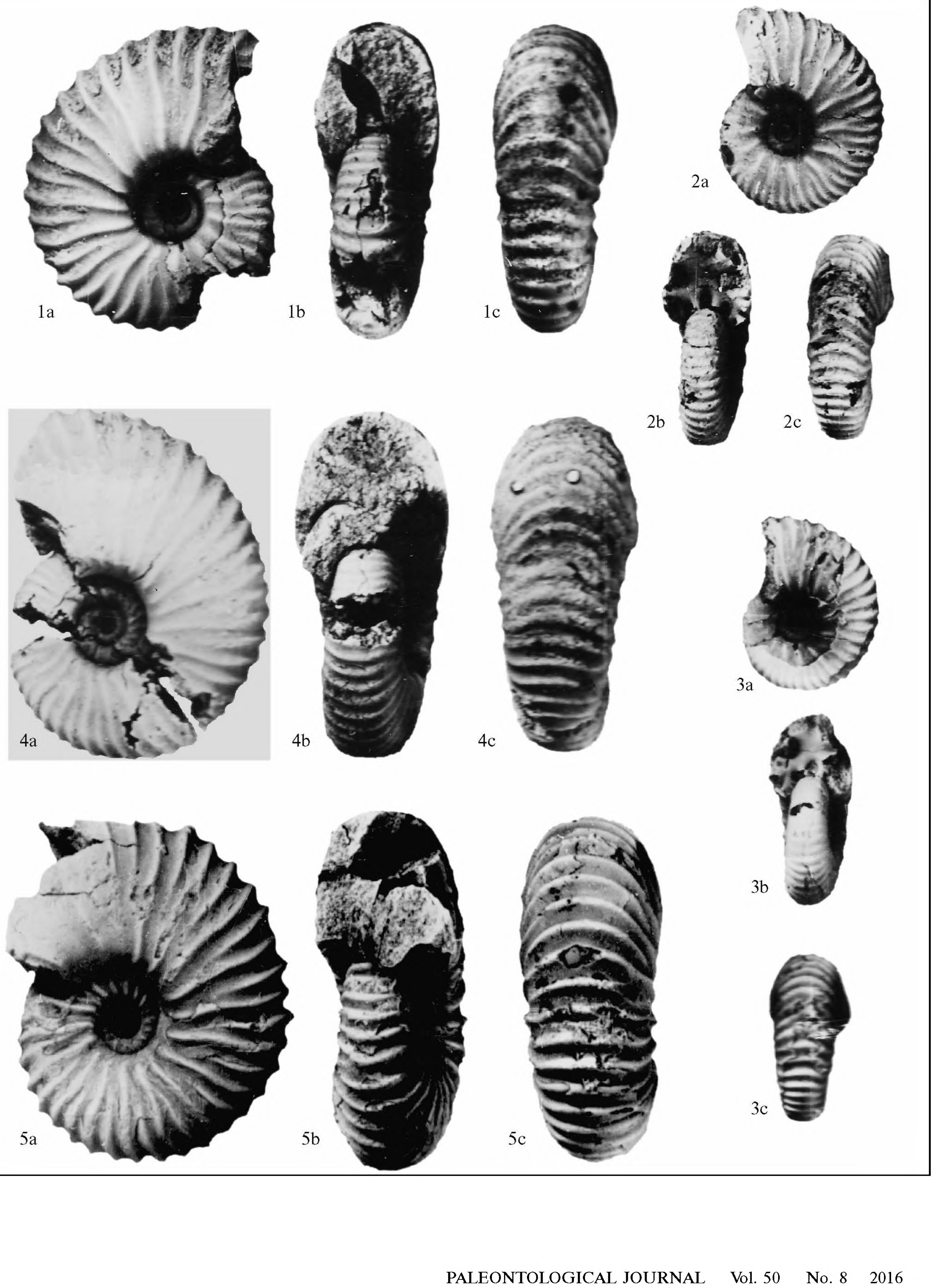
Plate 12



Explanation of Plate 12

Figs. 1 and 2. *Parahoplites irregularis* Casey, 1965; (1) specimen TsNIGR Museum, no. 12/10686; Great Balkhan, Utuludzha well; Middle Aptian, *Parahoplites melchioris* Zone; (2) specimen PIN, no. 5265/116; southern slope of Tuarkyr; the same age.

Plate 13



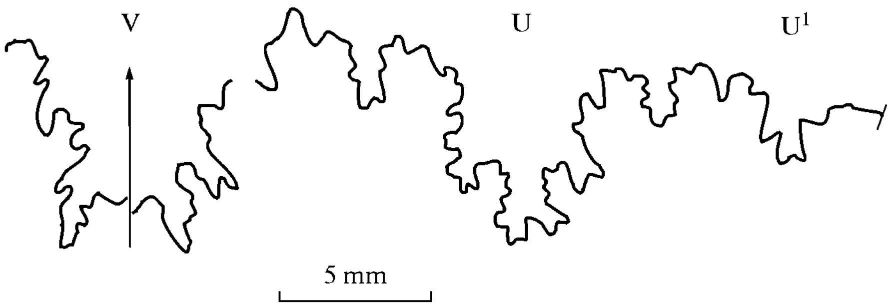


Fig. 55. Suture of *Parahoplites luppovi* Tovbina at WH = 11.1 mm; specimen TsNIGR Museum, no. 8/10686 (modified after Tovbina's manuscript); Great Balkhan, Utuludzha well; Middle Aptian, *Parahoplites melchioris* Zone.

C o m p a r i s o n. *P. irregularis* Casey is distinguished from the similar species *P. nutfieldiensis* (J. Sowerby) by the weaker, shorter, and less regular intercalary ribs.

O c c u r r e n c e. Turkmenistan (Great Balkhan); Middle Aptian, *Parahoplites melchioris* Zone; south England; Middle Aptian, *Parahoplites nutfieldiensis* Zone.

M a t e r i a l. Two large well-preserved specimens. Great Balkhan, Utuludzha well (TsNIGR Museum 12/10686); Tuarkyr, Babashi well (PIN 5265/116); Middle Aptian, *Parahoplites melchioris* Zone.

Parahoplites luppovi **Tovbina, 1982**

Plate 13, figs. 1–3

Parahoplites luppovi: Tovbina, 1982, p. 61, pl. 1, fig. l.

H o l o t y p e. TsNIGR Museum, no. 1/11909; specimen, figured by Tovbina (1982, pl. 1, fig. 1); Middle Aptian, *Parahoplites melchioris* Zone; Turkmenistan, Great Balkhan, Utuludzha section. Designated by the author of the species.

S h e l l s h a p e. The shell is semi-involute. The cross section is trapezoid. The whorl height is considerably greater than the width. The venter is rounded. The flanks are weakly flattened. The umbilical wall is steep. The umbilicus is relatively wide.

D i m e n s i o n s i n m m a n d r a t i o s:

Specimen TsNIGR Museum, no.	Dm	WH	WW	UW	WH/Dm	WW/Dm	UW/Dm
1/11909, holotype	30.5	14.3	13.7	7.5	0.47	0.45	0.25
59/10686	34.4	16.5	15.9	8.9	0.48	0.46	0.26
8/10686	37.2	16.3	15.0	11.1	0.44	0.40	0.30
9/10686, paratype	54.2	25.1	22.2	14.5	0.46	0.41	0.27

O r n a m e n t a t i o n. The ornamentation is represented by primary and intercalary ribs, distinct, even sharp, especially on the venter. The primary ribs begin in the upper part of the umbilical wall, increase shortly after, are weakly curved on the flanks and bent laterally and noticeably lean forward on the venter. The intercalary ribs begin near the mid-flank or somewhat lower; on the venter, they are identical to the primaries. One (in the early whorls, mainly two) intercalary ribs are usually located between the primary ribs.

S u t u r e. (Fig. 55). The sutural outline is typical of parahoplitids. Three lobes are observed on the outer side of the whorl: bifid ventral (V), asymmetrical trifid umbilical (U), almost as deep as the ventral lobe; a shallow first umbilical lobe (U^1) lies near the seam. The saddles (V/U) and (U/U^1) are wide, asymmetrically bifid.

C o m p a r i s o n a n d r e m a r k s. *P. luppovi* is intermediate between *P. melchioris* and *P. transitans.* It is distinguished from the former species by the narrower whorls and from the latter by slightly more widely spaced ribs.

Tovbina (1982, p. 62) confirmed the presence in *P. luppovi* of weak umbilical bullae, clearly distinct at the whorl height of 0.8 mm. In addition, she emphasized that this species was characterized by a prolonged (more than in other species) stage of smooth shell, which includes partly the third, the whole fourth, and partly fifth whorl, and the later appearance of distinct ornamentation (Tovbina, 1982, p. 63).

O c c u r r e n c e. Turkmenistan (Tuarkyr, Great Balkhan, Kopet Dagh); Middle Aptian, *Parahoplites melchioris* Zone.

M a t e r i a l. Five well-preserved medium-sized and small specimens. Tuarkyr, Babashi well (TsNIGR

E x p l a n a t i o n o f P l a t e 1 3

Figs. 1–3. *Parahoplites luppovi* Tovbina, 1982; (1) paratype TsNIGR Museum, no. 9/10686; Tuarkyr, Babashi well; Middle Aptian, *Parahoplites melchioris* Zone; (2) paratype TsNIGR Museum, no. 8/10686; (3) holotype TsNIGR Museum, no. 1/11909; Great Balkhan, Utuludzha well; the same age.

Fig. 4. *Parahoplites debilicostatus* I. Michailova, 1962; specimen TsNIGR Museum, no. 11/10686; Tuarkyr, Babashi well, Middle Aptian, *Parahoplites melchioris* Zone.

Fig. 5. *Parahoplites melchioris* Anthula, 1899; specimen TsNIGR Museum, no. 1/10686; Great Balkhan, Utuludzha well; Middle Aptian, *Parahoplites melchioris* Zone.

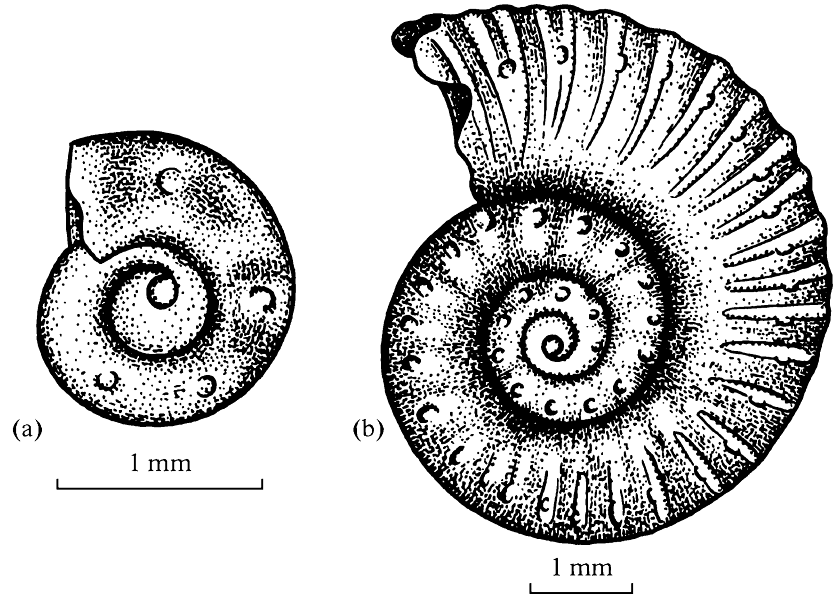


Fig. 56. Appearance and development of ornamentation in the genus *Colombiceras:* (a) *Colombiceras* sp. Dagestan, village of Akusha; Middle Aptian; (b) *Colombiceras* sp. northern Caucasus, Urukh River, Middle Aptian (Bogdanova and Mikhailova, 2007).

Museum, nos. 9/10686, 59/10686); Great Balkhan, Utuludzha well (TsNIGR Museum, nos. 1/11909, 8/10686), Oglanly well (TsNIGR Museum, no. 60/10686); Middle Aptian, *Parahoplites melchioris* Zone.

Family Acanthohoplitidae Stoyanow, 1949

D i a g n o s i s. Ornamentation mostly of almost straight primary and intercalary ribs, tubercles commonly present. In shell ontogeny, tubercles appearing in second–third whorls, but in some specimens, reduced with age. Ribs initially visible from tubercles to venter, and then, to umbilical wall (Fig. 56). Smooth shell at intermediate stage (characteristic of family Parahoplitidae) not observed.

S u t u r e. The suture is with a trifid, relatively symmetrical umbilical lobe and a bifid dorsal lobe.

C o m p o s i t i o n. The most detailed subdivision of the family Acanthohoplitidae Stoyanow is accepted in the *Atlas* ... (2005), which accepts three subfamilies: Colombiceratinae Tovbina, 1979, Diadochoceratinae Kvantaliani, 1978, and Acanthohoplitinae Stoyanow, 1949. The family Acanthohoplitidae (originally the subfamily) included the genera *Acanthohoplites* Sinzow, 1907; *Colombiceras* Spath, (1921) 1923; *Hypacanthoplites* Spath, (1921) 1923; *Gargasiceras* Casey, 1954, and *Diadochoceras* Hyatt, 1903. We synonymize the genera *Paracanthoplites* Stoyanow, 1949 and *Immunitoceras* Stoyanow, 1949 under *Acanthohoplites* Sinzow, although it is possible that further studies will allow reconsideration of Stoyanow's taxa, especially *Immunitoceras.* It is found in Europe, Asia, eastern North Africa, and America; Middle and Upper Aptian and also Lower Albian.

R e m a r k s. We disagree with Thomel (1980, pp. 176–180), who recognized among Gargasian ammonites the subgenus *Diadochoceras (Verguniceras)* with the type species *Ammonites pretiosus* d'Orbigny. The specimens described by Thomel and Dutour are externally similar to *Epicheloniceras,* hence, long time ago, Jacob (1907, pp. 93, 97) and, after him, Kilian and Reboul (1915, pp. 4, 203) assigned this species to *Douvilleiceras.* In addition, *Diadochoceras* is typical of the Clansayesian.

C o m p a r i s o n. The difference from the family Parahoplitidae is indicated above: (1) absence of the intermediate stage of a smooth shell in Acanthohoplitidae; (2) umbilical lobe is trifid, relatively symmetrical, and the dorsal lobe is bifid.

Genus *Acanthohoplites* Sinzow, 1907

Acanthohoplites: Sinzow, 1907, p. 478; Kilian, 1907–1913, p. 343; Kazansky, 1914, p. 66; Danilovich, 1923, p. 3; Spath, 1923, p. 64; Anderson, 1938, p. 64; Scott, 1939, p. 1052; Humphrey, 1949, p. 138; Stoyanow, 1949, p. 106; Basse, 1952, p. 655; Arkell et al., 1957, p. L386; Luppov and Drushchits, 1958, p. 103; Kudryavtsev, 1960, p. 319; Dimitrova, 1967, p. 184; Kvantaliani, 1971, p. 27; Wright et al., 1996, p. 275; Sharikadze et al., 2004, p. 400; Atlas ..., 2005, p. 397.

Acanthoplites (Acanthohoplites): Roman, 1938, p. 348.

Acanthoplites: Glazunova, 1953, p. 31; Eristavi, 1961, p. 55.

Nolaniceras: Casey, 1961a, p. 598.

Chaschupseceras: Kvantaliani, 1968, p. 62.

Protacanthoplites: Tovbina, 1970, p. 57.

T y p e s p e c i e s. *Parahoplites aschiltaensis* Anthula (Anthula, 1899, p. 117, pl. 10(9), figs. 3a–3c);

Russia, Dagestan, village of Ashilta, Middle and Upper Aptian. Designated by Roman (1938, p. 348).

S h e l l s h a p e. The shell is composed of five-six, less commonly, seven whorls. The cross section varies from low ellipsoidal to rounded quadratic and rounded rectangular. The change in the shape of the cross section is observed from the end of the third–beginning of the fourth whorls. In the fourth whorl, height in most species increases considerably faster than the width and becomes the same as the width and exceeds it. The umbilicus varies from relatively wide to wide.

O r n a m e n t a t i o n. The protoconch (Fig. 57) and first two whorls are smooth. Microscopic tubercles appear in the third whorl. At the end of the third whorl, hardly visible ribs appear or the shell in the three whorls remains smooth, whereas tubercles appear simultaneously with ribs. The combination of primary and intercalary ribs varies; at the transition to the last whorls, the number of intercalary ribs decreases and one intercalary rib occurs between the primaries. The tubercles always present at early stage, in one group of species remain at the adult stages, while in other group, they disappear.

S u t u r e. (Fig. 58). The prosuture and primary suture are connected near the seam. The fifth suture at the shell diameter around 0.5 mm still has a U^1 lobe and, in the ninth suture, this lobe is absent and the suture consists of four lobes: bifid ventral and entire umbilical, inner lateral and dorsal (VUID), and three saddles: external, umbilical, and inner.

At the beginning of the third whorl, the fifth U^1 is again formed at the top of the U/I saddle and the U^2 lobe appears in the middle of the fourth whorl. At the same time, the umbilical lobe becomes trifid, while the dorsal lobe almost simultaneously becomes trifid. Later, in the middle or at the end of the fourth whorl, the inner saddle becomes subdivided. Further changes occur by increased complexity of existing elements and increase in number of secondary lobes of the umbilical saddle, resulting in the development of the first umbilical, in some species second umbilical, and sometimes third umbilical lobe. This sutural morphogenesis is observed in *A. nolani* (Seunes) (Fig. 59) and *Acanthohoplites* sp. juv. (Fig. 60).

In a shell composed of five or six whorls, the suture is of two types: with an elongated, symmetrical umbilical lobe in species with a cross section elongated in height and with a short, frequently asymmetrical umbilical lobe in species with a rounded subquadrate cross section.

S p e c i e s c o m p o s i t i o n. Apart from the type species, this genus comprises more than 30 species, including *A. nolani* (Seunes, 1887), *A. bigoti* (Seunes, 1887), *A. uhligi* (Anthula, 1899); *A. laticostatus* Sinzow, 1907; *A. bigoureti* (Seunes, 1887); *A. abichi* (Anthula, 1899); *A. trautscholdi* (Simonovitch, Bačevitch et Sorokin, 1876); *A. subrectangulatus* Sinzow, 1907; *A. lautus* Glazunova, 1953; *A. multispinatus* (Anthula, 1899), *A. subangulicostatus* Sinzow, 1907; *A. migneni* (Seunes, 1887); *A. rectangularis* Kasansky, 1914; *A. compressus* Kasansky, 1914; *A. quadratus* Kasansky, 1914; *A. stephanoides* Kasansky, 1914; *A. anthulai* Kasansky, 1914; *A. angulicostatus* (d'Orbigny, 1841) sensu Anthula (1899); *A. bergeroni* (Seunes, 1887); *A. milletianus* (d'Orbigny); *A. multispinatoides* Rouchadze, 1938; *A. sparsicostatus* Rouchadze, 1938, and others. Species of the genus *Acanthohoplites* are widespread in the Middle and Upper Aptian beds of Russia (northern Caucasus), Georgia, Kazakhstan (Mangyshlak), and Turkmenistan. They are also known in France. Many unusual species are described from East Africa (Madagascar), United States (Arizona, California, Oregon), Mexico, and Japan.

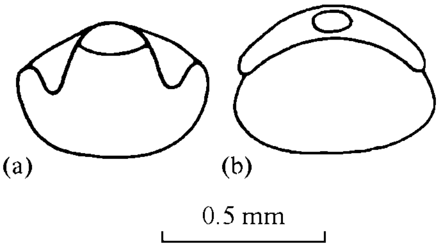


Fig. 57. Protoconch of *Acanthohoplites* sp. juv., specimen PIN, no. 5265/273: (a) upper view, (b) septal view; Tuarkyr, Babashi well, Upper Aptian.

R e m a r k s. Anthula (1899) recognized two groups in the genus *Parahoplites, P. melchioris* Anthula and *P. aschiltaensis* Anthula. Sinzow (1907) separated the second group of Anthula in a new genus, *Acanthohoplites,* and transferred to it some species from the *P. melchioris* group. Later, Spath (1923) established the genera *Colombiceras* and *Hypacanthoplites,* and the genus *Acanthohoplites* in its reduced sense is accepted by most authors, except for Roman (1938), who included *Colombiceras* and *Hypacanthoplites* in the genus *Acanthohoplites.*

Acanthohoplites aschiltaensis **(Anthula, 1899)**

Plate 14, figs. 1–3; Plate 15, figs. 1 and 2

Parahoplites aschiltaensis: Anthula, 1899, p. 17, pl. 10, figs. 2 and 3.

Acanthohoplites aschiltaensis: Sinzow, 1907, p. 478, pl. 6, figs. 19–21; Kazansky, 1914, p. 67, pl. III, fig. 47; Danilovich, 1923, pp. 10–11; Rouchadze, 1933, p. 197; Rouchadze, 1938a, p. 132.

Acanthoplites aschiltaensis: Glazunova, 1953, pp. 42, 43; pl. 8, figs. 1a, 1c, 2, 3a, and 3c; Eristavi, 1955, p. 97.

L e c t o t y p e. Specimen figured by Anthula (1899, p. 117, pl. 10 (9), fig. 3a); Aptian, *Parahoplites melchioris* Zone; Russia, Dagestan, village of Ashilta.[13]

S h e l l s h a p e. The shell is semi-evolute with whorls overlapping each other by approximately half a

[13]Kvantiliani (1971, p. 55) indicated the holotype, although Anthula described and figured two specimens.

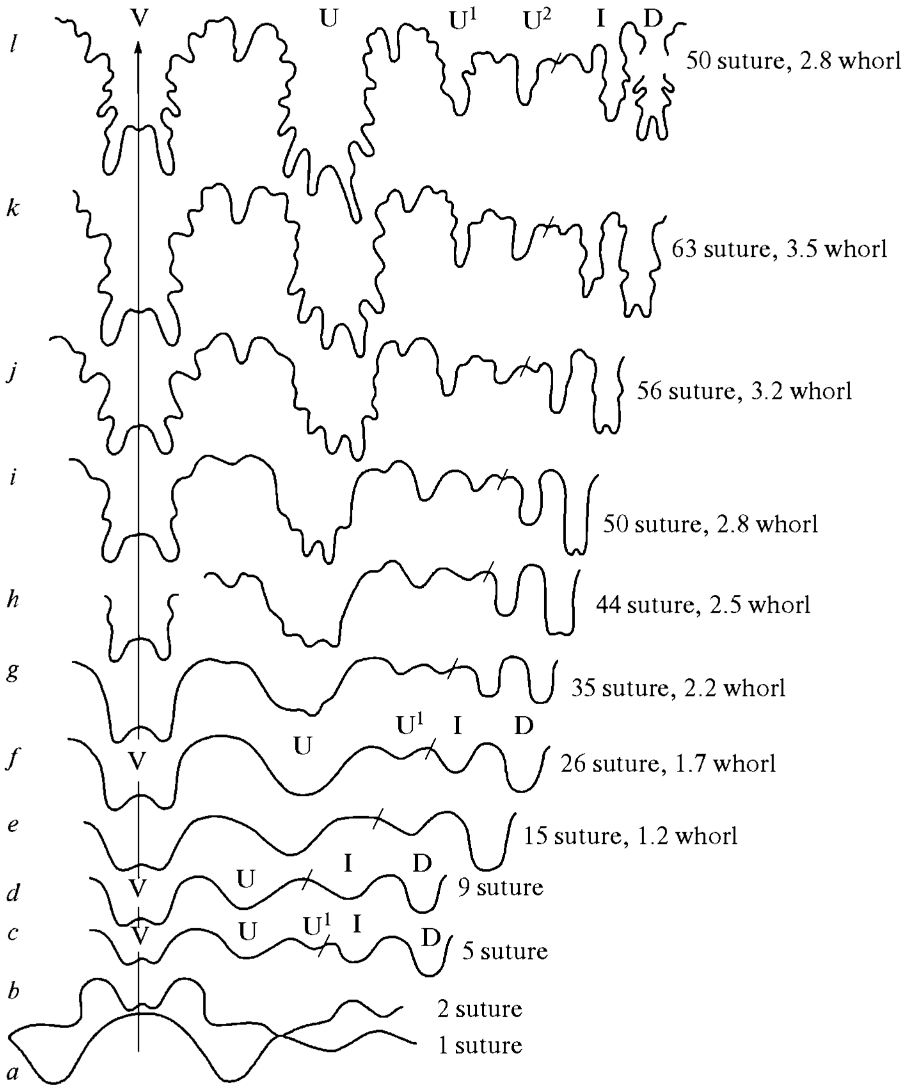


Fig. 58. Morphogenesis of the suture in *Acanthohoplites nolani* (Seunes); specimen PIN, no. 5265/275: (*a–e*) ×65, (*f*); ×45, (*g*) ×31, (*h*) ×23, (*i*) ×19, (*j*) ×15, (*k*) ×13, (*l*) ×6; northern Caucasus, Khokodz River; Upper Aptian.

whorl. The cross section varies from rounded quadratic to elongated rounded rectangular with a rounded venter and weakly convex flanks, gradually passing into a steep umbilical wall. The maximum whorl width is in the lower third of the flank.

D i m e n s i o n s in mm and ratios:

Specimen PIN, no.	Dm	WH	WW	UW	WH/Dm	WW/Dm	UW/Dm
5265/260	23.7	12.3	10.9	8.7	0.52	0.46	0.37
5265/215	51.1	25.5	21.1	17.4	0.50	0.40	0.34
5265/214	73.0	31.0	26.0	24.2	0.42	0.35	0.32
5265/216	73.8	32.2	26.7	24.3	0.42	0.36	0.30
5265/213	113.7	47.5	38.4	39.6	0.41	0.34	0.35

The umbilicus is relatively wide, at the diameter up to 20 mm, measuring 0.35–0.36 of the shell diameter, over this diameter it decreases to 0.30–0.32 and, finally, in specimens with the diameter more than 100 mm, again increases to 0.34–0.35.

O r n a m e n t a t i o n. At the diameter of 17.2 mm, in the last whorl, there are 40 ribs. The primary ribs begin from the seam, gradually increase and, in the mid-flank, possess thin spinous tubercles, from which they are divided into two branches, of which the anterior is the continuation of the primary rib and bent noticeably forward on the venter, and the posterior, less prominent, running almost straight on the venter. Two or three intercalary ribs lie between the primary ribs. They begin at the same level as the primaries, but are considerably thinner even on the venter.

The ornamentation is distinctly visible at the diameter about 7 mm; the ribs are uniform, very thin and tubercles on them are either absent or weak. At the diameter 32 mm, 21 ribs occur per half whorl. Some primary

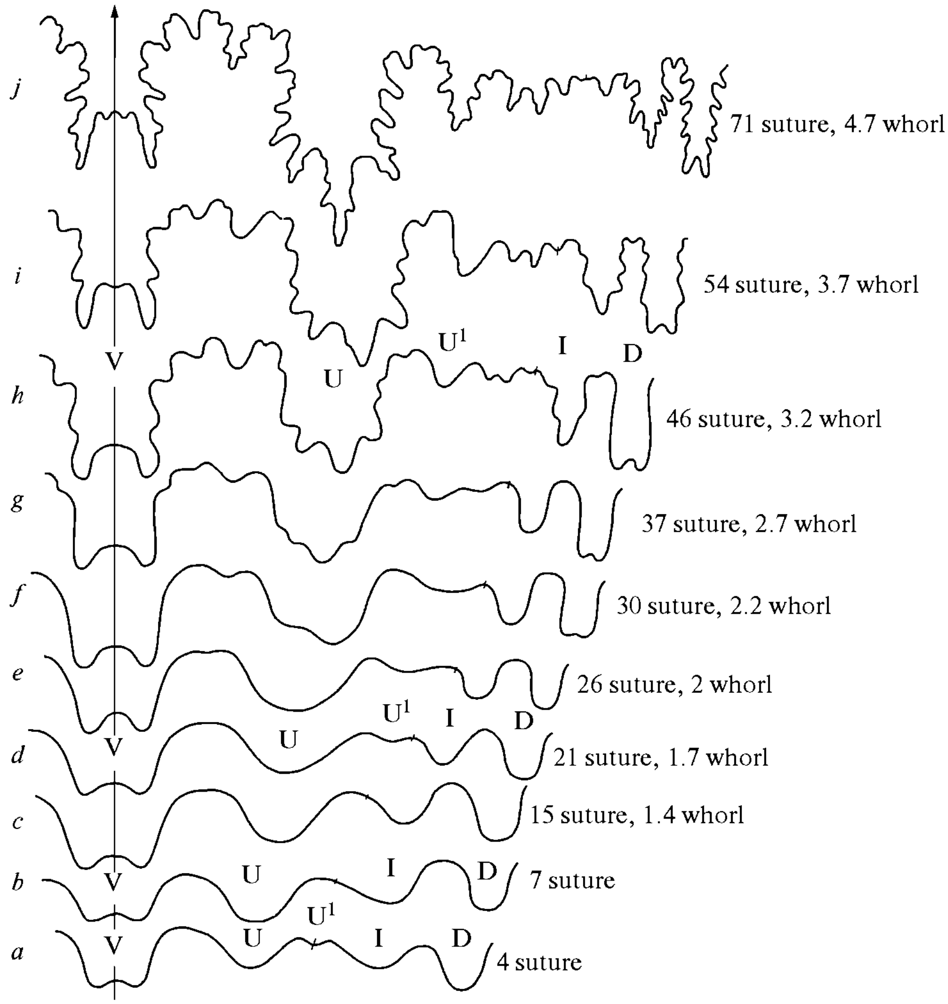


Fig. 59. Morphogenesis of the suture in *Acanthohoplites nolani* (Seunes); specimen PIN, no. 5265/274; northern Caucasus, Khokodz River; Upper Aptian.

ribs possess small lateral tubercles, gradually disappearing with age. One or two intercalary ribs occur between the primary ribs. At the diameter about 80 mm, the shell has 43 ribs, with one intercalary rib per each primary.

S u t u r e. The ventral lobe is bifid, with a low bifid median saddle. The relatively symmetrical umbilical lobe is with well-developed lateral branches. The first umbilical lobe is short, narrow, trifid, and relatively symmetrical. The deeper inner lateral lobe has well-developed central and inner branches. The dorsal lobe is bifid, in the lower half, with small digits, and in the upper part, with large digits.

The external and umbilical saddles are broad and high, asymmetrically bifid. The first umbilical saddle (U^1/I) is indistinctly asymmetrically trifid.

C o m p a r i s o n a n d r e m a r k s. The specimen figured by Anthula (1899, pl. 11, fig. 1) in the character of ornamentation is similar to *A. laticostatus* Sinzow, but larger size and incompleteness of this specimen do not allow exact comparison. Anthula (1899) mentioned the similarity of the sutures, but the suture was not illustrated.

Acanthohoplites aschiltaensis (Anthula) is morphologically similar to some species of *Acanthohoplites*. It is mostly similar to *A. laticostatus* Sinzow and *A. bigoureti* (Seunes). The former has denser ribs, tabulate venter with an angular ventrolateral shoulder, and, in medium-sized shells, a wider umbilicus. *A. bigoureti* (Seunes) is distinguished by the more widely spaced and coarser ribs, and the tubercles remain at larger shell diameters. Another similar species, *A. abichi* (Anthula), is characterized by the wide rounded whorls and less prominent ornamentation. Young whorls of *A. aschiltaensis* (Anthula) is similar to *A. rectangularis* Kasansky, but it has a distinctly angular whorl cross section, and less prominent ornamentation with earlier disappearance of tubercles.

Sinzow (1907) described *A. aschiltaensis* in detail and recognized two varieties: *aplanata* and *rotunda*.

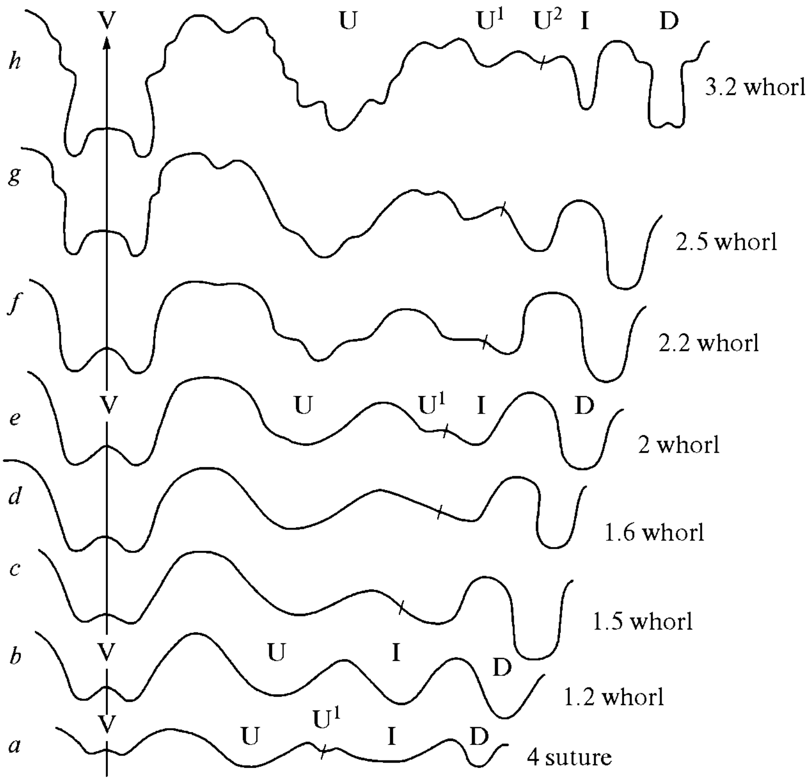


Fig. 60. Morphogenesis of the suture of *Acanthohoplites* sp. juv., specimen, PIN, no. 5265/273; Tuarkyr, Babashi well, Upper Aptian.

Later, he recognized the first variety as the separate species *A. aplanatus,* which has a distinctly tabulate venter and is closer to *A. multispinatus* than to *A. aschiltaensis.*

A. aschiltaensis var. *rotunda* was recognized by Sinzow as a thin-ribbed variety, with a wider cross section. Sinzow assigned Anthula's specimen (1899, pl. 10, fig. 4) to this variety. Eristavi (1955, p. 97) described but did not figure *Acanthoplites aschiltaensis* var. *rotunda* Sinzow. He did not agree with Rouchadze (1933, p. 133), who recorded this taxon for the northern Caucasus.

Among specimens that Sinzow assigned to typical *Acanthohoplites aschiltaensis,* those shown in pl. 5, figs. 1 and 8 cannot be assigned. The specimen figured in fig. 1 is less strongly ribbed and more strongly flattened with a wider umbilicus; in fig. 8 with a sharply angular cross section, resembling that of *A. multispinatus* (Anthula) and less developed primary ribs. Glazunova (1953) described and figured only young specimens up to 35 mm in diameter, making identification difficult.

O c c u r r e n c e. Russia (northern Caucasus, Dagestan), Kazakhstan (Mangyshlak), Turkmenistan (Kopet Dagh): Middle Aptian, *Parahoplites melchioris* Zone and Upper Aptian, *Acanthohoplites nolani* Zone; Kilian (1907–1913) indicated it from the Lower Aptian of Switzerland; in England, it is found in the Upper Aptian. *"Parahoplites"* cf. *aschiltaensis* was described from Peru (Sommermeier, 1913, p. 408), but this record could not be repeated in later years.

M a t e r i a l. There are 15 complete specimens and many fragments. The shell layer is almost always absent. Dagestan: Akusha (PIN, nos. 5265/215, 5265/216, 5265/260), Aya-Makhi (PIN, nos. 5265/213, 5265/214); Middle Aptian, *Parahoplites melchioris* Zone and Upper Aptian, *Acanthohoplites nolani* Zone.

Acanthohoplites laticostatus Sinzow, 1907

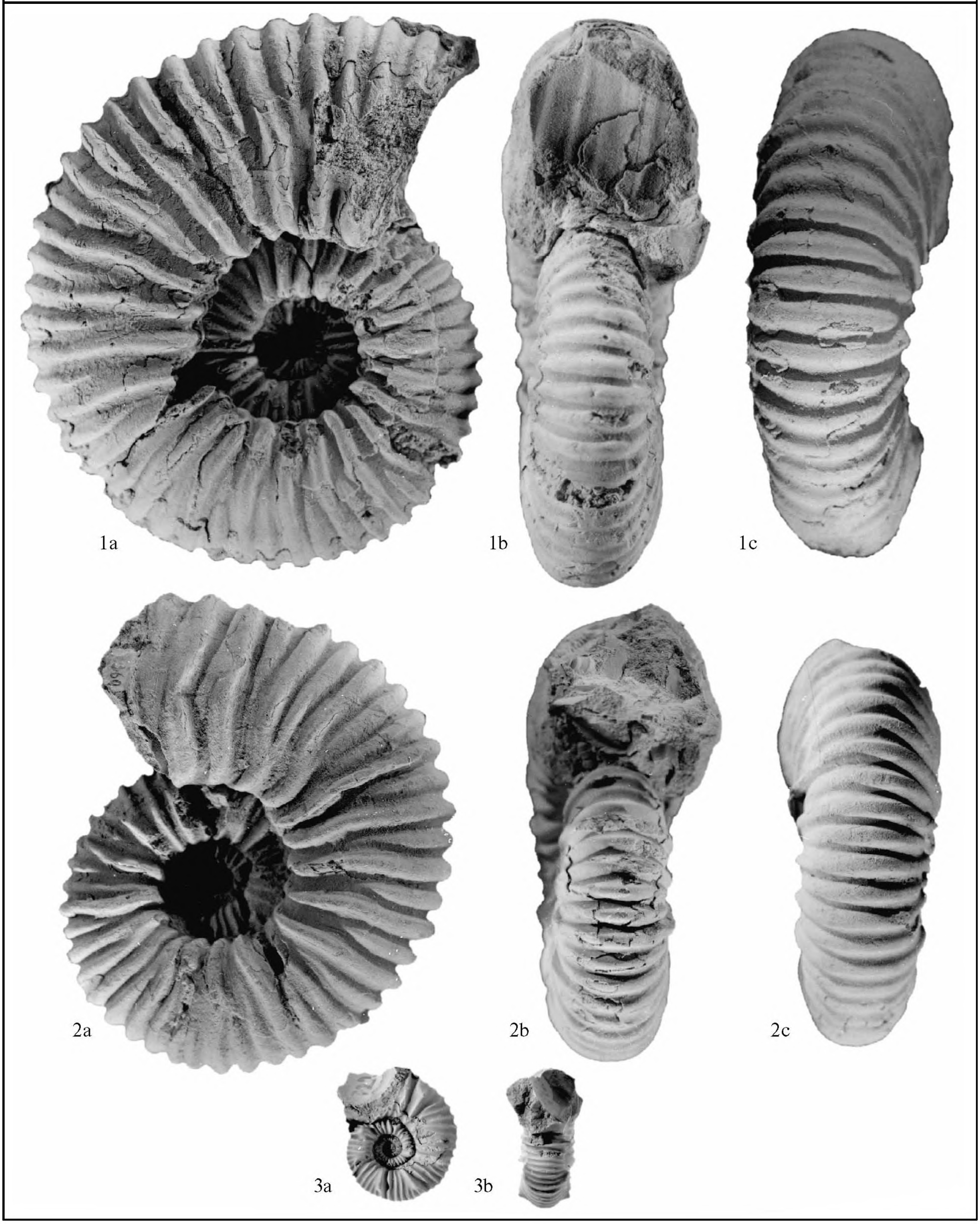
Plate 11, fig. 3, Plate 15, fig. 3

Acanthohoplites laticostatus: Sinzow, 1907, pp. 482, 483, pl. V, figs. 9–18; Kazansky, 1914, pp. 63, 69.

Acanthoplites laticostatus: Glazunova, 1953, p. 41, pl. VII, figs. 2a–2c; Eristavi, 1955, p. 98.

S h e l l s h a p e. The shell is semi-evolute, whorls embrace for less than half of the whorl height. The cross section is rounded rectangular with flattened venter and weakly convex flanks, with distinct ventrolateral shoulder. With age, the venter becomes more strongly rounded. The umbilical wall is low, obliquely descends to the umbilicus. The umbilicus is relatively wide. The whorl height is slightly larger than its width, or is the same as it.

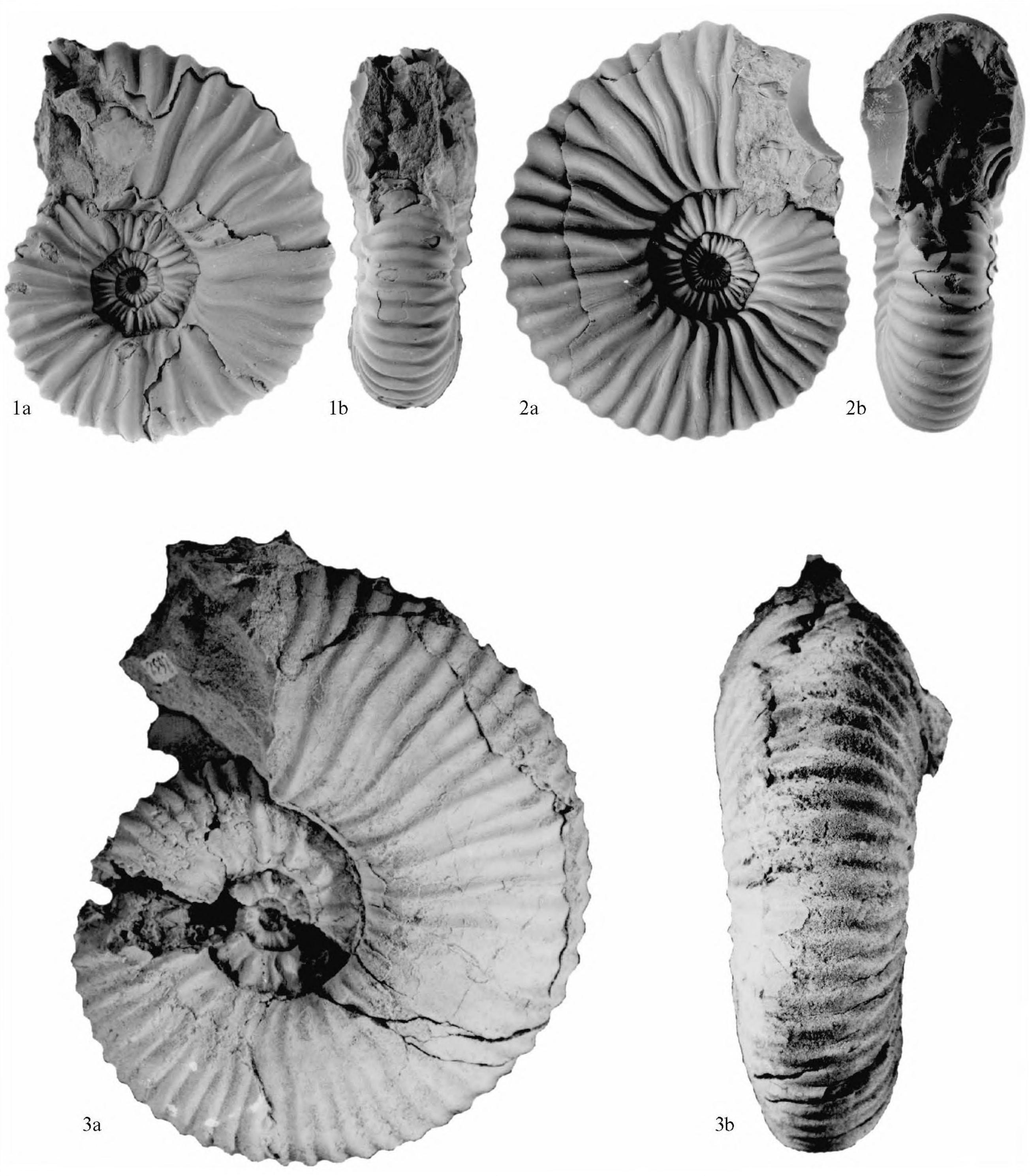
Plate 14



Explanation of Plate 14

Figs. 1–3. *Acanthohoplites aschiltaensis* Anthula, 1899; (1) specimen PIN, no. 5265/213; (2) PIN, no. 5265/214; Dagestan, village of Aya-Makhi, Middle Aptian, *Parahoplites melchioris* Zone; (3) PIN, no. 5265/260; Dagestan, village of Akusha, the same age.

Plate 15



Explanation of Plate 15

Figs. 1 and 2. *Acanthohoplites aschiltaensis* Anthula, 1899; (1) specimen PIN, no. 5265/216; (2) PIN, no. 5265/215; Dagestan, village of Akusha, Middle Aptian, *Parahoplites melchioris* Zone.

Fig. 3. *Acanthohoplites laticostatus* Sinzow, 1907; specimen PIN, no. 5265/219; Dagestan, village of Akusha, Middle Aptian, *Parahoplites melchioris* Zone.

Dimensions in mm and ratios:

Specimen PIN, no.	Dm	WH	WW	UW	WH/Dm	WW/Dm	UW/Dm
5265/217	52.0	21.0	19.9	18.1	0.40	0.38	0.35
5265/219	104.3	43.7	40.3	33.5	0.42	0.40	0.32

Ornamentation. At the diameter 30.5 mm, the shell has 48 ribs, of these 19 are primary, the rest are intercalary. The primary ribs begin from the seam, rapidly increase, almost radially cross the flanks, and are slightly flattened in its upper third, differing in this on the venter from the thinner intercalary ribs. Some primary ribs on the mid-flank possess small spinous tubercles, from which the ribs are divided into two parts.

With age, tubercles gradually disappear and intercalary ribs begin on the mid-flank, sometimes below, gradually increase and, on the venter, are not distinguished from the primaries. At diameter 104.3 mm, 30 ribs occur per half whorl. For one primary rib, there is one, less commonly two intercalary ribs.

Suture. The suture at the whorl height of 24.9 mm and width of 24.5 mm is relatively simple. The narrow deep ventral lobe has obtuse vertical prongs and high, bifid median saddle. The narrower, deep, asymmetrical, trifid umbilical lobe has an oblique external side and almost vertical inner side. The first umbilical lobe is shallow, trifid asymmetrical. The inner lateral lobe is deeper than the first umbilical lobe. Slightly deeper dorsal lobe has a bifid termination.

All saddles are bifid; the saddle V/U is widest, two next saddles are almost equal and saddle I/D is the narrowest.

Comparison. The species described is distinguished from *Acanthohoplites aschiltaensis* by the flattened venter, more closely spaced, often flattened ribs on the venter, and by the wider umbilicus. It differs from *A. rectangularis* Kasansky in the larger size, and more prominent and closely spaced ornamentation.

Remarks. *A. laticostatus* was described by Sinzow (1907) from dark clay of Mangyshlak and one small specimen comes from the northern Caucasus. The author of the species noted its similarity to *A. aschiltaensis* and, along with other differences, he noted the wider umbilicus in the species under description, whereas Glazunova (1953) noted the opposite, i.e., that *A. laticostatus* has a narrower umbilicus than *A. aschiltaensis*. Kazansky (1914) and Eristavi (1955) supported Sinzow's point of view.

Occurrence. Russia (northern Caucasus, Dagestan), Kazakhstan (Mangyshlak), Middle Aptian, *Parahoplites melchioris* Zone; Georgia, Middle Aptian.

Material. Two complete specimens and several fragments. Three of the fragments have partly preserved shell layer. The body chamber occupies half of the last whorl. Northern Caucasus: Nalchik River (PIN, no. 5265/217); Dagestan: village of Akusha (PIN, no. 5265/219); Middle Aptian, *Parahoplites melchioris* Zone.

Genus *Colombiceras* Spath, 1923

Colombiceras: Spath, 1923, p. 64.

Acanthoplites: Roman, 1938, p. 348 (pars).

Colombiceras: Humphrey, 1949, p. 150; Stoyanow, 1949, p. 121; Glazunova, 1953, p. 46; Arkell et al., 1957, p. L387; Kudryavtsev, 1960, p. 327; Eristavi, 1961, p. 65; Casey, 1965, p. 418; Egoian, 1969, p. 163; Luppov and Drushchits, 1958, p. 103; Kvantaliani, 1971, p. 60; Wright et al., 1996, p. 274; Sharikadze et al., 2004, p. 383; Atlas ..., 2005, p. 392; Dutour, 2005, p. 205.

Type species. *Ammonites crassicostatus* d'Orbigny, 1840; Upper Aptian, Gargasian, southeastern France. Designated by d'Orbigny (1840, p. 64).

Shell shape. The protoconch has a high median saddle, the caecum is oval in cross section (Fig. 61a). The shell is semi-evolute, composed of four–six whorls. The cross section varies from low ellipsoidal (first three whorls) to rounded quadratic, less commonly, rounded rectangular (Fig. 61b). The umbilicus varies from relatively wide to wide.

Ornamentation. The protoconch and the first whorl are smooth. Microscopic tubercles are visible on the second whorl (see Fig. 56). At the whorl diameter of 2.5 mm, there are visible weak ribs running from the tubercles to the venter, and the ribs become branched shortly after. The ribs are initially crested and, later, flattened.

In later whorls, the ornamentation is represented by coarse, flattened on the venter primary and intercalary ribs. The ribs alternate with each other over the one or two; the primary ribs often quite long retain lateral tubercles, from which the ribs are subdivided into two, less commonly, into three branches. In front of each primary rib, the interspace is deeper than behind it and between adjacent intercalary ribs. The ribs are grouped in two, three, or four. With age, the number of intercalary ribs decreses and, at the diameter of over 45 mm, one intercalary rib is usually between the primaries. At the same time, with the disappearance of tubercles, the branch of the primary rib is shifted forming an intercalary rib, and often ribs become rounded in large specimens.

Suture (Fig. 62). The total number of lobes is usually not more than five. The ventral lobe (V) has a bifid median saddle. The umbilical lobe (U) is as deep as the ventral lobe and has either relatively symmetrical or sharply asymmetrical outlines with a long central branch. The first umbilical lobe (U^1), which appeared as a result of deepening and expansion of the secondary lobe in the saddle U/I, is often bifid or quadripartite. The indistinctly trifid inner lateral lobe (I) is slightly deeper than the first umbilical lobe. The dorsal lobe is deep, narrow, and bifid.

Morphogenesis of the suture (Fig. 62). The primary suture is five-lobed: VUU^1ID: the ventral lobe is bifid, the others are entire, the small first umbilical lobe lies

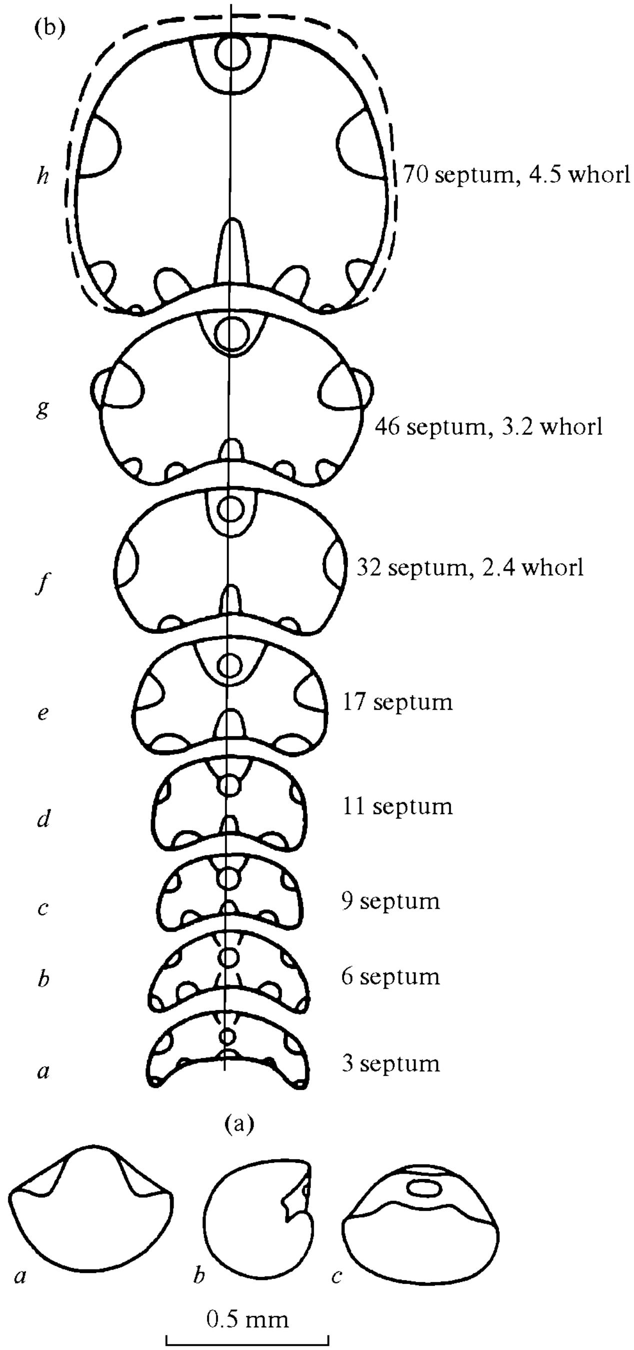


Fig. 61. *Colombiceras* ex gr. *crassicostatum* (d'Orbigny), specimen PIN, no. 5265/62: (a) protoconch, ×43: (*a*) upper view, (*b*) lateral view, (*c*) septal view; (b) morphogenesis of the whorl cross section: (*a–e*) ×31; (*f*); ×23; (*g*) ×12; (*h*) 6; northern Caucasus, Kuban River; Middle Aptian.

on the seam. Later, the U^1 lobe disappears and then is again formed in the U/I saddle in the middle of the third whorl and, by the end of this whorl, almost at the same time the external (V/U) and umbilical (U/U^1) saddle begin to divide into two and the umbilical lobe becomes bifid. Later, in the middle of the fourth whorl, the inner part of the suture becomes divided; the dorsal lobe becomes bifid and the inner saddle (I/D) becomes two-peaked.

Further changes reflect the increased complexity of existing elements. In the fifth–sixth whorls, the suture is complex. The sutural formula: $(V_1V_1)UU^1ID \rightarrow (V_1V_1)UID \rightarrow (V_1V_1)UU^1ID \rightarrow (V_1V_1)(U_2U_1U_2)U^1U^2I\,(D_1D_1)$.

S p e c i e s c o m p o s i t i o n. This genus includes the following species: *Colombiceras crassicostatum* (d'Orbigny, 1841); *C. treffrianus* (Karsten, 1856); *C. tobleri* (Jacob, 1906); *C. discoidale* (Sinzow, 1907); *C. subpeltoceroides* (Sinzow, 1907); *C. sinzowi* (Kasansky, 1914); *C. subtobleri* (Kasansky, 1914); *C. caucasicum* Luppov, 1949; *C. brumale* (Stoyanow, 1949); *C. elissoae* Kvantaliani, 1971; *C. bogdanovae* Tovbina, 1982; *C. korotkovi* sp. nov., and others. Russia (northern and southeastern Caucasus (Dagestan), Crimea); Europe (Switzerland, France, Spain); Asia (Kazakhstan (Mangyshlak), Turkmenistan, India); Africa (Madagascar); North and South America; Middle Aptian.

R e m a r k s a n d c o m p a r i s o n. The author of the genus *Colombiceras* (Spath, 1921, 1923) designated *Ammonites crassicostatus* d'Orbigny as the type species and assign it to the family Cheloniceratidae. He did not give a diagnosis of the new genus and did not comment on its composition. Later, species previously assigned to the *Ammonites crassicostatus* group were included in this genus.

Many authors after Spath placed the genus *Colombiceras* in the family Cheloniceratidae. However, genera of this family and the genus *Colombiceras* show clear differences in the morphogenesis of the suture and ornamentation. *Colombiceras* and *Cheloniceras* and also *Epicheloniceras* over the first two whorls have a similar suture. From the third whorl, new elements of the suture in the genus *Colombiceras* appear due to the division of the saddle U/I and, in the genera *Cheloniceras* and *Epicheloniceras,* due to the division of the lobes U and I. The dorsal lobe is also clearly different: bifid in *Cheloniceras* and trifid in *Cheloniceras* and *Epicheloniceras.* In addition, in *Cheloniceras,* the whorl is wider than high and the height increased with age less rapidly than in the genus *Colombiceras.* The above characters distinguish the genus *Colombiceras* from *Cheloniceras.* Therefore, we cannot support the assignment of the genus *Colombiceras* to the family Cheloniceratidae.

Avram (1973, pp. 4, 5) proposed to subdivide the genus *Colombiceras* into two subgenera: *Colombiceras (C.)* and *Colombiceras (Egoianiceras).*

In the stratotype region of the Gargasian, Dutour (2005) described *Colombiceras crassicostatum* (d'Orbigny), also recording this taxon for the lower level, *Dufrenoyia furcata* Zone.

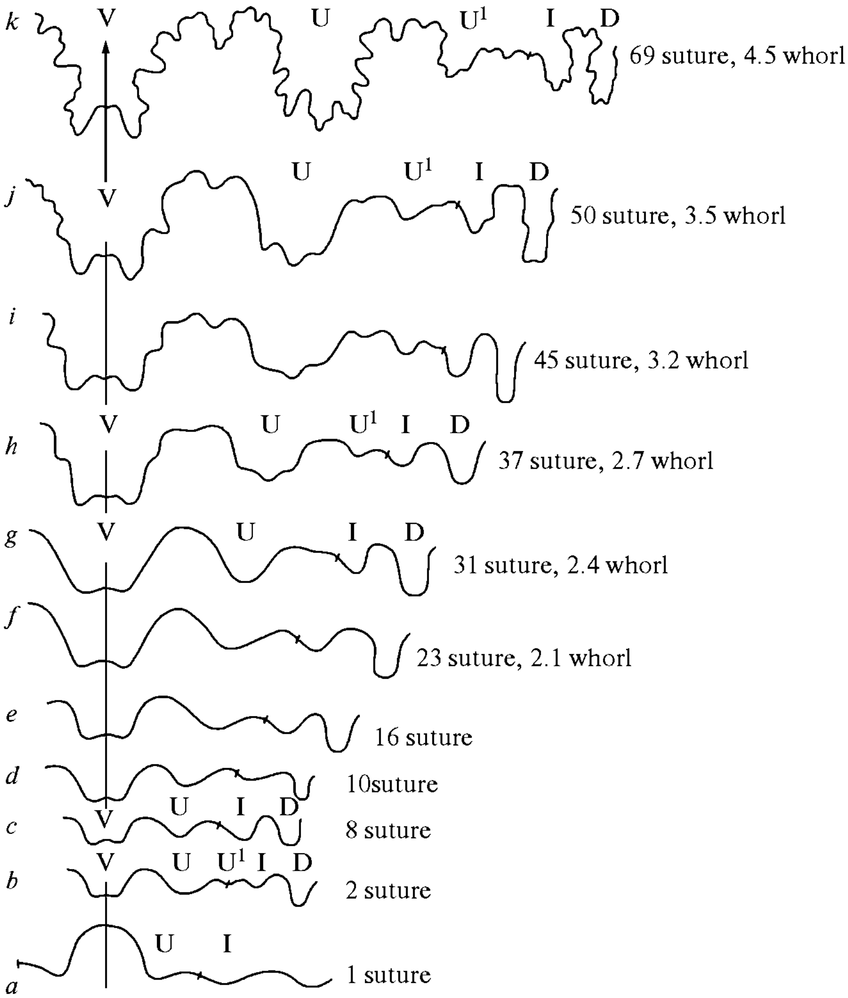


Fig. 62. Morphogenesis of the suture of *Colombiceras* ex gr. *crassicostatum* (d'Orbigny), specimen PIN, no. 5265/62: (*a–e*) ×12; (*f*) ×46, (*g*); ×39; (*h*) ×34; (*i*) ×25; (*j*) ×21; (*k*) ×10; northern Caucasus, Kuban River; Middle Aptian.

Colombiceras tobleri **(Jacob, 1906)**

Plate 16, figs. 1 and 2; Plate 17, figs. 1 and 2

Parahoplites tobleri: Jacob in Jacob and Tobler, 1906, p. 11, pl. 2, figs. 4, 5, and 6.

Acanthohoplites tobleri: Sinzow, 1907, p. 486, pl. 5, figs. 14 and 15; Sinzow, 1913, p. 113, pl. 6, figs. 2–2a.

Acanthoplites tobleri: Rouchadze, 1938a, pp. 138, 199.

Acanthoplites (Colombiceras) tobleri: Luppov in Luppov et al., 1949, p. 230, pl. 67, figs. 2 and 3.

Colombiceras tobleri: Glazunova, 1953, p. 47, pl. 11, figs. 1, 2a, 2c, 3, 4a–4q; Kudryavtsev, 1960, p. 328, pl. 14, figs. 1a, 1b, 2a, and 2b; Wiedmann and Dieni, 1968, p. 92, pl. 9, fig. 14; Stoykova, 1983, p. 87, pl. 1, fig. 2, pl. 3, figs. 2 and 3; Folmi, 1989, text-fig; Scharikadze et al., 2004, p. 384, pl. 63, fig. 2; pl. 64, fig. 2.

L e c t o t y p e. Specimen figured by Jacob and Tobler (1906, pl. 2, fig. 4); Aptian, Gargasian; Switzerland, Luter Zug. Designated herein.

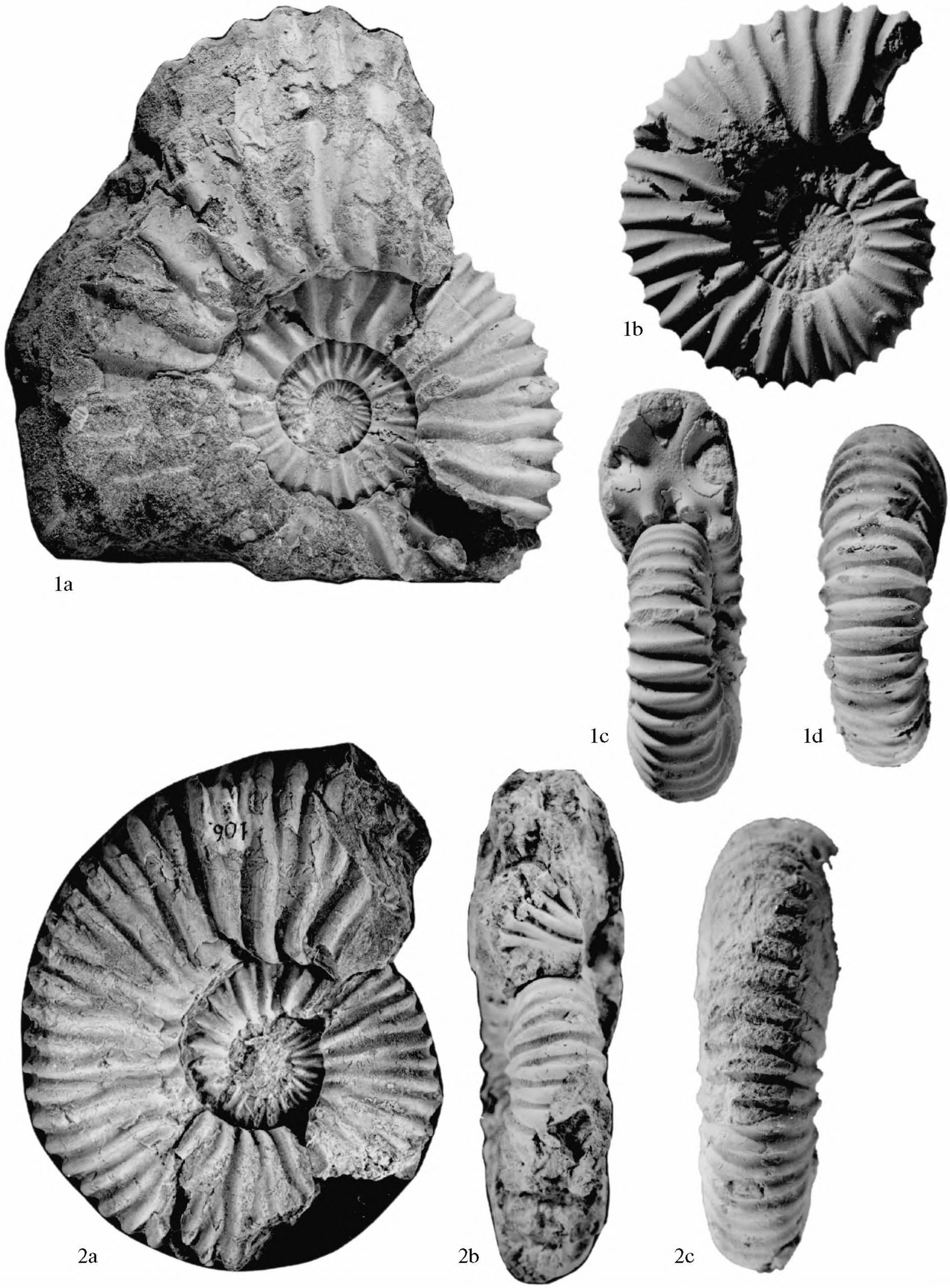
S h e l l s h a p e (Fig. 63a). The shell is semi-evolute, whorls embrace for less than a half. The cross section varies from ellipsoidal on the first whorls to rounded rectangular in the adult state. The venter and flanks are weakly convex with gradual transition to the low umbilical wall. The umbilicus is wide.

D i m e n s i o n s i n m m a n d r a t i o s:

Specimen PIN, no.	Dm	WH	WW	UW	WH/Dm	WW/Dm	UW/Dm
5265/181	51.8	22.7	15.2	14.8	0.44	0.30	0.29
5265/41	67.2	26.6	22.8	25.0	0.39	0.34	0.37
5265/42	84.0	35.8	28.8	28.8	0.42	0.34	0.34
5265/43	90.0	36.8	26.1	30.5	0.40	0.29	0.33
5265/44	93.8	37.6	28.8	32.0	0.40	0.30	0.34

O r n a m e n t a t i o n. The shell is covered by ribs (38 per the last whorl at the diameter of 68 mm). The primary ribs appear almost at the seam, gradually increase, weakly curve on the flank and run straight across the venter. The intercalary ribs, one between the primaries, begin in the middle of the flank or somewhat higher, gradually increase and, in the upper part of the flank, are not distinguished from the primaries. On the venter, all the ribs are crestlike and weakly flattened.

Plate 16



Explanation of Plate 16

Figs. 1 and 2. *Colombiceras tobleri* (Jacob, 1906); (1) specimen PIN, no. 5265/41; northern Caucasus, Kislovodsk; Middle Aptian, *Parahoplites melchioris* Zone; (2) specimen PIN, no. 5265/43; Dagestan, village of Dagva, the same age.

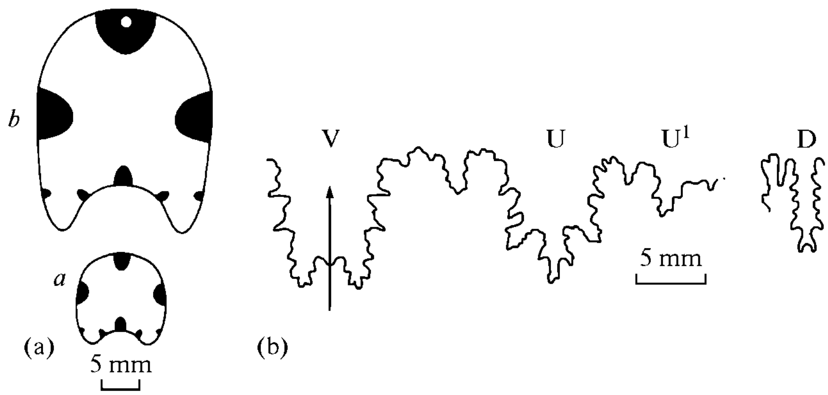


Fig. 63. *Colombiceras tobleri* (Jacob), specimen PIN, no. 5265/41: (a) whorl cross section at (*a*) WW = 4.2 mm and (*b*) WW = 21.0 mm; (b) suture at WW = 18.2; northern Caucasus, Kislovodsk; Middle Aptian.

Ribs visible on the penultimate whorl are more densely spaced. Per each primary rib there are from one to three intercalary ribs, which begin simultaneously with the primary ribs. In addition, primary ribs in the mid-flank have small spinous tubercles, at which they are subdivided into two branches. The anterior branch is curved forward, and the posterior branch crosses the venter straightly.

Suture (Fig. 63b). At the whorl width of 18.2 mm, the ventral lobe is bifid with a small bifid median saddle. The umbilical lobe is trifid, relatively symmetrical, as deep as the ventral lobe or deeper. The first umbilical lobe is half the depth of the umbilical lobe, trifid. The dorsal lobe is narrow, deep, bifid, with almost parallel serrated sides. The saddle V/U is high, asymmetrically bifid; saddle U/U^1 is narrower, lower, and weakly asymmetrical. The saddle I/D is narrow bifid with a deep secondary lobe.

Comparison. *Colombiceras tobleri* is similar to *C. discoidale* (Sinzow, 1906), from which it is distinguished by the narrower whorls. In contrast to *C. caucasicum* Luppov, it has less flattened crestlike ribs.

Remarks. The specimen figured by Sinzow (1907, pl. 5, figs. 14, 15) from a section in the vicinity of Pyatigorsk (northern Caucasus) completely corresponds to Jacob's description. Unfortunately, this specimen (no. 11068) is absent from the TsNIGR collection.

Occurrence. Russia (northern Caucasus, Dagestan), Kazakhstan (Mangyshlak), Turkmenistan (Great Balkhan, Kopet Dagh), Bulgaria, Switzerland, France; Middle Aptian, *Parahoplites melchioris* Zone; Georgia, Switzerland, Austria, Colombia; Middle Aptian.

Material. Five complete specimens and four well-preserved fragments. Northern Caucasus: Malka River (PIN, no. 5265/212), Kich-Malka River (PIN, no. 5265/235), Belaya River, village of Abadzekhskaya (PIN, no. 5265/42), Nalchik River (PIN, no. 5265/178), Belaya Rechka River (PIN, no. 5265/44), vicinity of Kislovodsk (PIN, no. 5265/41), Dagestan: village of Akusha (PIN, nos. 5265/181, 5265/182), village of Dagva (PIN, no. 5265/43); Middle Aptian, *Parahoplites melchioris* Zone.

Colombiceras discoidale (Sinzow, 1907)

Plate 18, figs. 1 and 2

Acanthohoplites tobleri Jacob var. *discoidalis:* Sinzow, 1907, p. 487, pl. 5, figs. 17–20.

Colombiceras tobleri Jacob var. *discoidalis:* Glazunova, 1953, p. 48, pl. 9, figs. 5a–5q.

Colombiceras tobleri discoidalis: Kudryavtsev, 1960, p. 328, pl. 6, fig. 2.

Colombiceras discoidale: Atlas ..., 2005, p. 393, pl. 101, figs. 3 and 4.

Lectotype. Specimen figured by Sinzow (1907, pl. 5, fig. 17, 18); Middle Aptian; Russia, northern Caucasus, vicinity of Pyatigorsk. Designated herein. Specimen no. 11068 is absent in the TsNiGR Museum.

Shell shape. The shell is semi-evolute. The whorls embrace each other slightly less than the half of the whorl height. The rounded rectangular cross section (Fig. 64a) is considerably higher than wide. The narrow venter is weakly rounded; the flanks are flattened. The umbilicus is wide. The umbilical wall is gently sloping.

Dimensions in mm and ratios:

Specimen PIN, no.	Dm	WH	WW	UW	WH/Dm	WW/Dm	UW/Dm
5265/45	40.7	14.1	13.5	16.1	0.34	0.33	0.22
5265/179	50.4	16.8	–	17.4	0.33	–	0.34
5265/46	55.0	20.7	16.7	19.5	0.38	0.30	0.35

Ornamentation. At the diameter 55 mm, there are 33 ribs in the last whorl. The primary ribs begin on the umbilical edge as prominent bullae, rapidly increase, bent weakly forward on the flank, and cross the venter straight. The intercalary ribs are one between the primaries, begin in the mid-flank, and are identical to the primaries on the venter, where both

Plate 17

Explanation of Plate 17

Figs. 1 and 2. *Colombiceras tobleri* (Jacob, 1906); (1) specimen PIN, no. 5265/44; northern Caucasus, Belaya Rechka River; Middle Aptian, *Parahoplites melchioris* Zone; (2) specimen PIN, no. 5265/42; northern Caucasus, Belaya River, village of Abadzekhskaya; the same age.

Figs. 3 and 4. *Colombiceras sinzowi* (Kasansky, 1914), (3) specimen PIN, no. 5265/47; (4) no. PIN, no. 5265/48; Dagestan, village of Akusha; Middle Aptian.

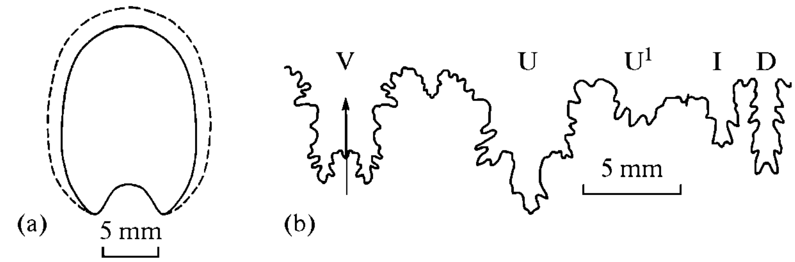


Fig. 64. *Colombiceras discoidalis* (Sinzow): (a) specimen no. 2894, whorl cross section at W = 14.7 mm; northern Caucasus, Baksan River; Middle Aptian; (b) specimen, PIN, no. 5265/46, suture at WH = 13.8 mm; northern Caucasus, Kheu River; Middle Aptian.

have a weakly flattened surface. Some intercalary ribs begin on the umbilical shoulder, similar to the primaries, but after leaving the venter, they reach only the mid-flank, where they disappear, i.e., resembling the wedging ribs of parahoplitids. The presence of the wedging and primary or intercalary ribs lead to the seeming proximity of the two primary or two intercalary ribs.

Specimen PIN, no. 5265/45 (Pl. 18, fig. 2) shows distinct ornamentation of the penultimate whorl. The number of the primary ribs, beginning on the umbilical shoulder and usually bearing thin spinous tubercles, reaches 11–12. Between these, there are two and, at the beginning of the whorl, three thin intercalary ribs appearing at the same level with the primaries, which are much coarser. At the tubercles, the primary ribs break into two branches. The ribs are slightly flattened on the venter.

Suture (Fig. 64b). The ventral lobe (V) is bifid, with strongly dissected almost parallel sides. The umbilical lobe (U) is deeper, trifid, and asymmetrical. The first umbilical lobe (U^1) is unusual in shape, has the base dissected into three almost equal digits. The inner lateral lobe (I) has three short digits at the base. A deep dorsal lobe (D) is typical of *Colombiceras*. All saddles are bifid and relatively symmetrical.

Variability. In the specimens studied, the outline of the cross section slightly varies. The cross section of our specimens is somewhat higher than that of Sinzow's specimens. In addition, specimen PIN, no. 5265/46 has a wider umbilicus.

Comparison. The difference from *Colombiceras tobleri* (Jacob) is given above.

Remarks. Kazansky (1914) proposed to recognize *Acanthohoplites tobleri* Jacob var. *discoidalis* Sinzow in a separate species, *Acanthohoplites sinzowi,* but he described and figured specimens dissimilar to the variety described by Sinzow. Rouchadze (1933) described *Acanthoplites sinzowi* Kasansky and included specimens described by Kazansky and Sinzow in the synonym list, although their measurements suggest considerably narrower whorls than indicated by Kazansky for *Acanthoplites sinzowi*. Glazunova (1953) noted the incongruence of *Colombiceras sinzowi* and *C. tobleri* Jacob var. *discoidalis* Sinzow.

Occurrence. Russia (northern Caucasus, Dagestan), Turkmenistan (Great Balkhan), Georgia; Middle Aptian.

Material. Three well-preserved specimens. Northern Caucasus: Gundelen River (PIN, no. 5265/179), Kheu River (PIN, no. 5265/46); Dagestan, village of Akusha (PIN, no. 5265/45); Middle Aptian.

Colombiceras sinzowi (Kasansky, 1914)

Plate 10, fig. 2; pl. 17, figs. 3 and 4

Parahoplites treffryanus: Anthula, 1899 (non Karsten, 1856), p. 127, pl. 21(?), fig. 2.

Acanthohoplites sinzowi: Kazansky, 1914, p. 73, pl. 3, figs. 52–55.

Colombiceras sinzowi: Kudryavtsev, 1960, p. 329, pl. 14, figs. 5 and 6.

Lectotype. Specimen figured by Kazansky (1914, pl. 3, fig. 52); Middle Aptian; Russia, Dagestan, village of Khodzhal-Machi. Designated here.

Shell shape. The protoconch is egg-shaped (Dm = 0.36 mm, W = 0.5 mm). The caecum and siphuncle extending from the first septum are well visible. The latter gradually narrows, located in the upper third of the whorl height and only gradually approach the venter.

The shell is small, semi-evolute, with relatively high and wide whorls embracing each other by slightly less than one-third of the whorl height. The cross section is rounded rectangular, with a rounded venter and weakly convex flanks. The umbilicus is relatively wide. The umbilical wall is steep. The cross section of three whorls is very low, ellipsoidal, the whorls weakly embrace each other and, beginning from the fourth whorl, the whorl height increases more rapidly than the width.

Dimensions in mm and ratios:

Specimen PIN, no.	Dm	WH	WW	UW	WH/Dm	WW/Dm	UW/Dm
5265/47	12.4	5.4	5.5	4.5	0.43	0.44	0.35
5265/48	37.0	16.0	14.8	11.2	0.43	0.40	0.31
5265/243	39.8	15.6	14.7	14.9	0.40	0.37	0.37
5265/180	44.5	20.0	17.2	14.8	0.44	0.38	0.33

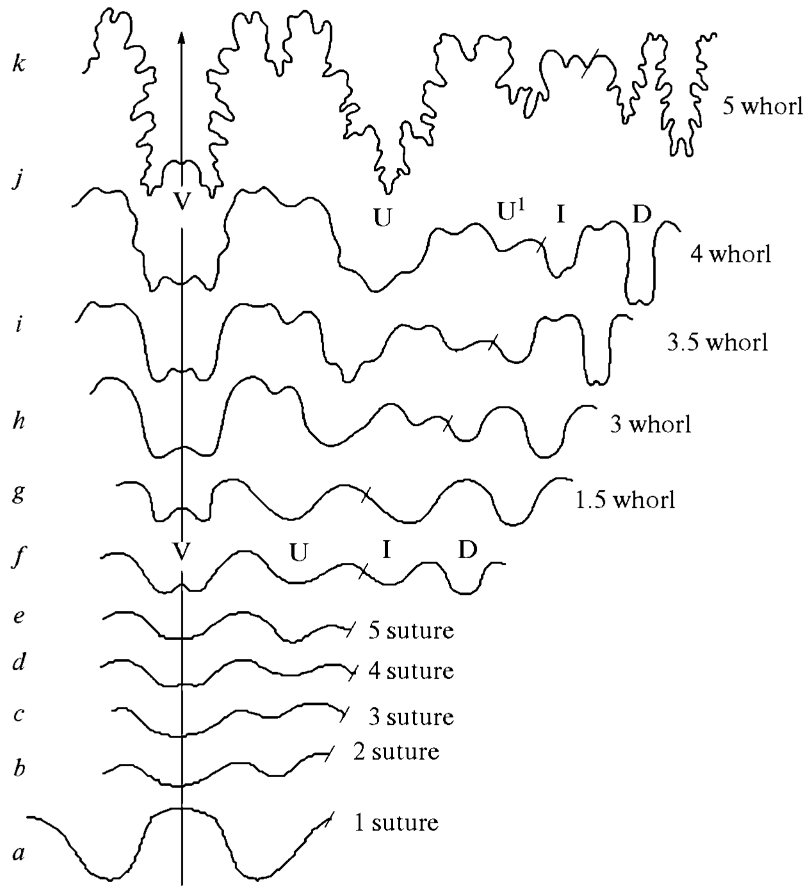


Fig. 65. Morphogenesis of the suture in *Colombiceras sinzowi* (Kasansky): (*a–j*) specimen no. 2300: (*a–g*) ×40; (*h*) ×34; (*i, j*) ×19; (*k*) specimen PIN, no. 5265/48, ×9; Dagestan, village of Akusha; Middle Aptian (after Mikhailova, 1960).

Ornamentation. At the shell diameter over 30 mm, the ornamentation is represented by primary and intercalary ribs and weak tubercles. The primary ribs begin almost at the seam, whereas the intercalary ribs appear about the mid-flank and reach the strength of the primaries near the venter. The total number of ribs is about 36–37 per whorl, all the ribs on the venter are flattened; the rib width is smaller than the intercostal spaces. The primary ribs possess tubercles, where in some cases the ribs break into two branches: a weaker posterior, and stronger anterior representing the continuation of the primary ribs. In some cases, the primary rib breaks into three branches; the tubercle becomes elongated, and the posterior branch is separated below the mid-flank. The intercalary ribs (one or two) begin on the umbilical shoulder near the primary, differing from them in the absence of tubercles.

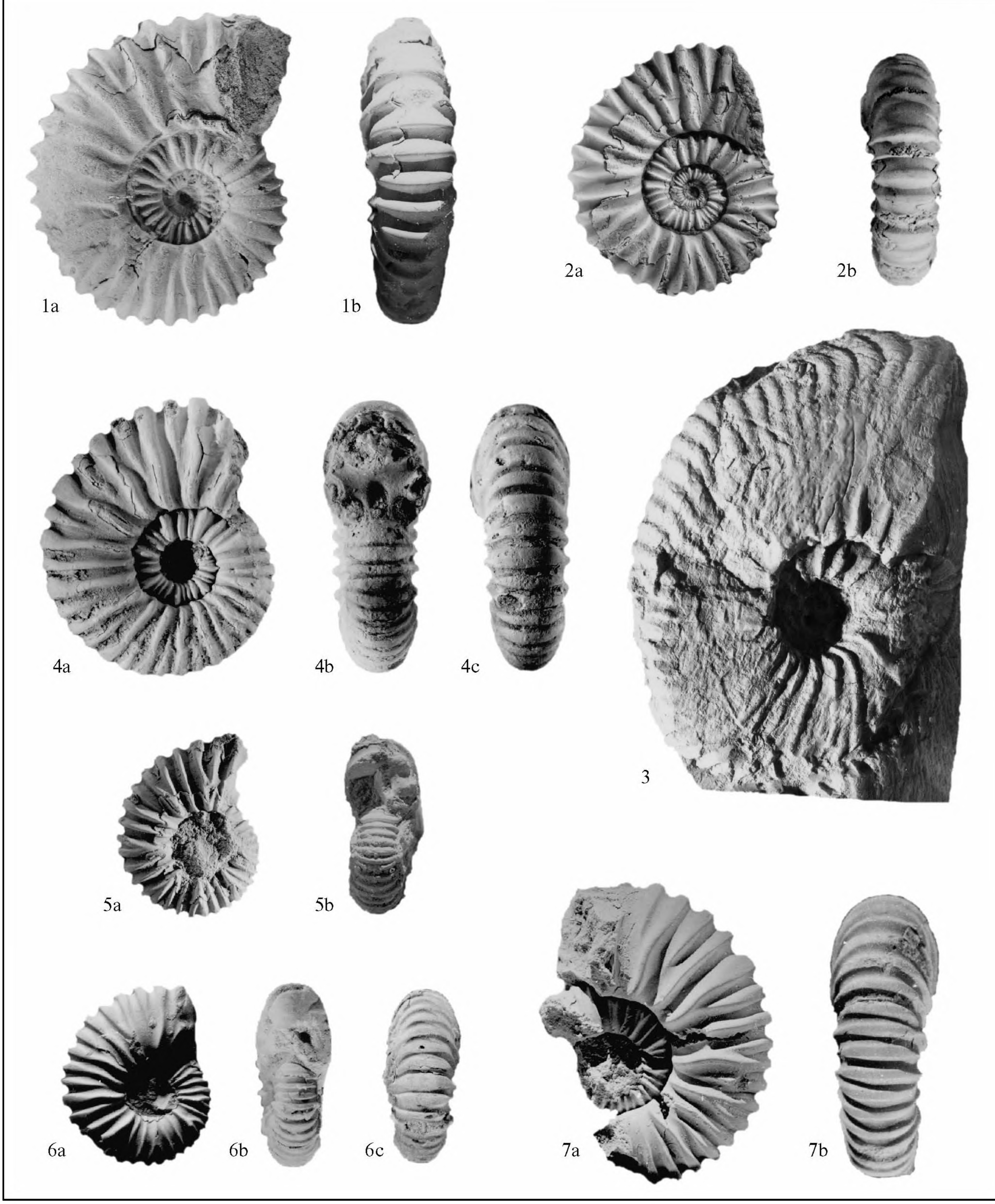
Ornamentation morphogenesis. The protoconch and first whorl are smooth. In the second whorl, i.e., approximately with Dm = 1 mm, tubercles in the mid-flank are well discernible and the umbilical lobe is curved around the tubercle. At Dm = 2.5 mm, it is possible to recognize ribs, beginning in the mid-flank from large or small tubercles. Somewhat later the ribs become branching. At Dm = 12.8 mm, 37 ribs occur on the venter, of which 12 are primary and the rest are intercalary. After Dm >30 mm, the number of tubercles is reduced.

Suture (Fig. 65). The suture of the fifth whorl is strongly dissected and the total number of lobes is five. The ventral lobe (V) is deep and bifid; the umbilical lobe (U) is almost as deep as the ventral lobe, relatively symmetrically trifid; the first umbilical lobe (U^1) is the

Explanation of Plate 18

Figs. 1 and 2. *Colombiceras discoidale* (Sinzow, 1907); (1) specimen PIN, no. 5265/46; northern Caucasus, Kheu River; Middle Aptian, *Parahoplites melchioris* Zone; (2) PIN, no. 5265/45; Dagestan, village of Akusha; the same age.
Fig. 3. *Colombiceras* sp; specimen MZ MGU, no. 79/4; southwestern Crimea, village of Mar'ino; Middle Aptian.
Figs. 4–7. *Colombiceras caucasicum* Luppov, 1949; specimens: (4) PIN, no. 5265/117; northern Caucasus, Urukh River; Middle Aptian; (5) PIN, no. 5265/50; northern Caucasus, Kich-Malka River; the same age; (6) PIN, no. 5265/51; (7) PIN, no. 5265/52; northern Caucasus, Kislovodsk; the same age.

Plate 18



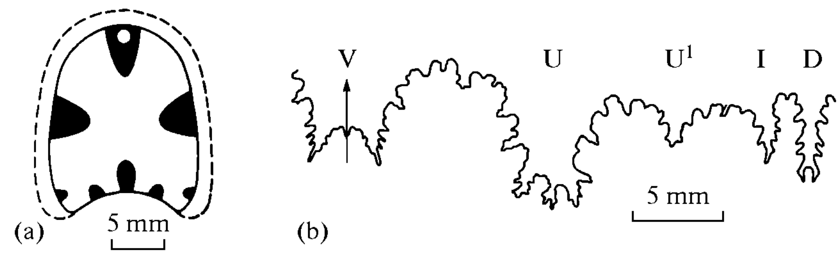


Fig. 66. *Colombiceras caucasicum* Luppov, specimen PIN, no. 5265/52: (a) whorl cross section at WW = 14.0 mm; (b) suture at WW = 13.2 mm; northern Caucasus, Kislovodsk; Middle Aptian.

shortest, asymmetrically bifid; the inner lateral lobe (I) is somewhat larger than the umbilical lobe, the bifid dorsal lobe (D) is deeper than the inner lateral and first umbilical lobe, but it is shorter and the ventral and umbilical lobes.

Morphogenesis of the suture. The prosuture is angustisellate, with a narrow median saddle. In the primary suture, small but broad dorsal and ventral lobe appears in place of the ventral and dorsal saddles; with the umbilical and inner lateral lobes between them. The base of the ventral lobe becomes flattened from the third suture and, in the fourth suture, this lobe is distinctly bifid. At the end of the third whorl, near the seam, a small depression appears on the external shell surface at the top of the umbilical saddle (U/I), leading to the formation of the first umbilical lobe (U^1). By the middle of the fourth whorl, the complexity of the existing elements increases: the umbilical lobe is distinctly trifid, the dorsal lobe becomes bifid, and three saddles (V/U, U/U^1, I/D) are two-peaked. Further fluting of the septum is reflected by the increased dissection of the elements of the suture.

Variability. The collection contains six specimens with fine, closely spaced ribs. The number of ribs increases to 40 per whorl. The sutural outline varies and even the ventral lobe is not totally symmetrical. The umbilical lobe in extreme cases is irregularly serrated, but, in the adjacent suture, it can be distinctly trifid. The variations result from different projections of the suture onto the ribs and interspaces and they can be observed in the adjacent sutures.

Comparison and remarks. The species is distinguished from *Colombiceras subtobleri* (Kasansky) by the denser ribbing; from *Colombiceras crassicostatum* (d'Orbigny), which has a similar ornamentation, by the ribs broken at the mid-flank into two branches; from *Colombiceras subpeltoceroides* (Sinzow) by the lower cross section and considerably smaller size. *Colombiceras sinzowi* is also similar to *C. korotkovi* sp. nov., especially specimen PIN, no. 5265/53, resembling a figured specimen of *C. sinzowi* in Kazansky (1914, pl. 3, fig. 52), but differing in the almost rounded whorls and the wider umbilicus. Since *Ammonites treffryanus* described by Karsten (1856, p. 109, pl. 4, fig. 1) is not identical to *Parahoplites treffryanus* described by Anthula (1899), the species name proposed by Kazansky (1914) is valid.

Occurrence. Russia (northern Caucasus, Dagestan); Middle Aptian.

Material. Eight complete well-preserved specimens and two fragments. The smallest specimen (PIN, no. 5265/47) is composed of almost four whorls with a completely preserved body chamber. The largest specimen is composed of more than five and a half whorls. The body chamber occupies about half of the last whorl. Northern Caucasus: Kuban River (PIN, nos. 5265/230, 5265/232), Malka River (PIN, nos. 5265/227, 5265/228), Kuma River (PIN, nos. 5265/225, 5265/226, 5265/243); Dagestan: village of Akusha (PIN, nos. 5265/47, 5265/48, 5265/180); Middle Aptian, *Colombiceras crassicostatum–Epicheloniceras subnodosocostatum* Zone.

Colombiceras caucasicum Luppov, 1949

Plate 18, figs. 4–7

Acanthoplites (Colombiceras) crassicostatum (d'Orbigny) var. *caucasica:* Luppov in Luppov et al., 1949, p. 230, pl. 67, fig. 1, text-fig. 58.

Colombiceras caucasicum: Luppov and Drushchits, 1958, pl. 47, fig. 5.

Colombiceras caucasica: Kudryavtsev, 1960, p. 330, pl. 5, fig. 3, pl. 6, fig. 3; Kvantaliani, 1971, p. 62, pl. 8, fig. 33, text-figs. 34 and 35; Sharikadze et al., 2004, p. 386, pl. 67, fig. 2, pl. 69, fig. 2, pl. 70, fig. 1 (?); Atlas ..., 2005, p. 393, pl. 101, fig. 5.

Holotype. TsNIGR Museum, no. 16/6801. Specimen figured by Luppov et al., (1949, pl. 67, fig. 1); Middle Aptian; Russia, northwestern Caucasus, Belaya River. Designated herein.

Shell shape. The shell is semi-evolute; whorls embrace each other for half of the whorl height or slightly less; the first whorls are wider than high. Later, the cross section (Fig. 66a) becomes rectangular oval. As the shell diameter increases, the relative whorl width increases. The venter and flanks are weakly convex. The umbilicus is relatively wide; the umbilical wall is steep.

Dimensions in mm and ratios:

Specimen PIN, no.	Dm	WH	WW	UW	WH/Dm	WW/Dm	UW/Dm
5265/242	27.1	13.8	11.5	12.7	0.50	0.42	0.47
5265/50	29.2	12.4	12.2	10.0	0.42	0.41	0.34
5265/231	31.0	11.5	11.0	9.8	0.37	0.35	0.32
5265/51	32.2	14.4	12.4	9.9	0.44	0.38	0.30
5265/117	45.8	19.6	16.5	14.9	0.42	0.36	0.32
5265/52	54.0	21.6	19.5		0.40	0.36	

Ornamentation. The ribs are strong and flattened. At Dm = 33 mm, there are 33 ribs in the last whorl, ten of which are primary, the rest are intercalary. The primary ribs begin in the lower part of the umbilical wall; on the umbilical shoulder, they form sharp umbilical bullae and further almost straight run across the flank, expanding and flattening in its upper third and cross the venter straight. The primary ribs at the mid-flank possess tubercles, from which the ribs are divided into two or three branches; the posterior intercalary rib often extend from the primary rib slightly higher than the umbilical shoulder. The intercalary ribs, usually two in a space between the primaries, begin at the same level as the primaries, but are considerably weaker than the latter and lack tubercles. With age, tubercles disappear, but in the lower third of the flank, the ribs often branch. Later, the intercalary ribs, which previously extended from the primaries, become separated and appear at the mid-flank. At this stage, one intercalary rib occurs per one primary rib.

Suture (Fig. 66b). At the whorl width of 13.2 mm, the ventral lobe is short, wide, and bifid, with obliquely diverging terminations. The umbilical lobe is deeper, trifid, and slightly asymmetrical. The first umbilical lobe is shallow, trifid, and relatively symmetrical. The inner lateral lobe is narrow, with a narrowing anterior end. The dorsal lobe is narrow deeper, and bifid. The broad two-peaked V/U saddle is slightly higher than the inner, narrow, bifid, relatively symmetrical saddle I/D. The saddles U/U^1 and U^1/I lying between them approximately of the same height and dissections.

Variability. The specimens studied show slight variations in the shape of the cross section: specimen PIN, no. 5265/50 has an almost tabulate venter, more than other specimens resembling the holotype. The suture is also variable. In specimen PIN, no. 5265/52, a weak asymmetry of the umbilical lobe in the penultimate whorl leads to a sharp asymmetry in the last whorl. In strongly ornamented shells, adjacent sutures can noticeably vary in details, resulting from different projections of the septa on the ribs or rib interspaces.

Comparison. The species described is similar to *Colombiceras crassicostatum* (d'Orbigny), but the latter has a tabulate venter and a higher cross section. In addition, ornamentation of *Colombiceras crassicostatum* is distinguished by being more regularly outlined, which is often observed in specimens that were drawn rather than photographed in early papers. *Colombiceras caucasicum* Luppov is similar to *C. sinzowi* Kasan., on the one hand, and to *C. tobleri* Jacob, on the other hand, but the former has wider whorls and, consequently, a differently shaped cross section, and also slightly denser ribbing; the latter has a wider umbilicus and much thinner and less flattened ribs on the venter.

Occurrence. Russia (northern Caucasus, Dagestan), Middle Aptian; *Colombiceras crassicostatum–Epicheloniceras subnodosocostatum* Zone; Georgia; Middle Aptian.

Material. Seven complete specimens and two fragments. Northern Caucasus: Kich-Malka River (PIN, nos. 5265/50, 5265/234), Kuban River (PIN, nos. 5265/229, 5265/231, 5265/233), Gundelen River (PIN, no. 5265/242), Urukh River (PIN, no. 5265/117); vicinity of Kislovodsk (PIN, nos. 5265/51, 5265/52); Middle Aptian, *Colombiceras crassicostatum–Epicheloniceras subnodosocostatum* Zone.

Colombiceras bogdanovae (Tovbina, 1982)

Plate 2, fig. 6

Protacanthoplites bogdanovae: Tovbina, 1982, p. 73, pl. 1, fig. 5.

Holotype. TsNIGR Museum, no. 5/11909; specimen figured by Tovbina (1982, pl. 1, fig. 5); Middle Aptian; Turkmenistan, western Kopet Dagh, Kyurendag Range, village of Danata. Designated by the author of the species.

Shell shape. The shell is semi-evolute. The cross section is oval, the height and width of the whorls are approximately the same. The venter is convex, the flanks are flattened. The umbilicus is wide.

Dimensions in mm and ratios:

Specimen no.	Dm	WH	WW	UW	WH/Dm	WW/Dm	UW/Dm
TsNIGR Museum 5/11909 holotype	40.0	16.0	14.8	16.3	0.40	0.37	0.40

Ornamentation. The shell possesses primary and intercalary ribs, almost radial on the flanks and flattened on the venter. The primary ribs are straight, begin on the umbilical wall. The anterior branch begins from the lateral tubercles approximately at the mid-flank; on the venter, the ribs are distinguished from one another. The lateral tubercles gradually decrease and disappear, and their starting point is shifted nearer to the umbilical shoulder. In addition, the space between the primary ribs has straight intercalary ribs, beginning at the same level as the primaries, but thinner than the primaries. Two–three and even four independent (intercalary) ribs occur between the primary ribs. The specimen described clearly shows change in the type of ribbing. In the first

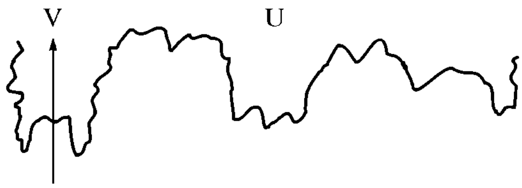


Fig. 67. Suture of *Colombiceras bogdanovae,* specimen TsNIGR Museum, no. 11/11909, WH= 4.8 mm; Lesser Balkhan, Chalsu gorge; Middle Aptian.

half of the whorl, the lateral tubercles are well developed and the number of thin intercalary ribs between the primaries is four. On the second half of the whorl, the number of intercalary ribs decreases to two–three; they become coarser; one trifid rib is present: the first branching on the umbilical shoulder and the second is in the mid-flank, with the anterior branch separated.

S u t u r e. The ventral lobe is bifid. The umbilical lobe is symmetrically trifid, with shortened branches (Fig. 67). The first umbilical lobe (U^1) is shallow; the inner lateral lobe (I) is weakly dissected. The saddles V/U and U/U^1 are bifid, serrated, but the first is considerably broader than the second.

C o m p a r i s o n a n d r e m a r k s. Tovbina described this species in the genus *Protacanthoplites* she proposed. However, the presence of the typical for *Colombiceras* flattened ribs makes us to change the generic attribution of this species, which is similar to *Colombiceras* ex gr. *crassicostatum* (d'Orbigny). This agrees with the data on the relatively low stratigraphic position of this species, which was also indicated by Tovbina (1982, p. 75).

O c c u r r e n c e. Turkmenistan (Tuarkyr, Great and Lesser Balkhan, Kopet Dagh); Middle Aptian, *Epicheloniceras subnodosocostatum* and lower horizons of the *Parahoplites melchioris* Zone.

M a t e r i a l. One well-preserved specimen. Kopet Dagh, Kyurendag Range, village of Danata (TsNIGR Museum, no. 5/11909); Middle Aptian, *Parahoplites melchioris* Zone.

Colombiceras korotkovi **Bogdanova et I. Michailova, sp. nov.**

Plate 11, fig. 4

?Acanthoplites aff. *sinzowi:* Rouchadze, 1938a, p. 139.

E t y m o l o g y. In memory of our friend and colleague Vladimir Aleksandrovich Korotkov.

H o l o t y p e. PIN, no. 5265/53. Middle Aptian, *Colombiceras crassicostatum*–*Epicheloniceras subnodosocostatum* Zone; Russia, northern Caucasus, vicinity of Kislovodsk.

S h e l l s h a p e. The shell is semi-evolute. The whorls embrace each other for about one-third of the height. The height of the cross section at small diameter is slightly greater than the width and, later in ontogeny, the width and height become almost the same. The cross section is oval, approximating the circle (Fig. 68a). The venter is broadly rounded; the flanks are weakly convex, without a sharp shoulder joining a low umbilical wall. The umbilicus is wide.

As the diameter increases, the relative whorl height and width noticeably decrease.

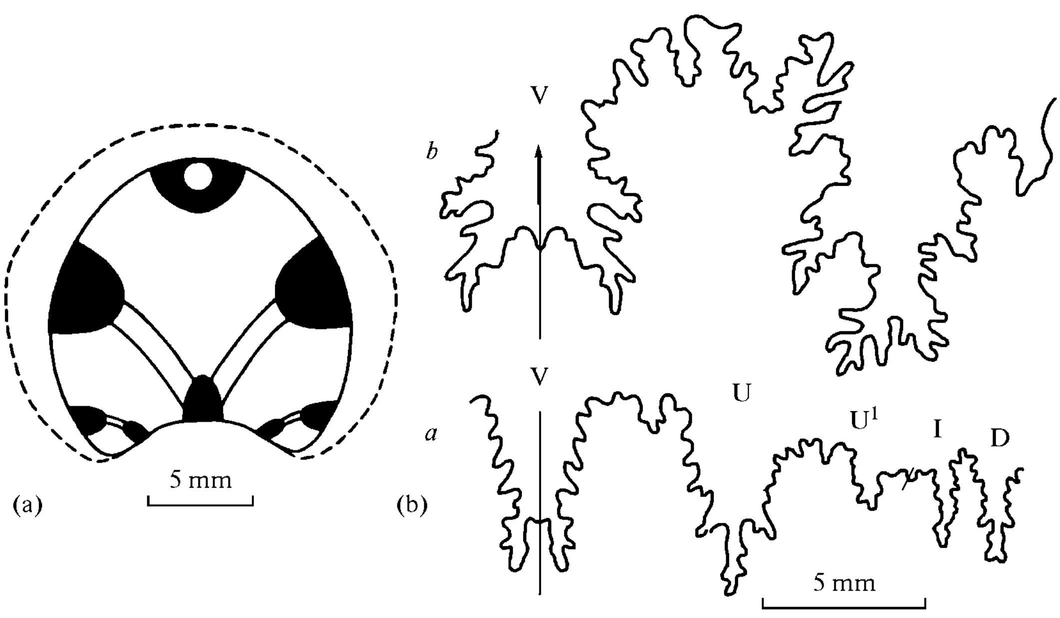


Fig. 68. *Colombiceras korotkovi* sp. nov., specimen PIN, no. 5265/53: (a) whorl cross section at Dm = 43.2 mm; (b) suture: (*a*) at Dm = 23.5 mm, (*b*) at Dm = 51.5 mm; northern Caucasus, Kislovodsk; Middle Aptian.

Dimensions in mm and ratios:

Specimen PIN, no.	Dm	WH	WW	UW	WH/Dm	WW/Dm	UW/Dm
5265/53*	21.1	10.5	9.0		0.50	0.43	
5265/53	29.8	12.9	12.0	11.4	0.43	0.40	0.38
5265/53	38.0	15.5	15.1	14.8	0.41	0.40	0.41
5265/53	45.4		18.7	18.0		0.41	0.39
5265/53	61.0	22.3	22.8	24.3	0.36	0.37	0.40

* Fragments are measured.

Ornamentation. The shell is covered by coarse ribs, the total number of which on the venter is 34. The primary ribs begin near the seam, at the mid-flank, possess an acuminate node, above which they break into two branches; a stronger anterior branch is curved forward on the flank, with a constriction before it.

Spaces between the primary ribs carry intercalary ribs beginning at the same level as the primary ribs. On the flanks, they are somewhat weaker than the primaries, whereas on the venter, they are sometimes identical to the latter. The regular arrangement of the primary and intercalary ribs is fixed by constrictions. The tubercles disappear with age, but the primary ribs bear elongated umbilical bullae, giving rise to two ribs with one intercalary rib between them. On the venter of shells over 13 mm in diameter, the ribs are flattened.

Suture. (Fig. 68b). The ventral lobe (V) is deep and bifid; the deeper umbilical lobe (U) is trifid, relatively symmetrical with a strongly elongated central branch; the first umbilical lobe (U^1) is the shallowest. The inner lateral lobe (I) is narrow; the dorsal lobe (D) is bifid, slightly deeper than the inner lateral lobe. The saddle V/U is high, asymmetrically bifid; the saddle U/U^1 is lower, bifid. The saddle U/U^1 is the lowest; the narrow saddle U^1/I is as high as the adjacent saddle.

Comparison. The new species is distinguished from *Colombiceras subpeltoceroides* (Sinzow) and *C. tobleri* (Jacob) by the wider umbilicus and different outline of the whorl cross section and from the second species, in addition, by the more strongly ornamented shell. *Colombiceras korotkovi* sp. nov. is most similar to *C. sinzowi* Kasansky, especially to the specimen figured by Kazansky (1914, pl. 3, fig. 52), but the latter has a narrower umbilicus, whereas the number of ribs at the same size reaches 31 instead 34 in our specimen.

Occurrence. Russia (northern Caucasus, Dagestan); Middle Aptian, *Colombiceras crassicostatum–Epicheloniceras subnodosocostatum* Zone.

Material. One complete well-preserved specimen with a partly preserved body chamber and several fragments. Northern Caucasus, vicinity of Kislovodsk (PIN, no. 5265/53); Middle Aptian, *Colombiceras crassicostatum–Epicheloniceras subnodosocostatum* Zone.

Superfamily Douvilleiceratoidea Parona et Bonarelli, 1897

Douvilleicerataceae: Mikhailova, 1983, p. 105; Wright et al., 1996, part L, vol. 4, p. 266.

Diagnosis. Shell with strongly inflated rounded or angular whorls; ornamented, with straight or slightly curved coarse ribs and tubercles (from one–two to eight rows on either side); tubercles typically absent on mid-venter. Protoconch and first whorl smooth. Tubercles on mid-flank appearing on second whorl, giving rise to ribs, bearing from one–two to eight rows of tubercles. Prosuture bilobed, with high ventral and lower dorsal saddles. Primary suture unstable five-lobed (VUU^1ID), fifth lobe (U^1) on first whorl reduced. New elements appearing by division of umbilical (U) and inner lateral (I) lobes, resulting in appearance of lobes U_1, U_2, I_2, I_1.

Sutural formula:

$$(V_1V_1)UU^1ID \rightarrow (V_1V_1)UID \rightarrow (V_1V_1)U_1U_2I_2I_1D.$$

Composition. Superfamily Douvilleiceratoidea is restricted to the family Douvilleiceratidae. Late Barremian–Early Albian; Europe, Asia, Africa, North and South America.

Remarks. The assignment to Douvilleiceratoidea of the families Trochleiceratidae Breistroffer, 1951 and Astiericeratidae Breistroffer, 1953 (Wright et al., 1996, p. 269) appears not well substantiated.

The inclusion (Wright et al., 1996, p. 266) in the superfamily Douvilleiceratoidea of the families Parahoplitidae Spath, 1922 and Deshayesitidae Stoyanow, 1949, i.e., lowering their taxonomic rank, is an extremely poor choice. This is not supported by the different patterns of the ontophylogenetic changes of the suture in Parahoplitoidea, Deshayesitoidea, and Douvilleiceratoidea. All the above superfamilies have an unstable five-lobed primary suture (VUU^1ID) inherited from the heteromorphic Ancyloceratoidea (suborder Ancyloceratina).

The evolution of Deshayesitoidea and Douvilleiceratoidea is documented with varying completeness. The first superfamily shows a succession from the heteromorphic *Heteroceras* to *Colchidites* and, later, to the monomorphic *Turkmeniceras,* which retain the relict characters of heteromorphism (umbilical perforation). *Turkmeniceras* gave rise to two genera, *Deshayesites* and *Paradeshayesites,* which have lost their perforation between the first and second whorls (Bogdanova and Mikhailova, 2004).

Douvilleiceratoidea possibly evolved from the genus *Paraspiticeras,* which most likely gave rise to the family Cheloniceratidae (subfamily Roloboceratinae). The genus *Paraspiticeras* was studied in detail by Wiedmann (1966; 1969). The suture figured (Wiedmann, 1969, fig. 15, p. 580) on its external portion almost completely corresponds to that in the family Douvilleiceratidae: hypertrophied saddle V/U and clearly bifid umbilical lobe U. In the Aptian, the umbilical lobe U of Douvilleiceratidae is divided into

Plate 19

two lobes (U_1 and U_2). With regard to the inner lateral lobe I, in *Paraspiticeras,* it still does not show a trend to the subdivision into I_1 and I_2.

There is a question: should *Paraspiticeras* be assigned to the superfamily Ancyloceratoidea or included in the superfamily Douvilleiceratoidea. The first variant is more preferred. However, the assumption of *Paraspiticeras* as a direct ancestor of Douvilleiceratoidea is contradicted by the fact that its occurrences are restricted to the Upper Hauterivian–Lower Barremian. The existing time gap between that and the first Cheloniceratidae is over 2 m.y. It is possible that the genus *Paraspiticeras* could be a descendant of the family Crioceratitidae rather than Ancyloceratidae (Baraboshkin and Mikhailova, 2009; Mikhailova and Baraboshkin, 2009). The monotypic Middle Albian family Astiericeratidae, in which the last whorl terminates in the lower scaphitoid hook, is a possible descendant of the superfamily Douvilleiceratoidea (Wright et al., 1996, p. 270).

C o m p a r i s o n. This superfamily differs from the superfamily Parahoplitoidea Spath in the appearance of new elements by the division of the umbilical and inner lateral lobes, and also in the hypertrophied saddle V/U.

Family Douvilleiceratidae Parona Et Bonarelli, 1897

Douvilleiceratidae: Arkell et al., 1957, L383; Wright et al., 1996, part L, vol. 4, p. 266.

D i a g n o s i s. Coincides with the diagnosis of the superfamily.

C o m p o s i t i o n. The family Douvilleiceratidae is subdivided into three subfamilies: Roloboceratinae Casey, 1961; Cheloniceratinae Spath, 1923; and Douvilleiceratinae Parona et Bonarelli, 1897. Genera and species described in this paper are assigned only to the subfamilies Cheloniceratinae and Douvilleiceratinae, the diagnoses of which are given below. Late Barremian–Early Albian; Europe, Asia, Africa, North and South America.

Subfamily Cheloniceratinae Spath, 1923

Cheloniceratinae: Arkell et al., 1957, L383; Wright et al., 1996, part L, vol. 4, p. 267.

D i a g n o s i s. Shell inflated, sometimes strongly inflated, semi-evolute. Cross section wide, rounded or angular. Ornamentation coarse, ribs with upper row of large lateral tubercles and lower row of smaller tubercles on umbilical shoulder. Suture typical of superfamily.

C o m p o s i t i o n. This subfamily includes the following genera: *Procheloniceras* Spath, 1923; *Cheloniceras* Hyatt, 1903 and *Epicheloniceras* Casey, 1954. Upper Barremian–Lower Albian; Europe, Africa, North and South America, Japan.

C o m p a r i s o n. The subfamily Cheloniceratinae is distinguished from the subfamily Douvilleiceratinae by the presence of at most three rows of tubercles.

Genus *Cheloniceras* Hyatt, 1903

Cheloniceras: Hyatt, 1903, p. 101; Spath, 1923, p. 64; Roman, 1938, p. 426; Scott, 1939, p. 1005; Arkell et al., 1957, p. L385; Luppov and Drushchits, 1958, p. 336; Kudryavtsev, 1960, p. 336; Casey, 1961a, p. 194; Dimitrova, 1967, p. 170; Kvantaliani, 1971, p. 105; Wright et al., 1996, p. 269; Sharikadze et al., 2004, p. 317; Atlas ..., 2005, p. 380; Dutour, 2005, p. 151.

T y p e s p e c i e s. *Ammonites cornuelianus* d'Orbigny, 1841 (d'Orbigny, 1840–1842, p. 364, pl. 112, fig. 1. 2); Lower Aptian, Paris Basin.

D i a g n o s i s. Shell large, medium-sized, less commonly small, inflated, semi-evolute with whorls, overlapping for less than half of whorl height. Umbilicus relatively wide, umbilical wall steep. Cross section wide, angular at level of tubercles, rounded between tubercles.

Shell with coarse ornamentation, consisting of ribs and two pairs of tubercles. Small lower tubercles lying on umbilical shoulder. Above seam, large tubercles confined to mid-flank. Primary ribs at lateral tubercles broken into two branches; anterior branch usually more prominent than posterior branch. In addition, shell having intercalary ribs, independent of primaries.

Sutural formula

$$VU_1U_2I_2I_1D.$$

S p e c i e s c o m p o s i t i o n. This genus includes many species, and two species are described below: *C. cornuelianum* (d'Orbigny, 1841) and *C. natarius* I. Michailova, 2009; Russia (northern Caucasus, Dagestan, Middle Volga Region), Kazakhstan (Mangyshlak), Turkmenistan, Georgia, Western Europe (France, England), Africa, North and South America, Japan; Lower Aptian.

R e m a r k s a n d c o m p a r i s o n. *Cheloniceras* is distinguished from *Procheloniceras* Spath by the presence of strong lateral and small umbilical tubercles.

Casey (1954, p. 113) subdivided the genus *Cheloniceras* into three subgenera: *Cheloniceras (Cheloniceras)* sensu stricto, *Ch. (Roloboceras)* subgen nov., and *Ch. (Epicheloniceras)* subgen nov. The first two subgenera are characteristic of the Early Aptian, and the third, of the Middle Aptian. Later, Casey (1954)

Explanation of Plate 19

Figs. 1 and 2. *Cheloniceras cornuelianum* (d'Orbigny, 1841); (1) specimen PIN, no. 5265/106; Volga Region near Ulyanovsk, village of Vilovka; Lower Aptian; (2) PIN, no. 5265/104; Dagestan, village of Akusha; the same age.

Figs. 3 and 4. *Pseudoaustraliceras pavlowi* (Wassiliewsky, 1908). (3) specimen no. GIN Georgia, no. 401/90; Kopet Dagh, Adzhidere, Middle Aptian, *Parahoplites melchioris* Zone; (4) GIN Georgia, no. 400/90; Great Balkhan, village of Oglanly; the same age.

Plate 20

raised the rank of *Roloboceras* to the generic level, described several new species of this genus, and studied morphogenesis of the suture of *Roloboceras hambrovi* (Forbes). This species clearly shows typical characters of Douvilleiceratoidea: the umbilical (U) and inner lateral (I) lobes are divided into two parts ($U \rightarrow U_1U_2$ and $I \rightarrow I_2I_1$) and also the saddle V/U being considerably higher than the adjacent saddles. This pattern completely corresponds to the morphogenesis of the suture in the genera *Cheloniceras* Hyatt, 1903 and *Epicheloniceras* Casey, 1954, and this rank was later accepted by many workers.

However, Casey (1961b, p. 193), Dimitrova (1967, p. 170), Arkell et al. (1957, L385), and Wright et al. (1996, p. 269) maintained their view that *Cheloniceras (Cheloniceras)* and *Cheloniceras (Epicheloniceras)* were subgenera.

These genera are clearly distinguished by the differences in ornamentation. The genus *Cheloniceras* has two rows of tubercles: lateral and umbilical rows, and *Epicheloniceras* has a third row of ventral tubercles.

Cheloniceras cornuelianum **(d'Orbigny, 1841)**

Plate 19, figs. 1 and 2; Plate 20, fig. 3

Ammonites cornuelianus: d'Orbigny, 1840–1842, p. 364, pl. 112, figs. 1 and 2; Sinzow, 1872, p. 30, pl. 5, figs. 1 and 2.

Douvilleiceras cornuelianum: Sinzow, 1906, p. 158, pl. 1, figs. 1 and 2; Kazansky, 1914, p. 63, pl. 3, figs. 40 and 41.

Douvilleiceras cornueli: Nikshich, 1915, p. 10, pl. 1. figs. 1–5.

Cheloniceras cornuelianum: Luppov et al., 1949, p. 234, pl. 70. fig. 1; Kudryavtsev, 1960, p. 336, pl. 18, figs. 1–3; Kotetishvili, 1970, p. 98, pl. 19, fig. 3; Thomel, 1980, p. 132, fig. 260; Bogdanova and Prozorovsky, 1999, p. 81, fig. k; Atlas ..., 2005, p. 381, pl. 93, fig. 4; Dutour, 2005, p. 152, pl. 19, figs. 1–6.

Cheloniceras (Cheloniceras) cornuelianum: Arkell et al., 1957, p. L385, fig. 501. 5; Casey, 1961a, p. 198, pl. 33, fig. 7; pl. 34, figs. 1–9; pl. 35, figs. 1 and 2; text-figs. 60–62, 67e–67f (this paper contains the most detailed synonymy list); Dimitrova, 1967, p. 170; Wright et al., 1996, p. 269, text-figs. 208, 4a, 4b.

Lectotype. Specimen figured by d'Orbigny (1840–1842, pl. 112, figs. 1, 2); Lower Aptian, clay with *Plicatula*; France, Haute Marne, Wassy. Designated by Casey, (1961a, p. 200).

Shell shape. The shell is medium-sized, less commonly small or large, semi-evolute. The whorl overlap is about a third of its height. The umbilicus is deep and moderately wide. The umbilical wall is high. The cross section is rounded angular. The venter is broadly rounded.

Dimensions in mm and ratios:

Specimen PIN, no.	Dm	WH	WW	UW	WH/Dm	WW/Dm	UW/Dm	WW/WH
5265/104	43.3	15.6	24.9	14.9	0.44	0.56	0.33	
5265/106		7.17	11.2					1.55
5265/105	44.2	17.8	25.6	15.0	0.40	0.57	0.33	

Ornamentation. The primary ribs have two rows of tubercles; the lower row is on the umbilical shoulder and the upper row lies about mid-flank. The upper lateral tubercles most strongly prominent; from them, the ribs break mostly into two, less commonly, into three branches. The intercalary ribs (one–three between the primaries) begin near the umbilicus and above it. In large specimens, all ribs on the venter are identical. The morphogenesis was studied in specimen PIN, no. 5265/56.

Suture (Fig. 69). The suture in adults is typical. The ventral lobe is bifid, with high median saddles, deeper than other lobes. The umbilical lobes are detached, asymmetrically trifid; U_1 is considerably deeper than U_2. The similar proportions are observed in the I_2 and I_1 lobes, but they are smaller. The dorsal lobe is narrow, with a single termination. The external saddle V/U_1 is extremely high, much higher than all other elements.

The morphogenesis of the suture is traced beginning from the fourth sutures, with five lobes: VUU^1ID. This number of lobes remains even in the eight sutures. At the beginning of the third whorl, the lobe U is divided into two uneven parts: the larger U_1 and slightly shallower (raised) U_2. These proportions remain to the middle of the fifth whorl. The lobes I and I_2 are similarly divided into two unequal parts $I \rightarrow I_2$ (shallower) and I_1 (deeper).

Comparison. This species is distinguished from *C. seminodosum* Sinzow by the ribs originating from the lateral tubercles, whereas in the latter species, branching at the later stage begins from the umbilical tubercles. In the early whorls, differences are less distinct.

Occurrence. Russia (northern Caucasus, Dagestan, Middle Volga Region); Kazakhstan (Mangyshlak); Turkmenistan, Georgia, France, Switzerland, England; Lower Aptian.

Material. Three specimens of varying state of preservation. Dagestan, village of Akusha (PIN, no. 5265/104); Middle Volga Region, village of

Explanation of Plate 20

Figs. 1 and 2. *Epicheloniceras tschernyschewi* (Sinzow, 1906); (1) specimen PIN, no. 5265/95; Mangyshlak, village of Aktash; Middle Aptian, *Epicheloniceras subnodosocostatum* Zone; (2) specimen PIN, no. 5265/94; Mangyshlak, Tushchibek well; the same age.

Fig. 3. *Cheloniceras cornuelianum* (d'Orbigny, 1841); specimen PIN, no. 5265/106; Volga Region near Ulyanovsk, village of Shilovka; Lower Aptian.

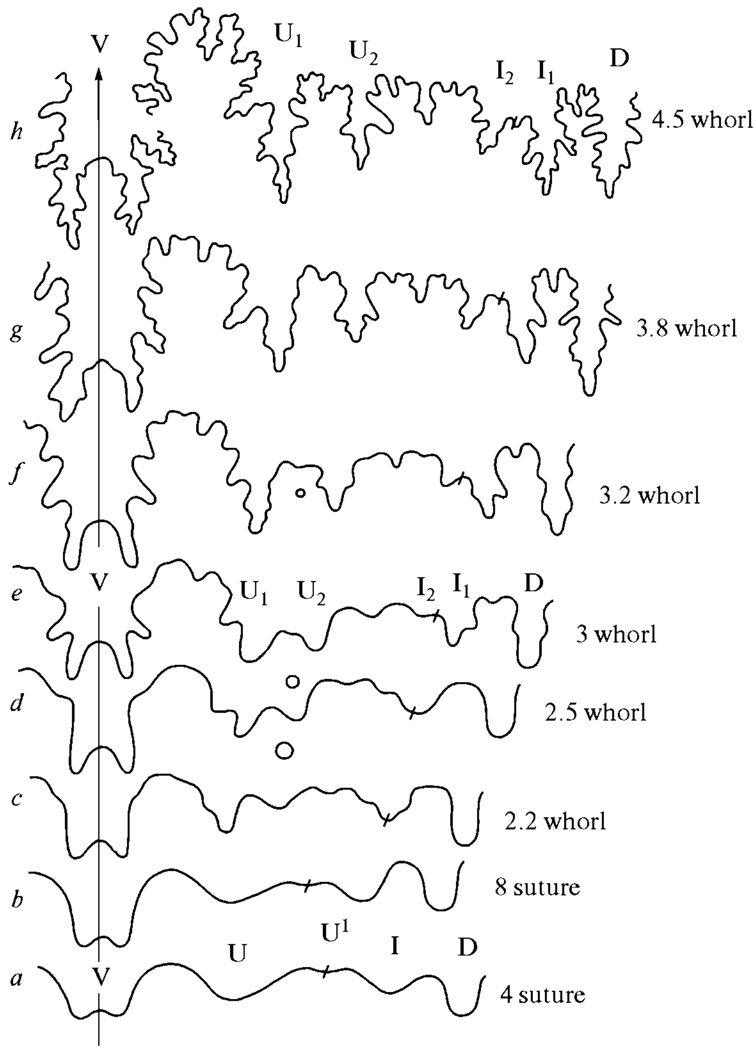


Fig. 69. Morphogenesis of the suture of *Cheloniceras cornuelianum* (d'Orbigny), specimen PIN, no. 5265/56: (*a*, *b*) ×97; (*c*) ×30; (*d*) ×23; (*e*) ×16; (*f*) ×13; (*g*)×8; (*h*) ×6; Dagestan, village of Akusha; Early Aptian.

Shilovka (PIN, no. 5265/106); Mangyshlak, Kugusem (PIN, no. 5265/105); Lower Aptian.

Cheloniceras natarius I. Michailova, 2009

Plate 21, fig. 1; Plate 22, fig. 1

Cheloniceras natarius: Mikhailova, 2009, pp. 24–26, pl. 1, fig. 1.

Holotype. Ulyanovsk, Museum "Simbirtsit" of the "Lita" company, specimen no. 1; Volga Region near Ulyanovsk; Lower Aptian, *Deshayesites deshayesi* Zone. Designated by the author of the species.

Shell shape. The shell is large, up to 370.0 mm in diameter. The whorl is 115.0 mm high and 140.0 mm wide. The umbilical width is 135.0 mm. In the middle whorls, the overlap is not more than a third of the whorl height and, by the end of the last whorl, the shell becomes almost evolute. The umbilicus is shallow and very wide. The umbilical wall is low and steep. The cross section is rounded; its width exceeds its height. The venter is broad and rounded.

Ornamentation. In the last whorl, the ornamentation is represented by 36 widely spaced ribs identical on the venter. On the first half of this whorl, the ribs break near the umbilical shoulders (near the lower umbilical tubercles) into two branches. The lower lateral tubercles are smaller and the upper lateral tubercles are larger. They are clearly fixed on the penultimate whorl. The suture is not observed.

Comparison. This species is distinguished from the most similar species *Ch. cornuelianum* (d'Orbigny) by the more strongly evolute shell and the shallow and very wide umbilicus.

Occurrence. Russia, Volga Region near Ulyanovsk; Lower Aptian.

Material. One large complete well-preserved specimen found by a fishermen near the village of Krushi and purchased by the "Lita" company (Ulyanovsk).

Volga Region near Ulyanovsk; village of Kriushi; Lower Aptian, *Deshayesites deshayesi/Audouliceras renauxianum* Zone.

Genus *Epicheloniceras* Casey, 1954

Cheloniceras (Epicheloniceras): Casey, 1954, p. 113; 1962, p. 235; Arkell et al., 1957, p. L385; Dimitrova, 1967, p. 173; Stoykova, 1983, p. 85; Wright et al., 1996, p. 269.

Epicheloniceras: Luppov and Drushchits, 1958, p. 117; Kudryavtsev, 1960, p. 338; Egoian, 1969, p. 182; Kvantaliani, 1971, p. 107; Mikhailova, 1976, p. 263; Mikhailova, Hosni, 1984, p. 85; Sharikadze et al., 2004, p. 339; Atlas ..., 2005, p. 383; Dutour, 2005, p. 159.

Type species. *Douvilleiceras tschernyschewi* Sinzow (Sinzow, 1906, p. 182), Middle Aptian; Mangyshlak. Designated by Case (1954, p. 113).

Diagnosis. Shell inflated, whorl overlap up to half of whorl height. Flanks convex; venter wide and rounded. Umbilicus deep, moderately wide. Umbilical wall high with rounded edge. Cross section between tubercles oval, when cut through tubercles octagonal.

Ornamentation. The primary ribs have three rows of tubercles; the intercalary ribs are weaker (branching off the primaries) or wedging.

Morphogenesis of ornamentation (Fig. 70). The protoconch and first whorl up to the primary constriction are smooth. In the second whorl, tubercles appear at the mid-flank and, on the third whorl, there are about seven tubercles, which are shifted nearer the umbilicus. The ribs appear from the beginning of the fourth whorl originally extending from some of the tubercles. By the end of the fourth whorl, the ornamentation ceases and, in the next, fifth whorl, primary and intercalary ribs extend from the lateral tubercles, and the second row of tubercles appears on the margins of the ventral side. There are seven–nine large lateral tubercles per whorl, giving rise to two branches; the posterior branch is wide and strong, with ventral tubercles, and the anterior branch is thin and less prominent. Sometimes, the shell possess weak isolated intercalary ribs similar to a smooth branch; a third row of small umbilical tubercles often appears. On the next, sixth (less commonly seventh) whorl, tubercles become weaker, sometimes almost completely disappear, primary and intercalary ribs either become uniform [*Epicheloniceras subnodosocostatum* (Sinzow) group] or more prominently different [*E. tschernyschewi* (Sinzow) group]. The sixth whorl, which reaches 31 mm in diameter, has 20 simple unbranching, strong, almost straight ribs, noticeably expanding towards the venter.

The suture is typical of the family.

Species composition. The genus *Epicheloniceras* includes more than 35 species, among which the Middle Aptian of Russia and adjacent countries contains *E. tschernyschewi* (Sinzow, 1906); *E. caucasicum* (Anthula, 1899); *E. waageni* (Anthula, 1899); *E. subnodosocostatum* (Sinzow, 1906); *E. pusillum* (Sinzow 1906); *E. orientale* (Jacob, 1906); *E. buxtorfi* (Jacob, 1906); *E. volgense* (Wassiliewsky, 1908); *E. stuckenbergi* (Kasansky, 1914); *E. intermedium* (Kasansky, 1914); *E. martinioides* Casey, 1961; *E. debile* Casey, 1961; *E. gracile* Casey, 1961, and others; Russia (northern Caucasus, Dagestan, Middle Volga Region); Kazakhstan (Mangyshlak); Turkmenistan; Georgia, England, Germany, France, Austria, Bulgaria, Switzerland; Africa (Madagascar), Iran, India, USA (California), Mexico, Colombia. Species of *Epicheloniceras* are restricted to the lower zone of the Middle Aptian.

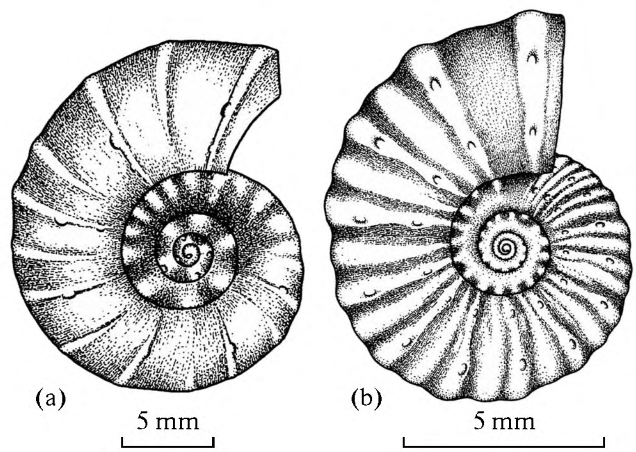


Fig. 70. Initiation and establishment of ornamentation in *Epicheloniceras:* (a) ×3.5; (b) ×7; Dagestan, village of Akusha; Early Aptian (after Bogdanova and Mikhailova, 2007).

Comparison. The genus is distinguished from *Cheloniceras* Hyatt by the presence of ribs with three pairs of tubercles, thinner ribs and narrower whorl cross section; from the genus *Douvilleiceras* Grossouvre by the fewer rows of tubercles, less coarse ribbing, and the wider venter.

Epicheloniceras tschernyschewi (Sinzow, 1906)

Plate 20, figs. 1 and 2; Plate 23, figs. 7–9

Douvilleiceras Tschernyschewi: Sinzow, 1906, p. 182, pl. 2, figs. 11–12; pl. 3, figs. 2–7; Wassiliewskyi, 1908a, p. 33; Nikshich, 1915, p. 25; pl. 2, figs. 2–9; pl. 3, figs. 1–2; pls. 4 and 5.

Cheloniceras tschernyschewi: Eristavi, 1955, p. 184; Eristavi, 1961, p. 64, pl. 3, figs. 9–10.

Cheloniceras (Epicheloniceras) tschernyschewi: Arkell et al., 1957, p. 385, fig. 503.1; Casey, 1962, p. 236, pl. 39, figs. 6 and 7 (detailed synonymy list); Stoykova, 1983, p. 85, pl. 4, figs. 2 ? and 3

Epicheloniceras tschernyschewi: Kudryavtsev, 1960, p. 339, pl. 19, figs. 2 and 3.

Epicheloniceras tschernyschewi: Sharikadze et al., 2004, p. 339, pl. 32, fig. 2; pl. 41. fig. 1; pl. 42, fig. 1; pl. 43, fig. 1; pl. 44, fig. 1; Atlas..., 2005, p. 383, pl. 94, fig. 1.

Lectotype. TsNIGR Museum, no. 16/11068. Specimen figured by Sinzow (1906, pl. 3, fig. 2); Aptian; Kazakhstan, Mangyshlak, Kyzyl-Kaspak Range. Designated by Casey (1962, p. 236).

Shell shape. The protoconch is elongated, 0.80 mm wide, and 0.58 mm in diameter (Fig. 71a). The shell is strongly inflated, semi-evolute, with moderately expanding whorls, overlapping for one-third of

Plate 21

Explanation of Plate 21

Fig. 1. *Chelonicerac natarius* I. Michailova, 2009, Museum «Simbirtsit» of the “Lita” company, specimen no. 1, ×43; Volga Region near Ulyanovsk, villadge of Kriushi, Lower Aptian, *Deshayesites deshayesi* Zone.

Plate 22

Explanation of Plate 22

Fig. 1. *Cheloniceras natarius* I. Michailova, 2009, Museum "Simbirtsit" of the "Lita" company. Specimen no. 1, ×43; Volga Region near Ulyanovsk, village of Kiushi, Lower Aptian, *Deshayesites deshayesi* Zone.

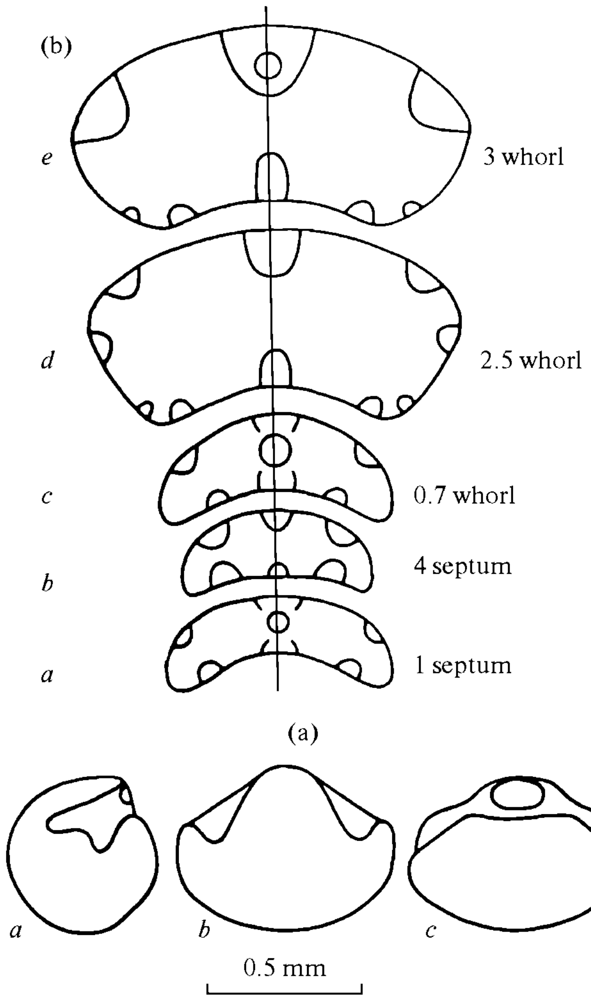


Fig. 71. *Epicheloniceras tschernyschewi* (Sinzow), specimen PIN, no. 5265/57: (a) protoconch: (*a*) lateral view, (*b*) ventral view, (*c*) septal view; (b) morphogenesis of the cross section: (*a*–*c*) ×43; (*d*) ×21; (*e*) ×6.

the whorl height. The flanks are slightly flattened, indistinctly delineated from the venter. The umbilicus is deep and moderately wide. The umbilical wall is high and steep. The whorl cross section changes considerably as the shell grows from broadly oval (angular if the section plane runs through the tubercles) to rounded oval (Fig. 71b).

Dimensions in mm and ratios:

Specimen PIN, no.	Dm	WH	WW	UW	WH/Dm	WW/Dm	UW/Dm
5265/95	17.5	10.0	13.0	7.5	0.57	0.74	0.42
5265/241	37.5	20.3	25.4	11.6	0.54	0.68	0.31
5265/251	45.5	19.0	26.5	11.0	0.42	0.58	0.24
5265/238	55.5	26.5	32.1	–	0.48	0.58	–
5265/97	59.1	28.8	36.1	17.8	0.48	0.61	0.30
5265/96	77.6	28.3	48.0	26.7	0.36	0.61	0.34
5265/94	87.7	36.6	53.2	23.7	0.42	0.61	0.31
5265/118	125	62.2	70.0	31.1	0.49	0.56	0.25

Ornamentation. The ornamentation is represented by ribs and tubercles. The ribs are primary and intercalary. The primary ribs are strong, possessing three pairs of tubercles; the ventral tubercles are very large, high, whereas the lateral tubercles are lower, and the umbilical tubercles are small. The primary ribs break into two branches from the lower row of the smallest tubercles: the posterior branch is stronger, with the middle and upper row of large tubercles, the anterior branch is weak, smooth. Two thinner and weaker intercalary ribs lie between the primary ribs. The lateral tubercles are pointed, acuminate. In the last whorl, they are often obtuse because the upper shell layer is not preserved. The acuminate nature of the lateral tubercles of the penultimate whorl is readily visible because of their position adjacent to the umbilical wall of the last whorl. The third pair of large tubercles occurs on the venter.

At the shell diameter more than 70 mm, about 50 ribs occur in one whorl. Three rows of tubercles are associated with strong primary ribs. From the lower tubercles, the ribs break into two branches; the anterior branch is always weak, with no tubercles, the posterior branch is strong and wide; a pair of high massive globular tubercles are present on the venter. In the mid-venter, the primary ribs are strongly flattened and widened. The intercalary ribs are weak, similar to the anterior branches of the primary ribs. In the second half of the whorl in specimen PIN, no. 5265/94 after diameter of 67 mm, the ventral tubercles and all ribs are similar in width.

For the ornamentation morphogenesis, see in the genus description.

Suture. Sutural formula:

$$(V_1V_1)UU^1ID \rightarrow (V_1V_1)UID$$
$$\rightarrow (V_1V_1)U_1U_2ID \rightarrow (V_1V_1)U_1U_2I_2I_1D.$$

Morphogenesis of the suture (Fig. 72). The prosuture has a high ventral saddle. The primary suture is five-lobed $(V_1V_1)UU^1{:}ID$. The first umbilical lobe in the first whorl is reduced and the number of lobes decreases to four. The ventral lobe is bifid already in the primary suture. In the third whorl, the umbilical lobe breaks into two parts (U_1, U_2). The first branch is deeper and larger than the second; later, in the third whorl, the inner lateral lobe I breaks into two new lobes (I_2 and I_1). Until the end of the third whorl, the dorsal lobe remains entire, without division, and becomes trifid in the fourth whorl. In this whorl, the sutural complexity increases.

Comparison and remarks. This species is distinguished from *E. subnodosocostatum* (Sinzow) by the wider whorl cross section, coarse primary ribs, greater number of intercalary ribs, and the fewer primary ribs.

Dutour (2005, p. 170, pl. 25, figs. 9–11) gives a description and illustration of *E. tschernyschewi* (Sinzow). However, Dutour's interpretation of the species is strikingly different from Sinzow's (1906). More so, Dutour synonymized *E. subnodosocostatum* (Sinzow)

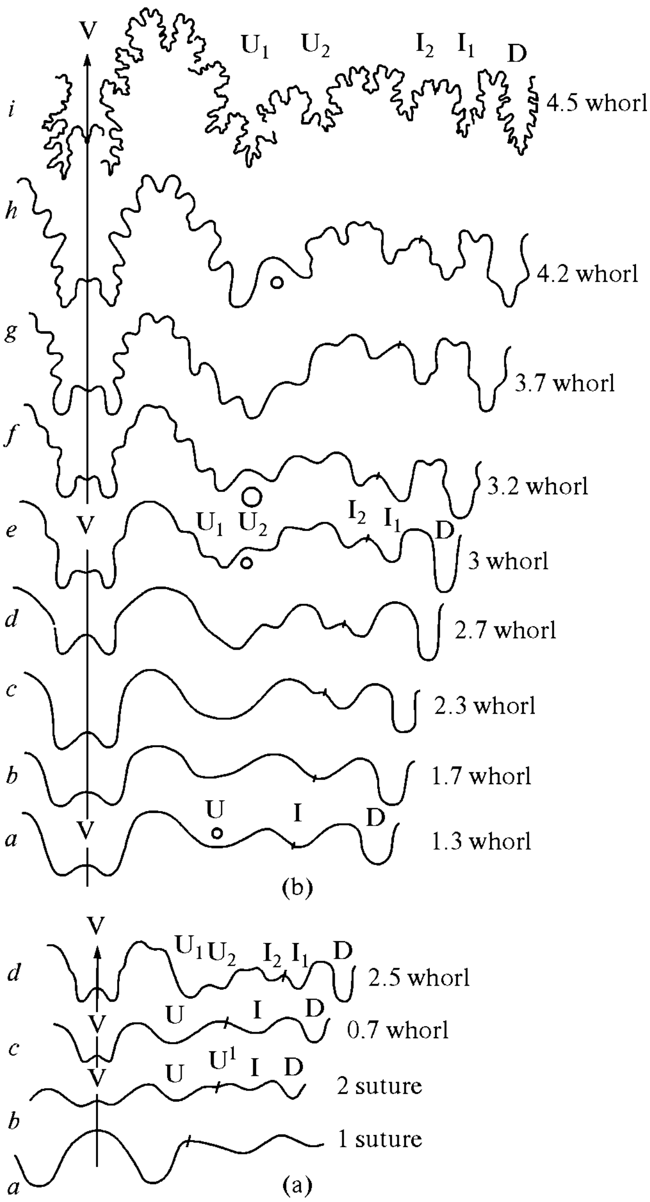


Fig. 72. *Epicheloniceras tschernyschewi* (Sinzow): (a) specimen PIN, no. 5265/57, early morphogenesis of the suture; Mangyshlak, Tushchibek; Middle Aptian: (*a, b*) ×75; (*c*) ×56; (*d*) ×22; (b) specimen PIN, no. 5265/58, morphogenesis of the suture; Great Balkhan, Bordzhakly well; Middle Aptian: (*a*) ×67; (*b*) ×48; (*c*) ×37; (*d*) ×33; (*e*) ×22; (*f*) ×22; (*g*) ×17; (*h*) ×12; (*i*) ×3.

under *E. tschernyschewi,* although the two species are fundamentally different (see below).

Aliev (1968, pp. 49–50, figs. 5–9), in a paper on ammonites of the southeastern Caucasus, described specimens identified as *E. tschernyschewi* (Sinzow) and *E. subnodosocostatum* (Sinzow). Judging from the illustration in his figs. 3, 4 and 7, these specimens do not belong to the genus *Epicheloniceras,* but they possibly belong to the genus *Diadochoceras* Hyatt.

Stoykova (1983) figured a large specimen (pl. 4, figs. 2, 3) completely corresponding to *E. tschernyschewi,* while the assignment to this species of a small specimen (pl. 4, fig. 2) is doubtful because of the almost complete absence of intercalary ribs.

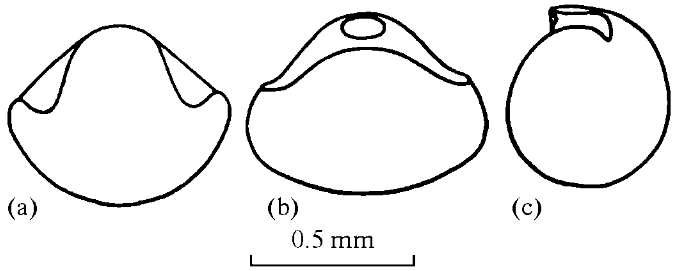


Fig. 73. Protoconch of *Epicheloniceras subnodosocostatum* (Sinzow), specimen PIN, no. 5265/59; northern Caucasus, village of Gundelen; Middle Aptian: (a) ventral view, (b) septal view, (c) lateral view.

O c c u r r e n c e. Russia (northern Caucasus, Dagestan), Middle Aptian, *Colombiceras crassicostatum–Epicheloniceras subnodosocostatum* Zone; Kazakhstan (Mangyshlak), Turkmenistan (Great Balkhan, Tuarkyr), Bulgaria, Georgia, Middle Aptian, *Epicheloniceras subnodosocostatum* Zone; France, Upper Aptian, *Epicheloniceras martini* Zone; England; Upper Aptian, *Epicheloniceras martinioides* Zone.

M a t e r i a l. Thirteen well-preserved specimens. Northern Caucasus, Malka River (PIN, no. 5265/238), Gundelen River (PIN, no. 5265/241), Kuma River (PIN, no. 5265/251); Middle Aptian, *Colombiceras crassicostatum–Epicheloniceras subnodosocostatum* Zone; Dagestan: village of Akusha (PIN, no. 5265/93); Mangyshlak: village of Aktash (PIN, no. 5265/95), Tushchibek well (PIN, nos. 5265/94, 5265/96, 5265/97, 5265/118); Great Balkhan: Utuludzha well (TsNIGR Museum, nos. 181/10367, 184/10367), Bordzhakly well (TsNIGR Museum, no. 186/10367); Tuarkyr, Babashi well (TsNIGR Museum, no. 183/10367); Middle Aptian, *Epicheloniceras subnodosocostatum* Zone.

Epicheloniceras subnodosocostatum **(Sinzow, 1906)**

Plate 24, figs. 1–8

Douvilleiceras subnodoso-costatum: Sinzow, 1906, p. 175, pl. 2, figs. 1–8; Nikshich, 1915, p. 40, pl. 6, figs. 4–7.

Douvilleiceras subnodosocostatum: Jacob in Jacob and Tobler, 1906, p. 14, pl. 1, figs. 4–6; Kazansky, 1914, p. 60; Spath, 1930, p. 452; Rouchadze, 1933, p. 195; Rouchadze, 1938a, p. 126.

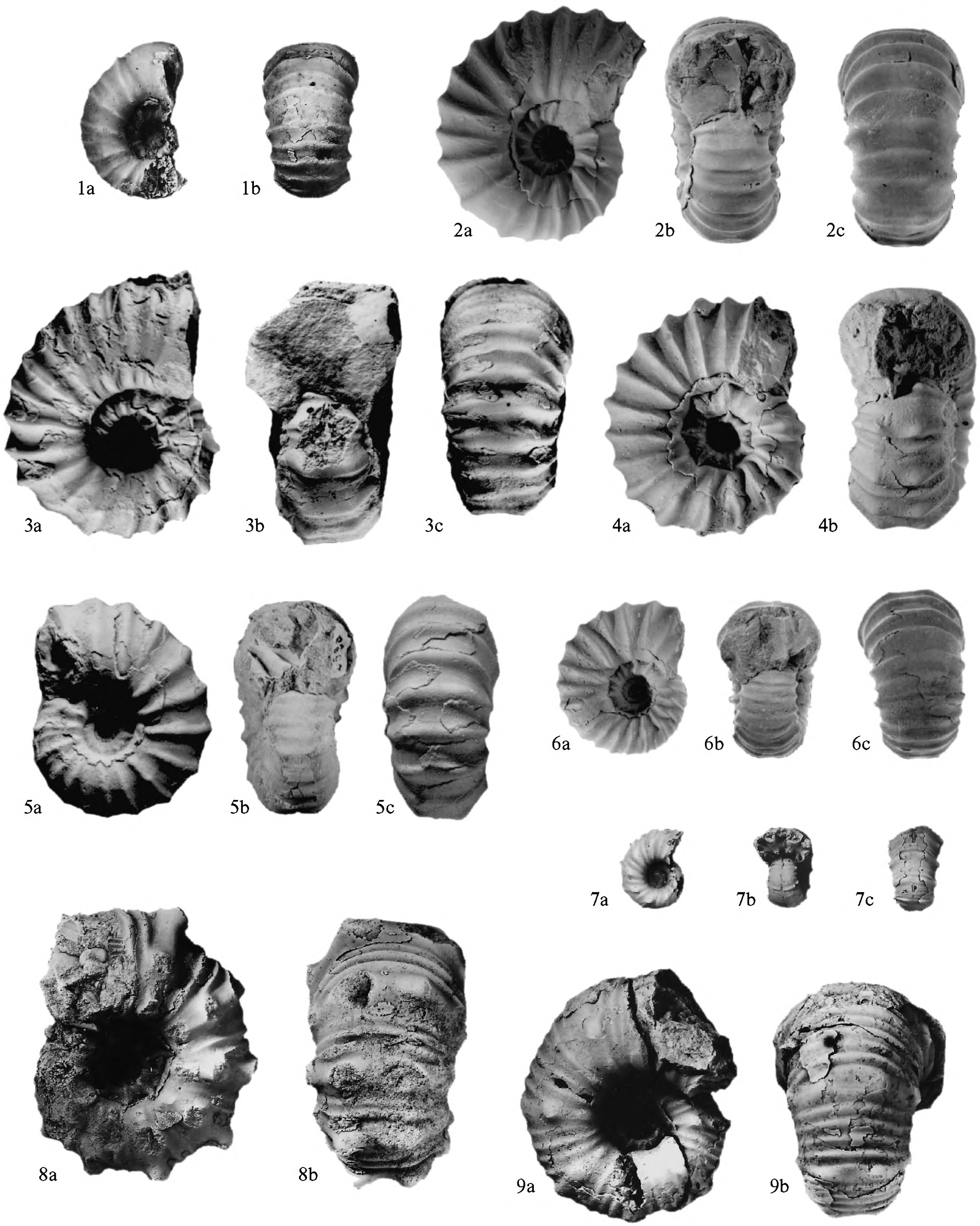
Cheloniceras subnodosocostatum: Eristavi, 1955, p. 148; 1961, p. 54, pl. 3, figs. 8 and 11.

Epicheloniceras subnodosocostatum: Kudryavtsev, 1960, p. 341, pl. 21, figs. 3a–3c; pl. 22, figs. 4a, 4b, and 5; Atlas ..., 2005, p. 383, pl. 95, fig. 1 (only).

L e c t o t y p e. TsNIGR Museum, no. 9/11066. Specimen figured by Sinzow (1906, pl. 2, fig. 1); Middle Aptian; Kazakhstan, Mangyshlak, Kyzyl-Kaspak Range. Designated here.

S h e l l s h a p e. The protoconch is elongated, 0.70 mm wide, and 0.58 in diameter (Fig. 73). The shell is relatively inflated and semi-evolute. The whorls

Plate 23



are slowly expanding, overlapping by one-third of the whorl height. The flanks are weakly rounded; the venter is broad, flattened in the middle. The umbilicus is deep and wide. The umbilical wall is steep and stepped. The cross section is broadly oval between the ribs and hexagonal when cut at the level of the tubercles.

Dimensions in mm and ratios:

Specimen PIN, no.	Dm	WH	WW	UW	WH/Dm	WW/Dm	UW/Dm
5265/64	11.5	4.8	7.2	5.3	0.41	0.62	0.46
5265/65	14.5	7.0	9.1	5.5	0.48	0.62	0.37
5265/66	18.2	9.6	12.9	6.9	0.52	0.70	0.37
5265/67	18.5	8.3	12.2	6.9	0.44	0.65	0.37
5265/74	19.5	10.8	14.2	7.5	0.55	0.72	0.38
5265/173	25.5	10.5	15.0	10.0	0.41	0.58	0.39
5265/68	30.5	14.3	19.2	10.5	0.46	0.62	0.34
5265/75	31.5	16.0	15.0	12.0	0.50	0.47	0.38
5265/107	32.0	14.1	17.8	9.8	0.44	0.55	0.31
5265/69	32.3	13.6	20.2	11.5	0.42	0.62	0.35
5265/70	34.2	19.6	20.5	12.5	057	0.59	0.36
5265/71	38.3	21.3	21.5	13.2	0.55	0.56	0.34
5265/119	39.5	16.5	21.5	–	0.41	0.54	–
5265/72	49.2	23.0	–	15.0	0.40	–	0.30
5265/73	51.0	21.9	28.5	18.2	0.42	0.55	0.35

Ornamentation. The ornamentation at the diameter of 45–50 mm is represented by coarse primary and weaker intercalary ribs and also by the ventral and lateral tubercles. The primary ribs begin on the umbilical wall, noticeably increase on the shoulder toward the flank, where in the first half of the whorl, there remains a lower row of small, gradually disappearing umbilical tubercles. Beginning from the acuminate lateral tubercles, the primary ribs are subdivided into two uneven branches; the posterior branch is strong with pronounced ventral tubercles, whereas the anterior branch is considerably less prominent. This difference is clearly observed approximately to diameter of 30 mm. Weak intercalary ribs can be present. At a larger diameter, the branching of the ribs does not occur, all ribs are strong and uniform.

The protoconch and first whorl are smooth. Six–seven tubercles appear in the second whorl at the midflank (Fig. 74). At the end of the third–beginning of the fourth whorl, the tubercles become acuminate. At the same time, a row of ventral tubercles appears and,

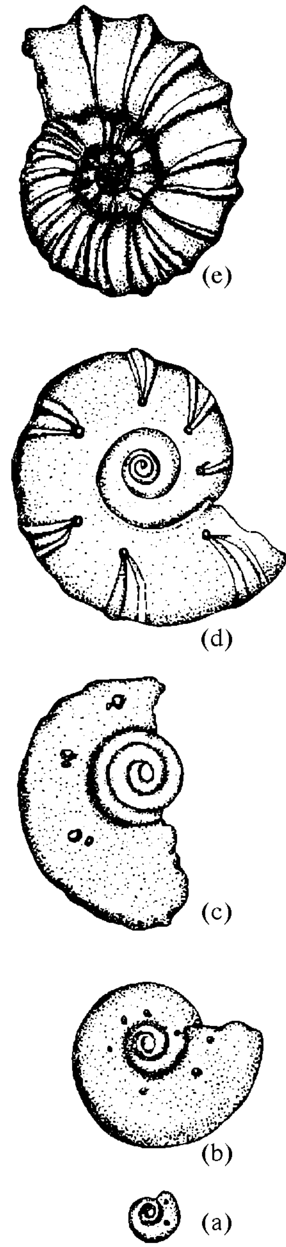


Fig. 74. Ornamentation morphogenesis in *Epicheloniceras subnodosocostatum* (Sinzow), specimen no. 7/1419; Dagestan, village of Akusha; Middle Aptian: (a) ×6; (b) ×7; (c) ×5.5; (d) ×4.5; (e) ×1.5.

Explanation of Plate 23

Figs. 1–6. *Epicheloniceras buxtorfi* (Jacob, 1906); specimens: (1) PIN, no. 5265/174; Kuba Dagh, Yangadzha Station; Middle Aptian, *Epicheloniceras subnodosocostatum* Zone; (2) PIN, no. 5265/86; (3) PIN, no. 5265/83; (4) PIN, no. 5265/85; (5) PIN, no. 5265/82; (6) PIN, no. 5265/84; Dagestan, village of Akusha; Middle Aptian, *Colombiceras crassicostatum–Epicheloniceras subnodosocostatum* Zone.

Figs. 7–9. *Epicheloniceras tschernyschewi* (Sinzow, 1906), (7) specimen TsNIGR Museum, no. 181/10367; (8) specimen TsNIGR Museum, no. 184/10367; Great Balkhan, Utuludzha well; Middle Aptian, *Epicheloniceras subnodosocostatum* Zone; (9) specimen TsNIGR Museum, no. 183/10367; Tuarkyr, Babashi well; the same age.

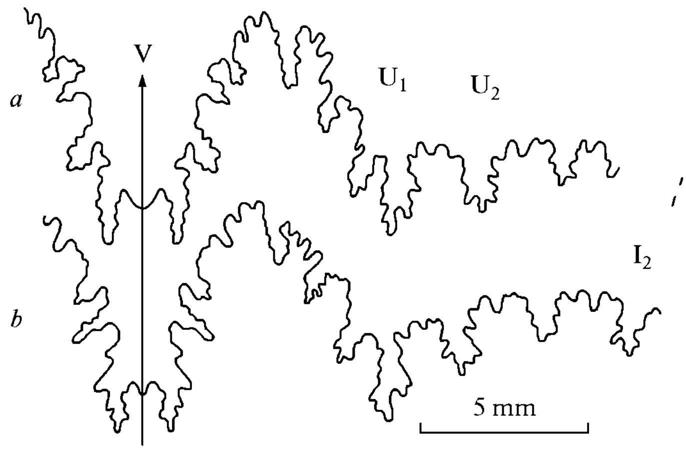


Fig. 75. Sutures of *Epicheloniceras subnodosocostatum* (Sinzow), specimen PIN, no. 5265/107; Dagestan, village of Akusha; Middle Aptian.

in the fourth–fifth whorls, ribs also appear. At this stage, the primary ribs bifurcate from the lateral tubercles; the anterior branch is sometimes nodose often hardly discernible. At younger stages (up to the end of the fourth whorl), the ornamentation is similar to that of *E. tschernyschewi* (Sinzow).

S u t u r e (Figs. 75, 76) The suture is strongly dissected. The ventral lobe is long, narrowed at the base. The umbilical lobe is subdivided into two asymmetrical lobes (U_1 and U_2), the first is deeper than the second. The inner lateral lobe is also subdivided into two separate lobes (I_2 and I_1). The dorsal lobe is trifid, as deep as the main branch of the umbilical lobe U_1.

The early morphogenesis of the suture confirms the presence of the first umbilical lobe (U^1) at the beginning of the first whorl and its disappearance at the end of this whorl (Fig. 76a). Later stages of the sutural morphogenesis (Fig. 76b) are similar to those of *E. tschernyschewi* (Sinzow).

C o m p a r i s o n. The species considered is similar to *E. volgense* (Wassiliewsky), but is distinguished from it by the lower whorl cross section and the more widely spaced primary ribs.

O c c u r r e n c e. Russia (northern Caucasus, Dagestan); Middle Aptian, *Colombiceras crassicostatum–Epicheloniceras subnodosocostatum* Zone; Kazakhstan (Mangyshlak); Turkmenistan (Tuarkyr, Great and Lesser Balkhans, Kopet Dagh), Georgia; Middle Aptian, *Epicheloniceras subnodosocostatum* Zone; Bulgaria, Middle Aptian, *Cheloniceras (Epicheloniceras) subnodosocostatum* Zone, England, Upper Aptian, *Cheloniceras (Epicheloniceras) martinioides* Zone; France, Upper Aptian, *Epicheloniceras martini* Zone; Colombia; Middle Aptian.

M a t e r i a l. Twenty well-preserved specimens. Northern Caucasus: Saverdon River (PIN, no. 5265/67), Malka River (PIN, nos. 5265/64, 5265/69, 5265/72, 5265/239), Baksan River, Kazansu River (PIN, no. 5265/221), Urukh River (PIN, no. 5265/66), Kuma River (PIN, nos. 5265/75, 5265/250), Kuban River (PIN, nos. 5265/252, 5265/253);Dagestan: village of Akusha (PIN, nos. 5265/65, 5265/68, 5265/70, 5265/71, 5265/74, 5265/107, 5265/119), Ullu-chai River (PIN, no. 5265/73); Middle Aptian, *Colombiceras crassicostatum–Epicheloniceras subnodosocostatum* Zone; Lesser Balkhan: Chalsu well (PIN, no. 5265/173); Middle Aptian, *Epicheloniceras subnodosocostatum* Zone.

Epicheloniceras orientale (Jacob, 1905)

Plate 25, figs. 5 and 6

Ammonites Martini: d'Orbigny, 1840–1842, p. 194, pl. 58, figs. 7 and 8 (non fig. 9).

Douvilleiceras Martini d'Orbigny var. *orientalis:* Jacob, 1905, p. 412; Jacob in Jacob and Tobler, 1906, p. 13, pl. 1, figs. 1 and 2 (non fig. 3); Wassiliewsky, 1908a, p. 35; Nikshich, 1915, p. 37, pl. 6, figs. 1–3.

Epicheloniceras martini orientalis: Kudryavtsev, 1960, p. 340, pl. 21, figs. 2 and 4; Atlas ..., 2005, p. 384, pl. 94, fig. 2.

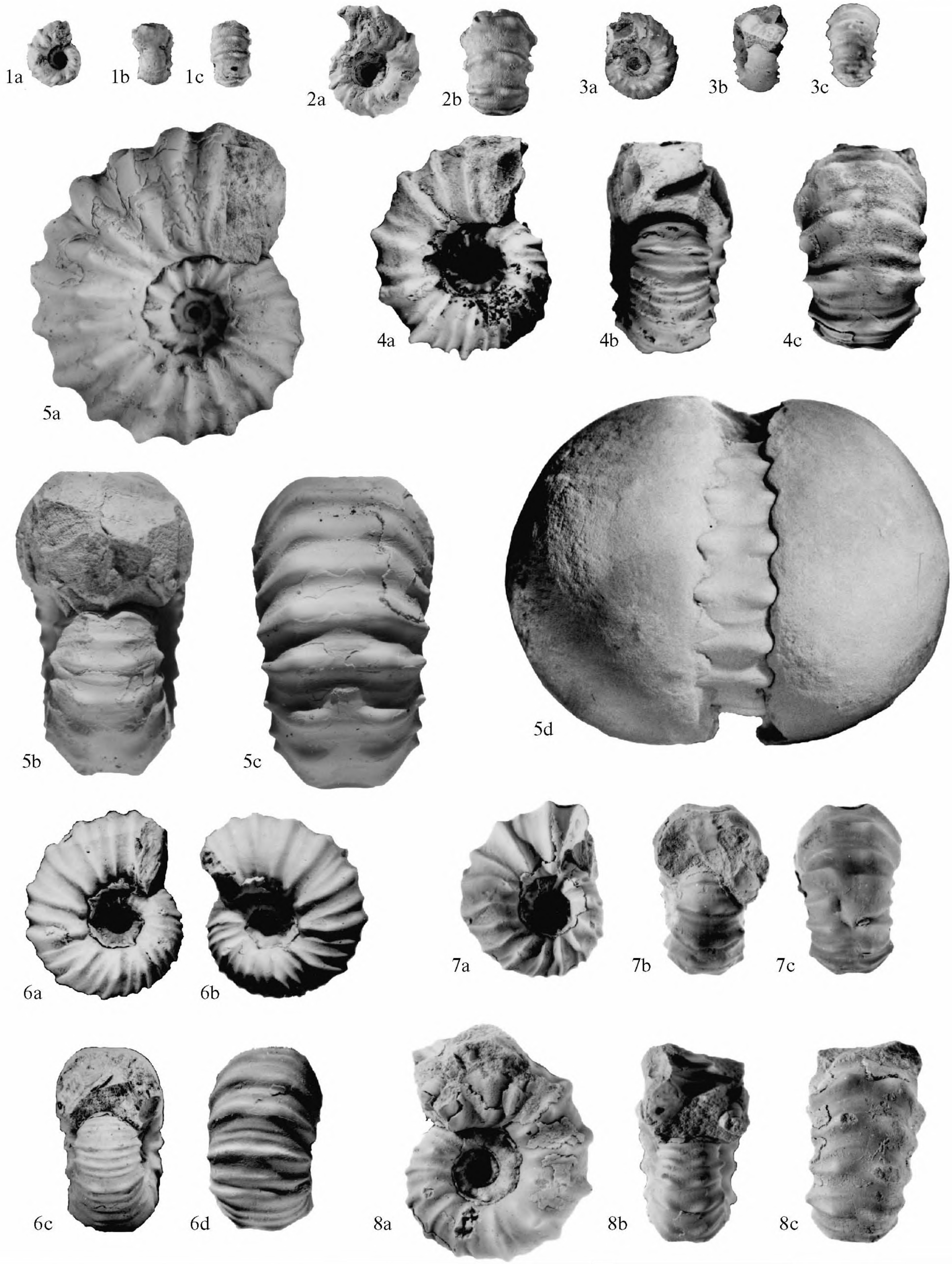
Cheloniceras (Epicheloniceras) martini orientalis: Stoykova, 1983, p. 86, pl. 4, fig. 1.

L e c t o t y p e. Specimen figured by d'Orbigny (1840–1842, pl. 58, figs. 7, 8); Aptian, Gargasian; southeastern France, village of Clansayes. Designated herein.

Explanation of Plate 24

Figs. 1–8. *Epicheloniceras subnodosocostatum* (Sinzow, 1906); specimens: (1) PIN, no. 5265/64; northern Caucasus, Malka River; Middle Aptian, *Colombiceras crassicostatum–Epicheloniceras subnodosocostatum* Zone; (2) PIN, no. 5265/66; northern Caucasus, Urukh River; the same age; (3) PIN, no. 5265/65; (4) PIN, no. 5265/70; Dagestan, village of Akusha; the same age; (5) PIN, no. 5265/73; Dagestan, Ullu-chai River; the same age; (6) PIN, no. 5265/107; (7) PIN, no. 5265/68; Dagestan, village of Akusha; the same age; (8) PIN, no. 5265/69; northern Caucasus, Malka River; the same age.

Plate 24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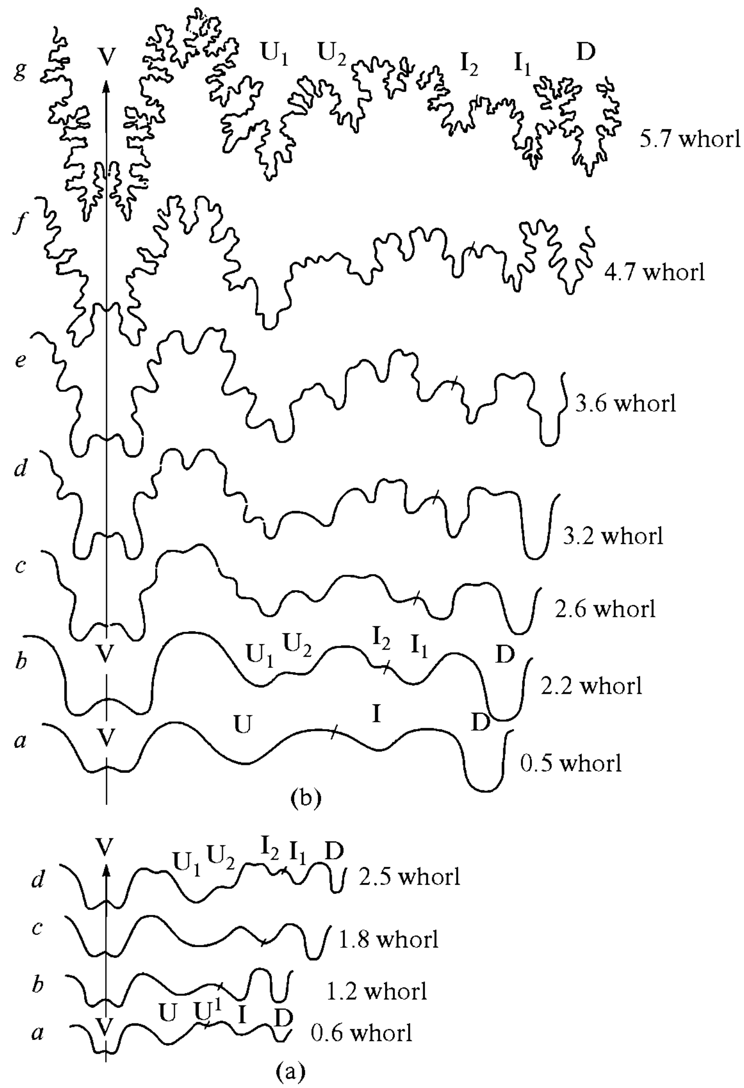


Fig. 76. (a) *Epicheloniceras subnodosocostatum* sp. juv., specimen PIN, no. 5265/59, early morphogenesis of the suture; northern Caucasus, village of Gundelen; Middle Aptian: (*a*) ×42; (*b*) ×42; (*c*) ×32; (*d*) ×20; (b) *Epicheloniceras subnodosocostatum* (Sinsow) specimen PIN, no. 5265/276, morphogenesis of the suture; Mangyshlak, Tushchibek; Middle Aptian: (*a*) ×70; (*b*) ×40; (*c*) ×24; (*d*) ×22; (*e*) ×18; (*f*) ×9); (*g*) ×3.

S h e l l s h a p e. The shell is semi-evolute, the whorls overlap for about one-third of the whorl height. The whorl cross section is crescentic and hexagonal if it cuts through the tubercles. The umbilicus is wide and deep. The umbilical wall is steep. The umbilical edge is angular.

D i m e n s i o n s i n m m a n d r a t i o s:

Specimen PIN, no.	Dm	WH	WW	UW	WH/Dm	WW/Dm	UW/Dm	WH/WW
5265/81	22.5	12.1	14.1	7.8	0.62	0.53	0.35	
5265/80		18.0	31.0					0.58

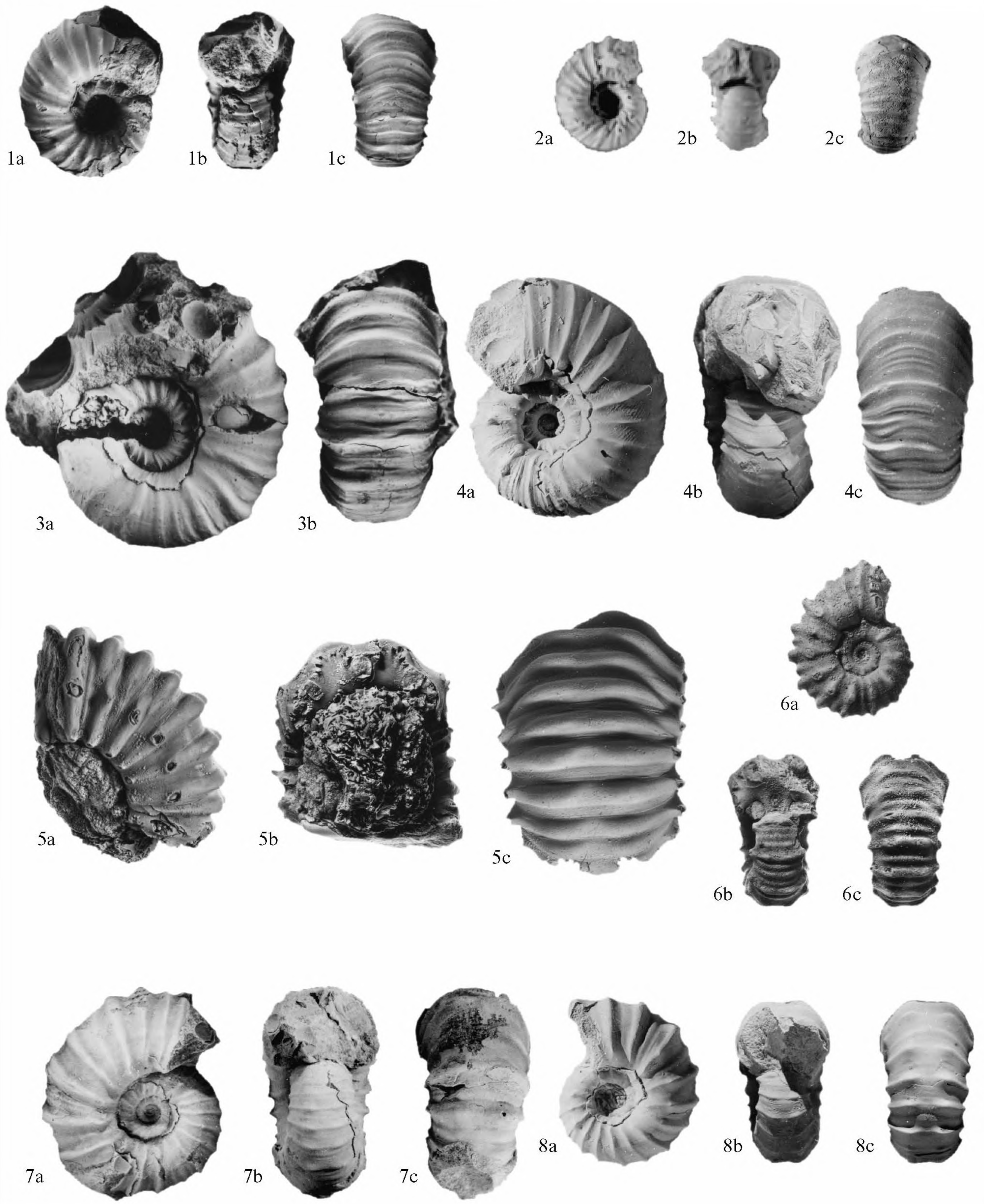
E x p l a n a t i o n o f P l a t e 25

Figs. 1–4. *Epicheloniceras pusillum* (Sinzow, 1906); specimens: (1) PIN, no. 5265/88; (2) PIN, no. 5265/89; (3) PIN, no. 5265/91; (4) PIN, no. 5265/90; Dagestan, village of Akusha; Middle Aptian, *Colombiceras crassicostatum–Epicheloniceras subnodosocostatum* Zone.

Figs. 5 and 6. *Epicheloniceras orientale* (Jacob, 1905), (5) specimen PIN, no. 5265/80; northern Caucasus, Pshekha River; Middle Aptian, *Colombiceras crassicostatum–Epicheloniceras subnodosocostatum* Zone; (6) PIN, no. 5265/81; northern Caucasus, Urukh River; the same age.

Figs. 7 and 8. *Epicheloniceras intermedium* (Kasansky, 1914), (7) specimen PIN, no. 5265/121; (8) specimen PIN, no. 5265/55; Dagestan, village of Akusha; Middle Aptian, *Colombiceras crassicostatum–Epicheloniceras subnodosocostatum* Zone.

Plate 25



Ornamentation. The ornamentation is represented by primary and intercalary ribs. The primary ribs possess lateral and ventral tubercles. The lateral tubercles are strong; the ventral tubercles are weaker, elongated. The umbilical tubercles in the young whorls are weak and, in adults, are stronger. The ribs branch from the lateral tubercles; the intercalary rib lies immediately before a primary. A pair of elongated ventral tubercles are present on the intercalary ribs of adult whorls.

Suture. The suture is similar to that of *E. tschernyschewi* (Sinzow). The external saddle V/U_1 is extremely high. The ventral lobe (V) and external branch of the umbilical lobe (U_1) are approximately equal in depth.

Comparison and remarks. Jacob (1905, p. 412) considered that d'Orbigny (1840–1842) as *Ammonites martini* figured two varieties from different localities. One of these, called by Jacob as *Douvilleiceras martini* d'Orb. var. *orientalis* (d'Orbigny, 1840–1842, pl. 58, figs. 7, 8), was found in the vicinity of the village of Clansayes. Subsequently, this variety was regarded as a subspecies. The second variety (d'Orbigny, 1840–1842, pl. 58, fig. 9) comes from the vicinity of Apt (near the villages of Gargasian and Carniol), from the outcrops (according to Kilian) of the so-called western Aptian facies. Jacob suggested that this variety should be called *Douvilleiceras martini* d'Orb. var. *occidentalis*. We agree with Jacob's view that *Douvilleiceras martini* var. *orientalis* from the Gargasian is an intermediate form between *D. martini* var. *occidentalis* from the Bedoulian and *D. clansayense* (Jacob, 1905, p. 413) from the Clansayesian.

Varieties proposed by Jacob were assigned to different subgenera, which we consider to be separate genera. The variety of *"D." martini* d'Orbigny var. *occidentalis* (Jacob) should be referred to as *Cheloniceras martini* (d'Orbigny), i.e., to retain the original species name, whereas *"D." martini* d'Orbigny *orientalis* (Jacob) should be identified as *Epicheloniceras orientale* (Jacob). The necessity of this solution is based on the presence in the second variety of three rows of tubercles, which is characteristic of the genus *Epicheloniceras*.

In contrast, Dutour (2005), considers the species *martini* belonging to *Epicheloniceras* and, according to that, dates this zone as the Late Aptian. Unfortunately, he did not analyze Jacob's (1905, p. 412) study, where he described two varieties of *martini*, which come from different stratigraphic levels and, according to which the species *martini* occurred in the Early Aptian (see above).

Occurrence. Russia (northern Caucasus); Middle Aptian, *Colombiceras crassicostatum–Epicheloniceras subnodosocostatum* Zone; Georgia, *Epicheloniceras subnodosocostatum* Zone; Bulgaria, Middle Aptian, *Cheloniceras (Epicheloniceras) subnodosocostatum* Zone; England, Upper Aptian, *Epicheloniceras martinioides* Zone.

Material. Eight well- and moderately well-preserved specimens. Northern Caucasus: Urukh River (PIN, no. 5265/81), Pshekha River (PIN, no. 5265/80), Malka River (PIN, nos. 5265/240, 5265/244), Kich-Malka River (PIN, no. 5265/245), Gundelen River (PIN, no. 5265/246), Kuban River (PIN, nos. 5265/247, 5265/248); Middle Aptian, *Colombiceras crassicostatum–Epicheloniceras subnodosocostatum* Zone.

Epicheloniceras buxtorfi (Jacob in Jacob et Tobler, 1906)

Plate 23, figs. 1–6

Douvilleiceras Buxtorfi: Jacob and Tobler, 1906, p. 15, pl. 1, figs. 9–11; Nikshich, 1915, p. 45, pl. 6, figs. 8–10.

Cheloniceras (Epicheloniceras) buxtorfi: Casey, 1962, p. 253, pl. 39, fig. 8.

Epicheloniceras buxtorfi: Sharikadze et al., 2004, p. 341, pl. 34, fig. 2; pl. 40. fig. 3.

Lectotype. Specimen figured by Jacob and Tobler (1906, pl. 1, fig. 9); Aptian, Gargasian; Switzerland, village of Luter Zug. Designated by Casey (1962, p. 253).

Shell shape. The shell is semi-evolute and inflated. The whorl cross section is oval; when it cuts through tubercles, it is octagonal. Each subsequent whorl embraced by one-third of the whorl height. The umbilicus is wide and deep. The umbilical wall is steep. The umbilical shoulder is rounded.

Dimensions in mm and ratios:

Specimen PIN, no.	Dm	WH	WW	UW	WH/Dm	WW/Dm	UW/Dm
5265/174	27.5	12.2	17.1	10.9	0.45	0.62	0.39
5265/84	28.5	13.1	16.1	9.5	0.50	0.56	0.33
5265/87		14.5	20.6				
5265/82	38.1	16.1	19.1	11.1	0.42	0.50	0.29
5265/85	41.5	16.1	20.8	14.4	0.39	0.50	0.35
5265/86	43.0	18.1	24.2	14.1	0.42	0.56	0.33
5265/83	46.0	21.2	24.8	13,9	0.46	0.56	0.30
5265/76	64.6	27.2	34.8	19.5	0.42	0.54	0.30

Ornamentation. The ornamentation is represented by ribs and tubercles. The ribs are primary and intercalary. The primary ribs are strong. The intercalary ribs are thin in early whorls and strong at the later stages. The intercalary ribs begin at the mid-flank, usually one between two primaries. Tubercles are not very large, arranged in three rows on the primary ribs. The umbilical tubercles are weak. Ventral tubercles are present on the intercalary ribs in adult whorls.

Suture. (Fig. 77a). The suture is strongly dissected. The ventral lobe (V) is deep, comparatively narrow, with a high secondarily bifid median saddle. The external branch of the umbilical lobe (U_1) is more strongly dissected than the inner branch (U_2). The external saddle (V/U) is extremely high, more strongly dissected.

Comparison. This species differs from *E. tschernyschewi* (Sinzow) in the less strongly inflated shell and fewer intercalary ribs; from *E. subnodosocostatum* (Sinzow) in the appearance of intercalary ribs on the flanks and the presence of one row of tubercles in adult whorls.

Occurrence. Russia (northern Caucasus, Dagestan); Middle Aptian, *Colombiceras crassicostatum—Epicheloniceras subnodosocostatum* Zone, Kazakhstan (Mangyshlak); Turkmenistan (Kuba Dagh); Middle Aptian, *Epicheloniceras subnodosocostatum* Zone; England, Upper Aptian, *Chelonicras (Epicheloniceras) martinioides* Zone; France, Upper Aptian, *Epicheloniceras martini* Zone; Switzerland, Colombia; Middle Aptian.

Material. Ten well-preserved complete shells and five fragments. Northern Caucasus: Kuban River (PIN, nos. 5265/255, 5265/256), Kuma River (PIN, no. 5265/249), Kazansu River (tributary to the Baksan River) (PIN, no. 5265/222), Gundelen River (PIN, no. 5265/254), Malka River (PIN, no. 5265/257), Kich-Malka River (PIN, no. 5265/258); Dagestan: village of Akusha (PIN, nos. 5265/82, 5265/83, 5265/84, 5265/85, 5265/86, 5265/87); Middle Aptian, *Colombiceras crassicostatum—Epicheloniceras subnodosocostatum* Zone; Mangyshlak: Tushchibek well (PIN, no. 5265/76), Kuba Dagh: Yangadzha station (PIN, no. 5265/174); Middle Aptian, *Epicheloniceras subnodosocostatum* Zone.

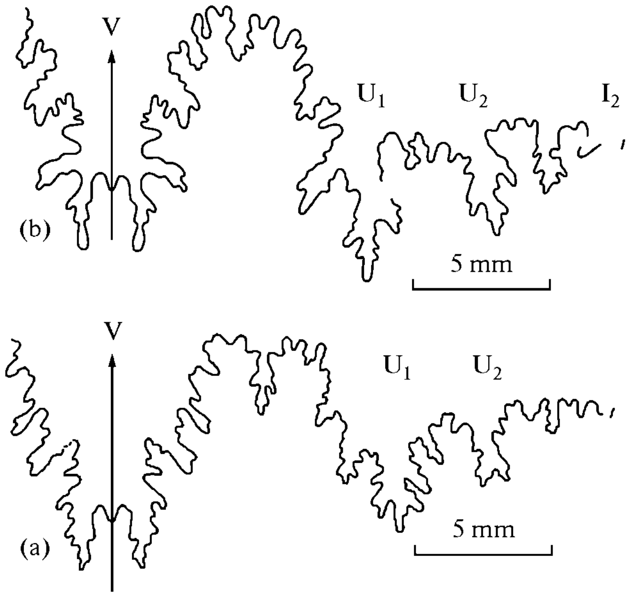


Fig. 77. Suture: (a) *Epicheloniceras buxtorfi* (Jacob), specimen PIN, no. 5265/86 at WH = 16.5 mm and WW = 18.3 mm; (b) *Epicheloniceras pussilum* (Sinzow), specimen PIN, no. 5265/90 at WH = 12.1 mm and WW = 15.7 mm; Dagestan, village of Akusha; Middle Aptian.

Epicheloniceras pusillum (Sinzow, 1906)

Plate 25, figs. 1–4

Douvilleiceras subnodoso-costatum var. *pusilla:* Sinzow, 1906, p. 180, pl. 2, figs. 9 and 10.

Douvilleiceras subnodosocostatum var. *pusilla:* Jacob and Tobler, 1906, p. 15, pl. 1, figs. 12–14.

Douvilleiceras pusilla: Kazansky, 1914, p. 57, pl. 2, figs. 30–32; Rouchadze, 1938a, p. 128.

Epicheloniceras pusillum: Kudryavtsev, 1960, p. 341, pl. 22, figs. 2 and 3.

Lectotype. Specimen figured by Sinzow (1906, pl. 2, fig. 9); Middle Aptian; Russia, northern Caucasus, Kislovodsk. Designated here, a smaller and better preserved specimens of two specimens from Sinzow's collections. In places, the second specimen (Sinzow, 1906, pl. 2, fig. 10) has strong ventral tubercles. Unfortunately, specimen indicated by Sinzow as no. 11068 (housed in the TsNIGR Museum) is missing from the collection.

Shell shape. The shell is small, semi-evolute, with whorls overlapping less than half of the whorl height. The umbilicus is relatively wide. The cross section is broadly oval. The umbilical wall is steep, joining the flank without a sharp shoulder ; the venter is broad and rounded.

Dimensions in mm and ratios:

Specimen PIN, no.	Dm	WH	WW	UW	WH/Dm	WW/Dm	UW/Dm
5265/108	16.0	7.3	9.4	6.5	0.45	0.59	0.40
5265/89	18.5	8.9	12.5	7.2	0.39	0.67	0.39
5265/92	21.3	10.3	14.0	7.8	0.48	0.65	0.37
5265/110	22.0	10.2		7.3	0.46		0.33
5265/109	26.0	11.8	14.5	8.2	0.45	0.55	0.31
5265/88	28.1	14.5	16.2	9.5	0.51	0.58	0.34
5265/90	38.5	17.3	20.1	11.9	0.48	0.52	0.31
5265/91	45.7	18.1	22	16.9	0.40	0.48	0.37

Ornamentation. The ornamentation consists of primary and intercalary ribs. In specimen PIN, no. 5265/91 (Dm ca. 46 mm), ten primary ribs occur per half whorl, and 11 in specimen PIN, no. 5265/90. The primary ribs on the venter are more raised than on the flanks. Tubercles are rarely observed on the venter (PIN 5265/90). Lateral tubercles gradually decrease with age and are clearly visible only on the penultimate whorl. No rib branching is observed. From one to three intercalary ribs occur between the primaries. These intercalary ribs are thin and weak, and sometimes appear as low bands.

Suture. The suture is typical of the genus *Epicheloniceras* (Fig. 77b).

Comparison and remarks. *E. pusillum* is distinguished from *Ep. subnodosocostatum* by the less strong and almost smooth primary ribs.

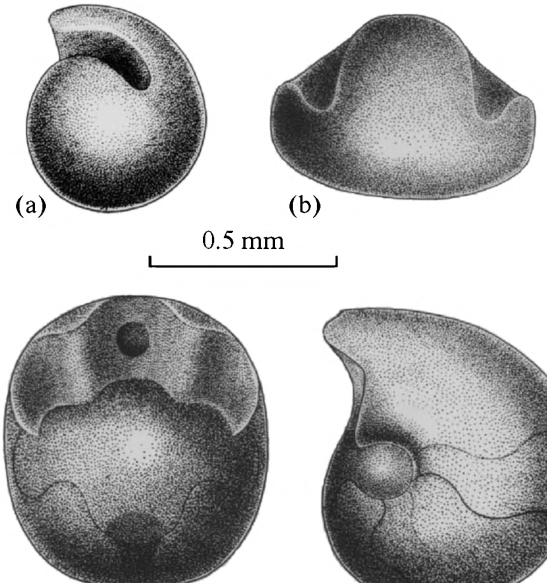

(a) (b)
0.5 mm
(c) (d)
0.5 mm

Fig. 78. Protoconch of *Epicheloniceras intermedium* Kasansky: (a) lateral view, (b) upper view, (c, d) protoconch and several chambers; Dagestan, village of Akusha; Middle Aptian (after Mikhailova, 1960).

Rouchadze (1938a) identified three specimens of *Douvilleiceras pusillum* from the Kislovodsk section and gave measurements, which agree with the measurements of our specimens. The original drawing of the suture is very generalized, but even so, it shows that the external saddle V/U_1 is significantly higher than the lateral saddles and unequal branches U_1 and U_2.

O c c u r r e n c e. Russia (northern Caucasus, Dagestan); Middle Aptian, *Colombiceras crassicostatum—Epicheloniceras subnodosocostatum* Zone; Switzerland; Middle Aptian.

M a t e r i a l. Eight well-preserved specimens. Dagestan: village of Akusha (PIN, nos. 5265/88, 5265/89, 5265/90, 5265/91, 5265/92, 5265/108, 5265/109, 5265/110); Middle Aptian, *Colombiceras crassicostatum—Epicheloniceras subnodosocostatum* Zone.

***Epicheloniceras stuckenbergi* (Kasansky, 1914)**

Plate 26, figs. 1–3

Douvilleiceras Stuckenbergi: Kazansky, 1914, p. 55, pl. 2, figs. 27 and 29 (only).

L e c t o t y p e. Specimen figured by Kazansky (1914, pl. 2, fig. 27); Middle Aptian; Russia, Central Dagestan, village of Khodzhal-Machi. Designated herein.

S h e l l s h a p e. The shell is inflated, rounded angular, with whorls overlapping by one-third of the height. The umbilicus is relatively wide and the umbilical wall is steep.

D i m e n s i o n s i n m m a n d r a t i o s:

Specimen PIN, no.	Dm	WH	WW	UW	WH/Dm	WW/Dm	UW/Dm
5286/77	40.5	14.7	28.8	15.3	0.36	0.70	0.37
5286/78	42.8	17.9	25.5	13.0	0.40	0.59	0.34

O r n a m e n t a t i o n. The ornamentation is coarse, composed of the primary and intercalary ribs and three rows of tubercles. The primary ribs (six per half of the last whorl) (at Dm ca. 40 mm) begin on the umbilical wall, thicken on the umbilical shoulder, with a small umbilical tubercle, extending from which they can break into two branches (anterior branch is weaker than the posterior branch). The lateral and ventral tubercles are strong. One–two identical intercalary smooth thinner ribs lie between the primary ribs.

S u t u r e. The suture is typical of the genus *Epicheloniceras.*

C o m p a r i s o n a n d r e m a r k s. Of four specimens listed by Kazansky (1914), those figured in pl. 2, figs. 26 and 28 are only tentatively assigned to this species, as in these specimens ornamentation is significantly weaker in the second half whorl.

This species is distinguished from *E. subnodosocostatum* by the coarser ventral tubercles and from *E. tschernyschewi* by the fewer intercalary ribs.

O c c u r r e n c e. Russia (northern Caucasus, Dagestan); Middle Aptian, *Colombiceras crassicostatum—Epicheloniceras subnodosocostatum* Zone; Turkmenistan (Tuarkyr, Great Balkhan, Kuba Dagh, Kopet Dagh); Middle Aptian, *Epicheloniceras subnodosocostatum* Zone.

M a t e r i a l. Seven well-preserved and moderately well-preserved specimens. Northern Caucasus: Kuban River (PIN, no. 5265/184); Dagestan: village of Akusha (PIN, nos. 5265/78, 5265/79, 5265/183); Middle Aptian, *Colombiceras crassicostatum—Epicheloniceras subnodosocostatum* Zone; Great Balkhan: Bordzhakly well (PIN, nos. 5265/77, 5265/111); Kuba Dagh, Yangadzha station (PIN, no. 5265/259); Middle Aptian, *Epicheloniceras subnodosocostatum* Zone.

***Epicheloniceras intermedium* (Kasansky, 1914)**

Plate 25, figs. 7 and 8

Douvilleiceras intermedium: Kazansky, 1914, p. 59, pl. 2, figs. 33–36.

L e c t o t y p e. Specimen figured by Kazansky (1914, pl. 2, fig. 33); Middle Aptian; Russia, village of Dagestan, Khodzhal-Makhi. Designated herein.

S h e l l s h a p e. The protoconch is elongated (Fig. 78), 0.64 mm wide and 0.51 mm in diameter. The ventral saddle is rounded angular. At the end of the first whorl, the siphuncle is almost central. The cross section at this stage is low ellipsoidal, with a broadly rounded venter and weakly convex flanks. The whorl width is more than twice the whorl height. In the later

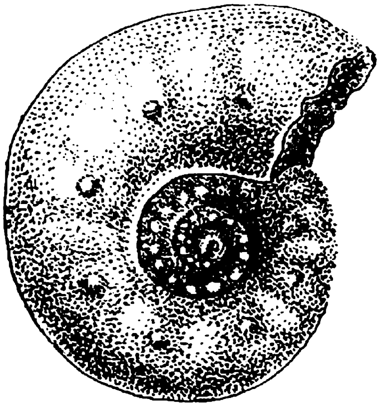


Fig. 79. *Epicheloniceras* sp., lateral view; Dagestan, village of Akusha; Middle Aptian (after Mikhailova, 1960).

whorls, the height increases more rapidly than the width, but remains slightly less than the width. The shell is relatively small, semi-evolute; the whorls overlap each other by less than half of their height. Cross section is wide, when cutting through the tubercles, angular. The umbilicus is relatively wide, the umbilical wall is steep.

Dimensions in mm and ratios:

Specimen PIN, no.	Dm	WH	WW	UW	WH/Dm	WW/Dm	UW/Dm
5265/55	29.7	12.1	15.5	10	0.40	0.52	0.37
5265/121	36.3	15.3	18.7	12.4	0.40	0.54	0.34

Ornamentation. The ornamentation is represented by coarse primary and weaker intercalary ribs. The primary ribs with prominent elongated ventral tubercles and smaller acuminate lateral tubercles. The lower row of elongate tubercles on the umbilical shoulder gives rise to the primary ribs. The intercalary ribs are weaker, mostly one between a pair of primary ribs. In the first third of the last whorl, the ornamentation is less prominent, but on the primary ribs, the ventral and lateral tubercles are present.

Ornamentation morphogenesis. The first whorl is smooth, but tubercles appear immediately after the constriction at the mid-flank; at the level where the whorls are most convex, tubercles appear (Fig. 79). The first ribs are visible at a shell diameter of about 10 mm; they first appear only on the venter, extending from one node to another. At the diameter over 15 mm, ribs at the transition to the umbilical wall become stronger, forming elongated bullae. Weak intercalary ribs are occasionally present.

Suture (Fig. 80). At the diameter of 18 mm, the suture is composed of strongly dissected saddles and lobes. The ventral bifid lobe is considerably larger than all the other lobes. The first umbilical lobe (U_1) is asymmetrical, with the sides of different height. The umbilical lobe (U_2) is slightly larger than the second inner lateral lobe (I_2), and the last lies on the outer side if the whorl. The first inner lateral lobe (I_2) is differently high and asymmetrical. The dorsal lobe is as deep as the umbilical lobe. The external saddle (V/U_1) is considerably wider than the others. The umbilical saddle (U_2/I_2) is low, but wider than the inner saddle (I_1/D). Two small auxiliary saddles appear on either side of the inner saddle.

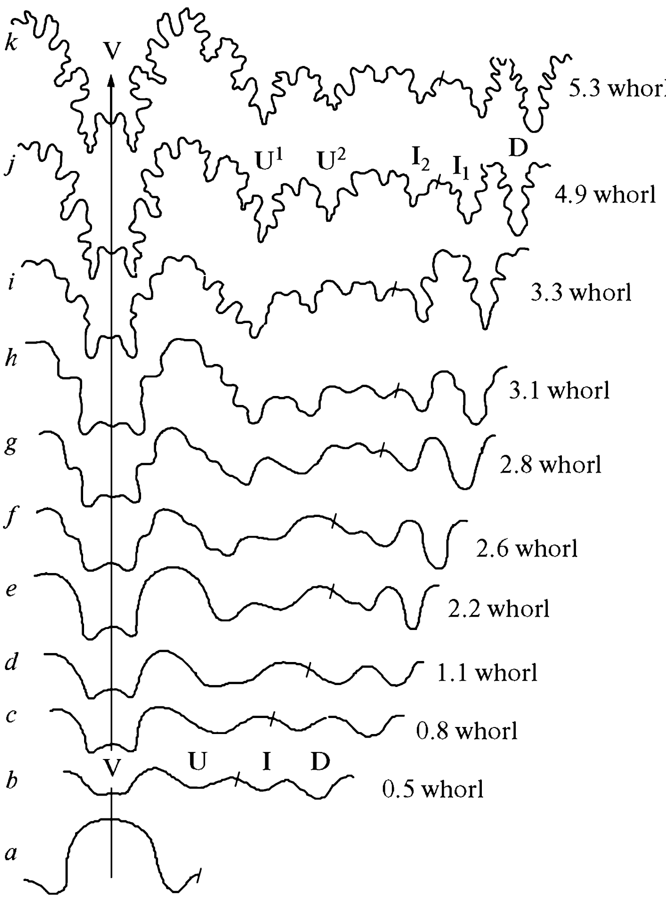
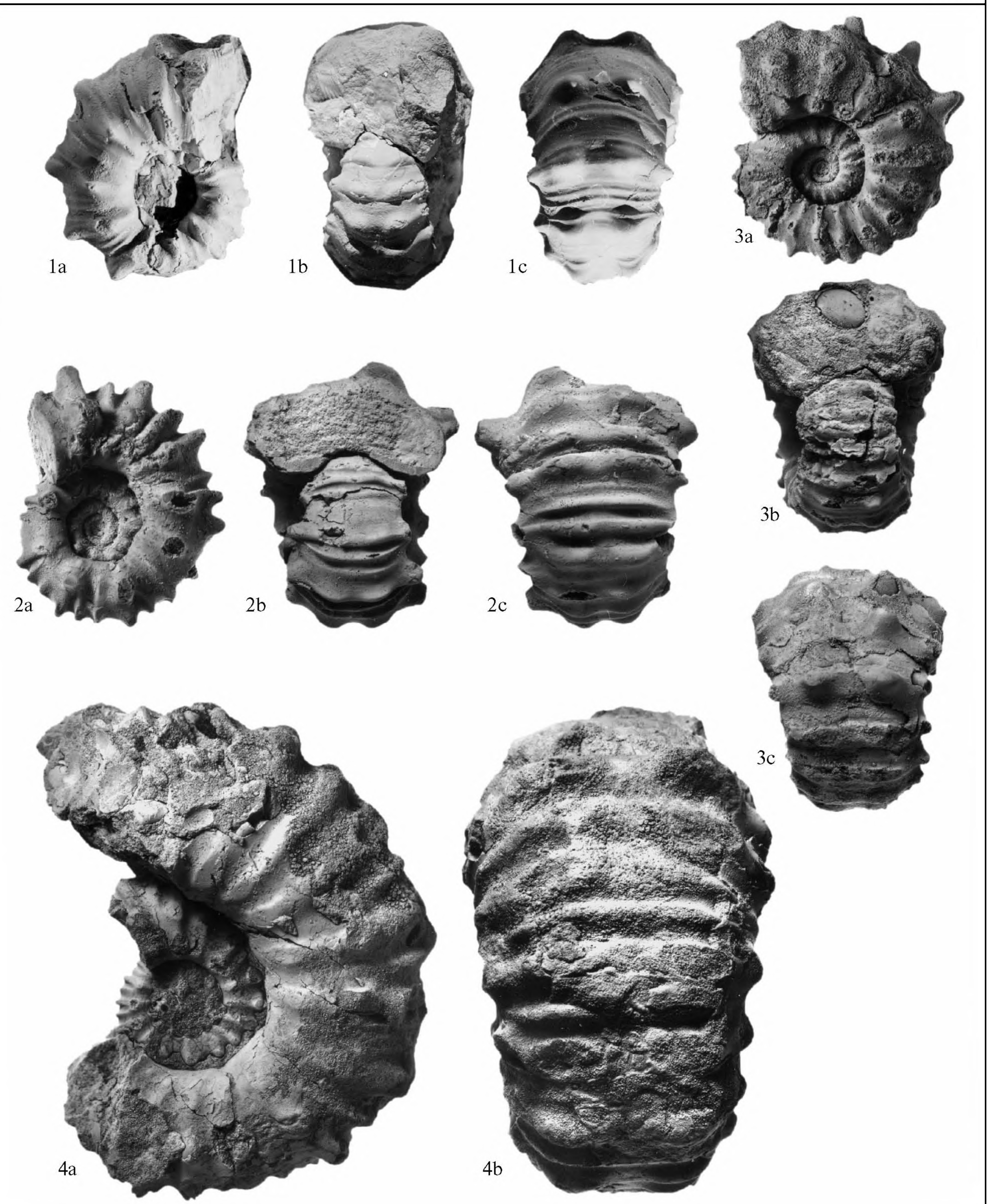


Fig. 80. Morphogenesis of the suture of *Epicheloniceras intermedium* (Kasansky), specimen PIN, no. 5265/55; Dagestan, village of Akusha; Middle Aptian: (*a–d*) ×14, (*e*) ×12.5, (*f*) ×12, (*g*, *h*) ×10, (*i*) ×8, (*j*) ×6, (*k*) ×4.

Morphogenesis of the suture. The prosuture is with a high median saddle. At the diameter of 0.9 mm, four lobes are observed. At the shell diameter of 2 mm, the base of the umbilical lobe becomes flattened. At the diameter of 2.7 mm, a secondary saddle dividing this lobe into two parts begins developing on the inner side of the ventral lobe. At the same stage, the base of the inner lateral lobe flattens. Later, the external and internal sides of the external saddle become serrated and, at the diameter of 5.5 mm, such changes are also observed in the inner saddle. Later in ontogeny, branches of the umbilical and second inner lateral

Plate 26



Explanation of Plate 26

Figs. 1–3. *Epicheloniceras stuckenbergi* (Kasansky, 1914); specimens: (1) PIN, no. 5265/78; Dagestan, village of Akusha; Middle Aptian, *Colombiceras crassicostatum–Epicheloniceras subnodosocostatum* Zone; (2) PIN, no. 5265/111; (3) PIN, no. 5265/77; Great Balkhan, Bordzhakly well; the same age.

Fig. 4. *Epicheloniceras martinioides* Casey, 1961; specimen PIN, no. 5265/262; northern Caucasus, Malka River; Middle Aptian.

lobes are differentiated. Since they appear as a result of subdivision of lobes rather than saddles, the lobes are designated as U_1, U_2, and I_2, I_1.

Morphogenesis of the suture of *E. intermedium* (Kasansky) was first illustrated and analyzed by one of us (Mikhailova, 1957, 1958) and, shortly after, it was repeated by Casey (1961a, p. 196, text-fig. 60) and in *Osnovy paleointologii* (Ruzhencev, 1962, p. 285, text-fig. 61). It should be said that neither Casey nor authors of the *Osnovy paleointologii* noted rapid disappearance of the fifth lobe (U^1) and, because of this, the primary suture was universally interpreted as four-lobed. Later, it was established that there is a large group of Aptian ammonoids with an unstable five-lobed primary suture.

C o m p a r i s o n. This species is distinguished from *E. subnodosocostatum* (Sinzow) and *E. stuckenbergi* (Kasansky) by the less prominent ornamentation and from *E. pusillum* by the stronger ornamentation.

O c c u r r e n c e. Russia, Dagestan; Middle Aptian, *Colombiceras crassicostatum–Epicheloniceras subnodosocostatum* Zone.

M a t e r i a l. Two well-preserved specimens from the section near the village of Akusha, Central Dagestan (PIN, nos. 5265/55, 5265/121); Middle Aptian, *Colombiceras crassicostatum–Epicheloniceras subnodosocostatum* Zone.

Epicheloniceras martinioides Casey, 1961

Plate 26, fig. 4

Cheloniceras (Epicheloniceras) martinioides: Casey, 1961b, p. 595, pl. 84, figs. 2a and 2b, text-figs. 14d and 14e; Casey, 1962, p. 239, pl. 27, figs. 1a–1c, pl. 28, figs. 3a and 3b, pl. 29, text-figs. 83, 86g, and 86h; Glazunova, 1967, p. 174; Dutour, 2005, p. 163, pl. 20, figs. 1–4, pl. 21. fig. 1, pl. 22, figs. 1 and 2, pl. 23, fig. 1, non pl. 24, figs. 1–6.

H o l o t y p e. GSM 98603, Hythe Beds (Boughton Group), Skinner's quarry, Boughton Mount near Maidstone, Kent (Casey's collection).

S h e l l s h a p e. The shell is medium-sized, inflated, with wide whorls, rounded angular in cross section when cutting through the tubercles. The umbilicus is relatively wide; the umbilical wall is steep.

D i m e n s i o n s i n m m a n d r a t i o s:

Specimen PIN, no.	Dm	WH	WW	UW	WH/Dm	WW/Dm	UW/Dm
5265/262	83.4	36.0	52.5	28.8	0.43	0.63	0.35

O r n a m e n t a t i o n. The ornamentation is represented by coarse primary and less pronounced intercalary ribs. The primary ribs begin near the seam; on the umbilical shoulder, they are associated with the lower row of small tubercles. The middle row of larger lateral tubercles is slightly above. The upper row of auricle-shaped ventral tubercles is typical of this species. Thin intercalary ribs (one–two between the primaries) also have elongated auricle-shaped ventral tubercles. In the preceding whorl, the difference between the primary and intercalary ribs is less pronounced. The umbilical row of tubercles is almost indiscernible and the lateral and ventral rows are distinct.

S u t u r e. Our specimen has only fragments of the suture. Casey (1961a, 1964) two times illustrated the suture, with all typical characters of such of the superfamily Douvilleiceratoidea. The deviation is observed in the saddle V/U, which can be slightly higher and narrower than usual.

C o m p a r i s o n. This species is distinguished from other species of the genus *Epicheloniceras* by the presence of the auricle-shaped ventral tubercles and from the type species *E. tschernyschewi* (Sinzow) by the considerably fewer intercalary ribs.

Among *E. martini* (d'Orbigny), Dutour (2005, p. 163) recognized the macroconchs and microconchs. Macroconchs dominate (Dutour, 2005, pl. 20, figs. 1–4, pl. 21, fig. 1, pl. 22, figs. 1, 2, pl. 23, fig. 1, pl. 25, figs. 1–4, 12), which correspond to *E. martinioides* Casey. Smaller specimens, microconchs (Dutour, 2005, pl. 24, figs. 1–6, pl. 25, figs. 5–8) do not have clearly elongated ventral tubercles and resemble *E. buxtorfi* (Jacob). However, specimens, figured in pl. 25, figs. 1–3 have more intercalary ribs and more strongly resemble *E. tschernyschewi* (Sinzow).

O c c u r r e n c e. Russia (northern Caucasus), Middle Aptian; France, England, Upper Aptian.

M a t e r i a l. One moderately well-preserved specimen. Northern Caucasus, Malka River (PIN, no. 5265/262); Middle Aptian, *Parahoplites melchioris* Zone.

Subfamily Douvilleiceratinae Parona et Bonarelli, 1897

Douvilleiceratinae: Arkell et al., 1957, L387; Wright et al., 1996, part L, vol. 4, p. 269.

D i a g n o s i s. Shell inflated, from semi-evolute to almost evolute. Cross section wide and angular. Ornamentation coarse; at early stages, ribs with three pairs of tubercles, later, with multiple tubercles. Suture typical of superfamily Douvilleiceratoidea.

C o m p o s i t i o n: Genera *Eodouvilleiceras* Casey and *Douvilleiceras* Grossouvre, 1894 from the Upper Aptian–Lower Albian of Europe, Asia, and South America.

C o m p a r i s o n. The difference from the subfamily Cheloniceratinae is stated above.

Genus *Eodouvilleiceras* Casey, 1961

Eodouvilleiceras: Casey, 1961a, p. 191; Obata, 1969, p. 166; Wright et al., 1996, p. L269; Sharikadze et al., 2004, p. 369; Atlas..., 2005, p. 387.

Epicheloniceras (Eodouvilleiceras): Egoian, 1969, p. 182.

T y p e s p e c i e s. *Douvilleiceras horridum* Riedel, 1938 (Riedel, 1938, p. 29, pl. 6, figs. 1, 2); Upper Aptian; Colombia. Designated by the author of the genus (Casey, 1961a, p. 191).

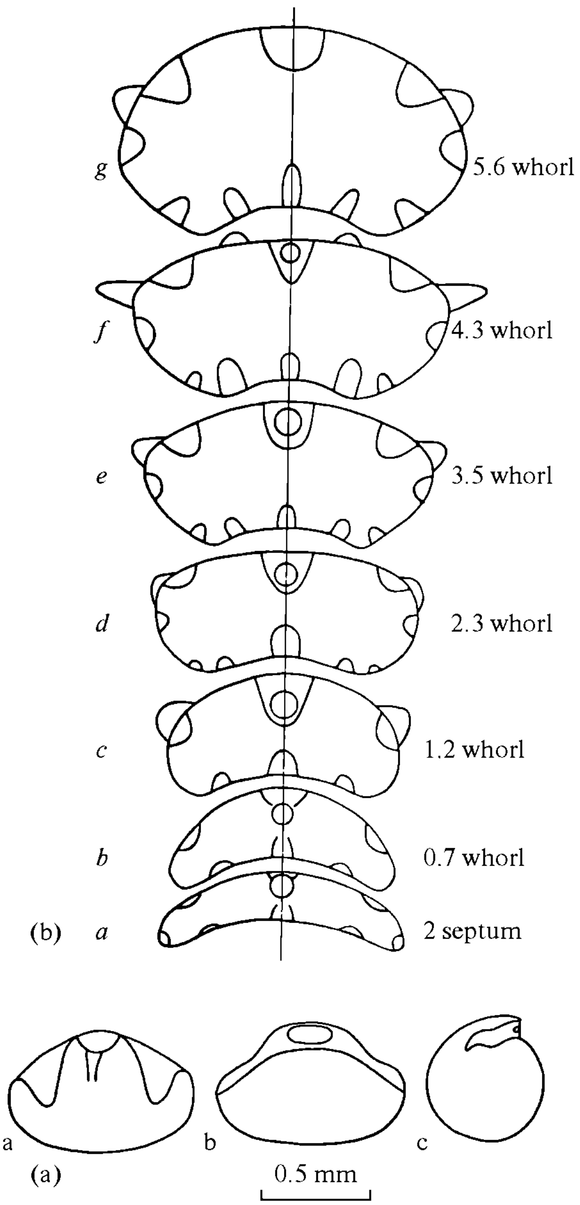


Fig. 81. *Eodouvilleiceras clansayense* (Jacob), specimen no. 87/7212: (a) protoconch: (*a*) upper view, (*b*) proseptum view, (*c*) lateral view; (b) morphogenesis of the cross section: (*a*–*c*) ×44; (*d*) ×20; (*e*) ×10; (*f*) ×5; (*g*) ×2; Tuarkyr, Babashi well, Late Aptian.

D i a g n o s i s. Shell medium-sized, semi-evolute. Each subsequent whorl overlaping preceding one by one-third of whorl height. Cross section rounded and, when cutting through tubercles, angular. Whorl width equal to, or higher than, height. Umbilical wall steep. Umbilicus wide and stepped.

The ornamentation is represented by ribs and tubercles. The umbilical wall is smooth. The ribs are coarse, appear on the umbilical shoulder, and, in medium-sized whorls, are subdivided into primary and intercalary ribs (similar to the primaries). Tubercles in adult whorls are arranged in three rows on the umbilical shoulder, flanks, and venter. In the young whorls, initially lateral and, then, ventral tubercles appear. The lateral tubercles in all whorls remain the highest. With age, the shape of the ventral tubercles changes from conical to elongated, flattened, bifid, and in the later to trifid. The ribs are lowered between the ventral tubercles.

The suture is complexly dissected. The ventral lobe (V) is deep, relatively narrow, and bifid. In ontogeny, the umbilical lobe is divided into two parts: a larger U_1 and smaller U_2. The external saddle V/U is somewhat asymmetrical, extremely high, and approximately twice as high as adjacent saddles.

S p e c i e s c o m p o s i t i o n: *E. horridum* (Riedel, 1938); *E. clansayense* (Jacob, 1905); *E. santafecinum* (Burckhardt, 1925); *E. badkhyzicum* (Urmanova, 1962); *E. aphanasievi* Egoian, 1969; *E. extenuatum* Egoian, 1969; *E. matsumotoi* Obata, 1969; *E. trituberculatum* Sakharova, 1985. Russia (northern Caucasus, Dagestan), Turkmenistan (Tuarkyr, Badkhyz), Georgia, France, USA (California), Colombia, Venezuela, Japan; Upper Aptian.

R e m a r k s. The genus *Eodouvilleiceras* is intermediate between Middle Aptian *Epicheloniceras* and Early Albian *Douvilleiceras,* because the ventral tubercles tend to break into two or three peaks with their gradual divergence and separation, like in *Douvilleiceras.* The suture is similar to that of *Epicheloniceras* (Fig. 72) and *Eodouvilleiceras.*

C o m p a r i s o n. The genus in question differs from *Epicheloniceras* Casey, 1954 in the shape of tubercles. In *Eodouvilleiceras,* they are higher; in adult whorls, ventral tubercles are bifid and trifid. It is distinguished from *Douvilleiceras* Grossouvre, 1894 by the presence of only three rows of tubercles, instead of six–eight rows. However, these genera are similar in having increased tubercles in adult whorls.

***Eodouvilleiceras* clansayense (Jacob, 1905)**

Plate 27, figs. 1–4

Douvilleiceras clansayense: Jacob, 1905, p. 413, pl. 13, fig. 4; Jacob in Jacob and Tobler, 1906, p. 14, pl. 1. figs. 7, 8.

H o l o t y p e. Specimen figured by Jacob (1905, pl. 13, figs. 4a, 4b, 4c); Aptian; southeastern France, Clansayes. Designated by Egoian (1965, p. 156) by monotypy.

S h e l l s h a p e. The protoconch is elongated; the caecum is oval in cross section (Fig. 81a). The shell is medium-sized, semi-evolute, inflated, with whorls overlapping each other by more than half of the whorl height. The cross section is rounded oval or sharply angular, if it goes through the tubercles (Fig. 81b). The umbilicus is relatively wide and stepped. The umbilical wall is steep.

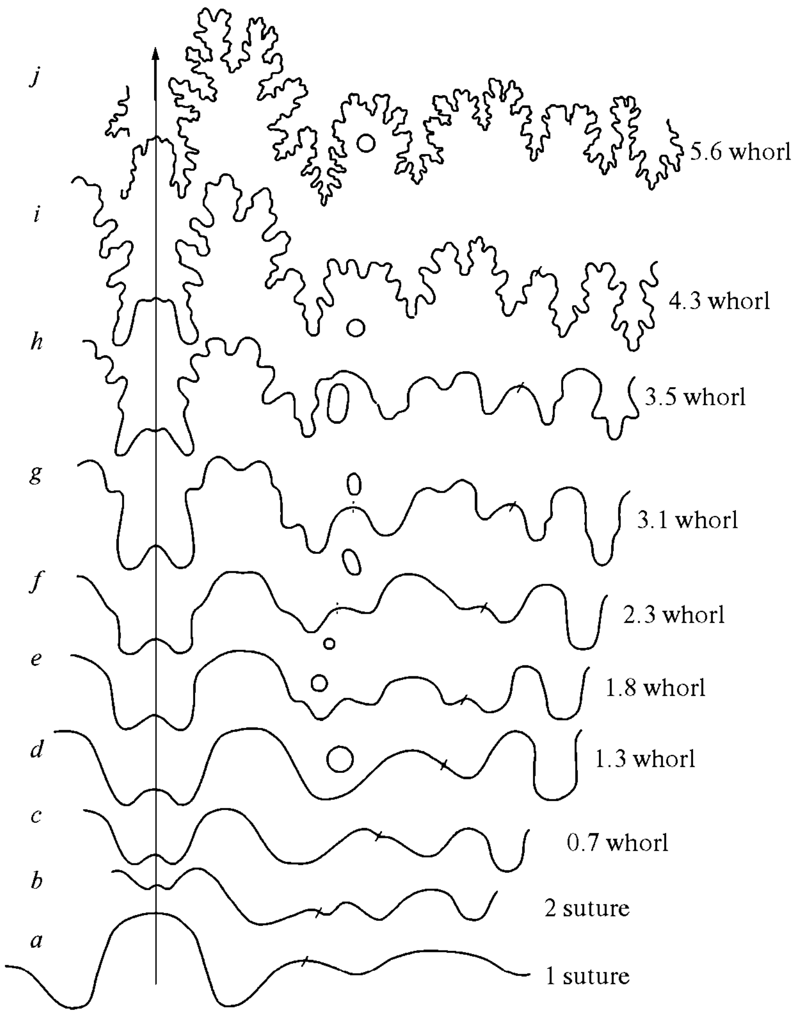


Fig. 82. Morphogenesis of the suture of *Eodouvilleiceras clansayense* (Jacob), specimen no. 87/7212: (*a–d*) ×72; (*e*) ×52; (*f*) ×40; (*g*) 23, (*h*) ×17; (*i*) ×9; (*j*) 4; Tuarkyr, village of Babashi, Late Aptian.

Dimensions in mm and ratios:

Specimen PIN, no.	Dm	WH	WW	UW	WH/ Dm	WW/ Dm	UW/ Dm
5265/98	21.2	8.2	12.5	9.6	0.40	0.50	0.45
5265/138	31.0	14.0	19.5	~11.8	0.45	0.62	0.38
5265/99	32.0	12.2	19.6	12.7	0.38	0.60	0.40
5265/137	45.1	19.8	24.5	~17.8	0.43	0.54	0.39
5265/100	49.5	20.7	25.4	17.3	0.42	0.51	0.35

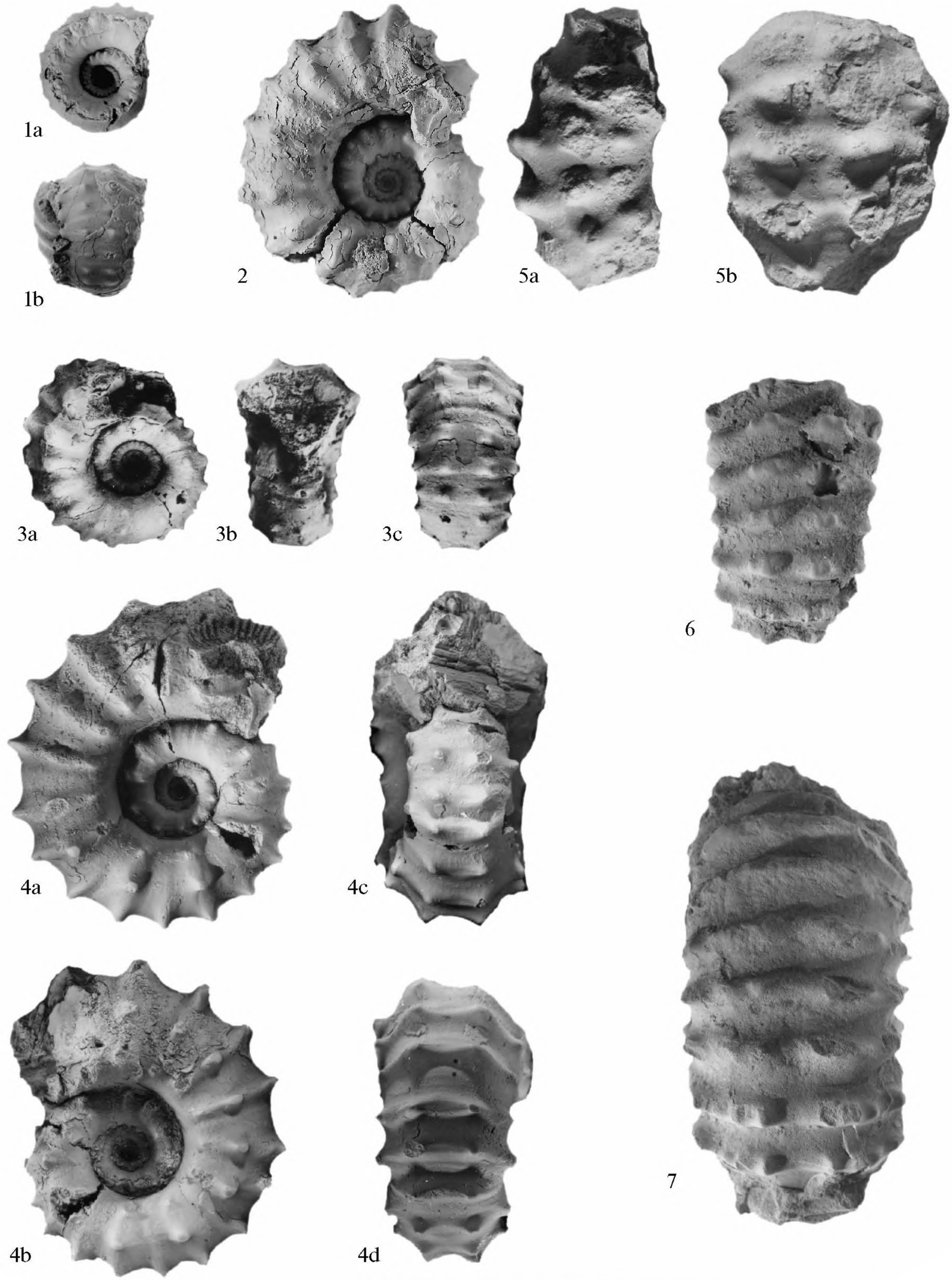
Ornamentation. The ornamentation is represented by coarse ribs with three rows of tubercles. The tubercles appear considerably earlier than ribs. The lateral tubercles, approximately 12 tubercles per one whorl, first appear in the second whorl, whereas the ventral tubercles appear much later. Shortly after, ribs appear between the lateral and ventral tubercles. The ribs become lower toward the plane of symmetry.

Over the diameter of 20 mm, the ornamentation is uniform. The primary ribs are clearly dominant; the intercalary ribs are widely spaced, irregular, either intercalary or extending from the lateral tubercles. A row of small umbilical tubercles is the last to develop at the diameter of 25.0 mm on the umbilical shoulder. At this stage, the primary ribs begin from the umbilical tubercles, whereas the widely spaced intercalary ribs either extend from the lateral tubercles or begin at the same level with them.

Suture. (Fig. 82). The morphogenesis of the suture of this species reflects features characteristic of the superfamily Douvilleiceratoidea. The prosuture is with high median saddle and two lobes U and I. The primary suture is five-lobed, VUU^{1}ID. The ventral lobe is shallow and bifid; the small but distinct first umbilical lobe U^1 is present. In the ninth suture, a rudiment of this lobe is present, but later it disappears.

At the end of the second whorl, there are four lobes, VUID. The umbilical lobe is asymmetrical trifid and the inner lateral lobe is bifid. The asymmetrical subdivision of the umbilical and inner lateral lobes is com-

Plate 27



Explanation of Plate 27

Figs. 1–4. *Eodouvilleiceras clansayense* (Jacob, 1905); specimens: (1) PIN, no. 5265/98; northern Caucasus, Khokodz River; Upper Aptian; (2) PIN, no. 5265/277; (3) PIN, no. 5265/99; (4) PIN, no. 5265/100; Tuarkyr, Babashi well, the same age.

Fig. 5. *Eodouvilleiceras badkhizicum* (Urmanova, 1962); specimen PIN, no. 5265/103; Dagestan, Burdeki Village; Upper Aptian.

Figs. 6 and 7. *Eodouvilleiceras trituberculatum* Sacharova, 1985; (6) specimen PIN, no. 5265/102; (7) specimen PIN, no. 5265/101; Dagestan, village of Akusha, Upper Aptian.

pleted by the subdivision of each into two separate lobes: U → U_1 and U_2, I → I_2 and I_1. Lateral digits gradually appear on the lateral sides of the ventral lobe and it becomes narrow and deep, with complex dissection. The dorsal lobe is acuminate. The external saddle V/U rapidly increases in height, exceeding at the terminal stage all other saddles approximately twofold.

The arrangement of the lateral tubercles, beginning from the 17th suture is shown in Fig. 82. The marginal curves of the septum go around the tubercles, which are projected on the umbilical lobe and, after its subdivision, lie between the U_1 and U_2 lobes.

Comparison and remarks. *E. clansayense* is distinguished from congeners by the presence of undivided acuminate ventral tubercles. At the same time, the ribbing with the almost complete absence of intercalary ribs precludes assignment of this species to the genus *Epicheloniceras.*

The specimen described and figured by Egoian (1965, p. 156, pl. 13, fig. 1; pl. 14, figs. 1–3) as *E. clansayense* has a denser ribbing and lower whorls; therefore, it is not included in the synonymy list. Jacob (1905, p. 413) considered *Eodouvilleiceras clansayense* as the terminal form of the evolutionary lineage *Cheloniceras martini* d'Orb. → *Epicheloniceras orientale* (Jacob).

The comparison of the sutural morphogenesis in this species with that of Gargasian *E. tschernyschewi* Sinzow (see Fig. 72) shows a lesser dissection of its elements in the latter species. Perhaps, this resulted from acceleration, as one species is Gargasian, and another is Clansayesian.

Occurrence. Russia (northern Caucasus); Turkmenistan (Tuarkyr); Georgia, Colombia; Upper Aptian.

Material. Six well-preserved specimens. Northern Caucasus: Khokodz River (PIN, no. 5265/98); Tuarkyr: Babashi well (PIN, nos. 5265/99, 5265/100, 5265/137, 5265/138, 5265/277); Upper Aptian.

Eodouvilleiceras badkhyzicum **(Urmanova, 1962)**

Plate 27, fig. 5

Epicheloniceras badkhyzicum: Urmanova, 1962 Egoian, 1969, p. 185, pl. 20. fig. 2.

Holotype. TsGM, no. 8174; Turkmenistan, Badkhyz, Gerirud Anticline; Upper Aptian. Designated by the author of the species.

Shell shape. The cross section is low, hexagonal; the height is much less than the width. The umbilical wall is low and steep. The flanks have a sharp bend in the middle part, especially if the cross section cuts through the tubercles. A wide venter is slightly raised above the lateral sides.

Ornamentation. The ornamentation is mostly composed of coarse, evenly spaced primary ribs with three rows of tubercles running along the ribs. The ventral tubercles are clearly bifid, the lateral tubercles (on the mold) are slightly obtuse and the umbilical tubercles are small and pointed. The ventral tubercles expand at the base of ribs and approximate the lateral tubercles. The expansion of the ventral tubercles leads to their subdivision. The primary ribs begin from the acuminate umbilical tubercles.

Suture. The suture is typical of the family Douvilleiceratidae. The adjacent sutures depending on the ornamentation can be different in outline. However, the proportions of the ventral lobe (V), first and second umbilical lobes (U_1 and U_2), first and second inner lateral lobes (I_2 and I_1), and the dorsal (D) lobe and the prevalence in size of the external saddle V/U_1 are retained.

Comparison and remarks. Egoian (1969) assigned to the species considered a specimen figured by him in pl. 19, fig. 2, but it has a less dense ribbing compared to the type species and, hence, it is not included in the synonymy list.

E. badkhyzicum is distinguished from *E. extenuatum* (Egoian) by the earlier bifurcation of the ventral ribs and remaining with age of prominent tubercles. It differs from *E. aphanasievi* Egoian in the more closely spaced ribs.

Occurrence. Russia (Dagestan); Turkmenistan (Badkhyz); Upper Aptian.

Material. One shell fragment. Dagestan, village of Burdeki (PIN, no. 5265/103); Upper Aptian.

Eodouvilleiceras trituberculatum **Sakharova, 1985**

Plate 27, figs. 6 and 7; Plate 28, figs. 1 and 2

Eodouvilleiceras trituberculatum: Sakharova, 1985, p. 174, pl. 8, figs. 1 and 2.

Holotype. MZ MGU, no. 1/85, specimen figured by Sakharova (1985, pl. 8, fig. 1); Dagestan, village of Akusha; Upper Aptian, *Acanthohoplites nolani* Zone.

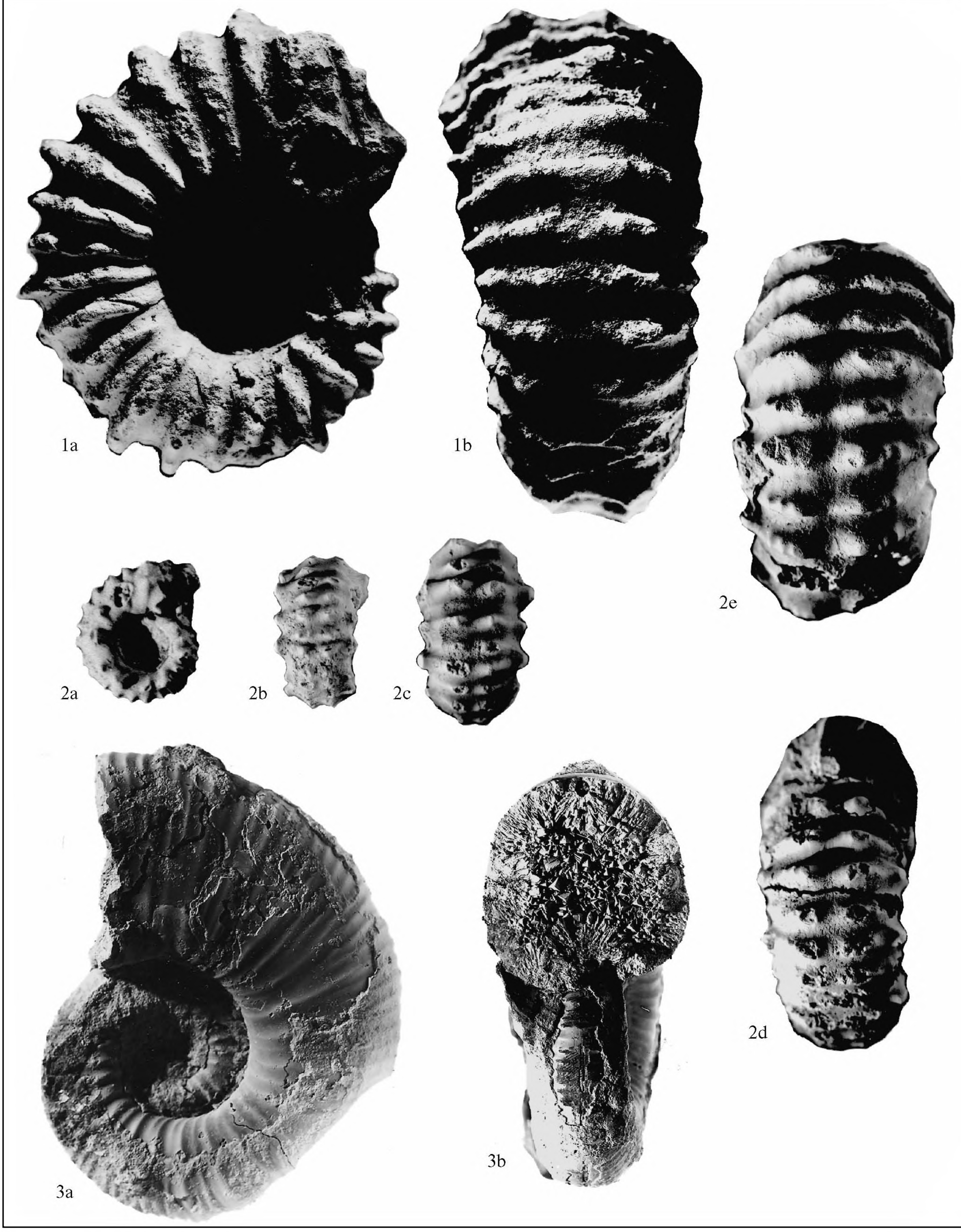
Shell shape. The shell is semi-evolute with whorls overlapping the preceding one by a third of the height. The cross section is low and angular. The umbilical wall is rounded, steeply descending to the wide umbilicus.

Dimensions in mm and ratios:

Specimen no.	Dm	WH	WW	UW	WH/Dm	WW/Dm	UW/Dm
MZ MGU 2/85	74.0	26.0	34.0	27.0	0.35	0.46	0.36
MZ MGU 1/85 holotype	79.0	25.0	36.0	28.0	0.31	0.45	0.36
PIN 5265/114	87.0	30.2	47.8	28.9	0.38	0.55	0.33

Ornamentation. The ornamentation is represented by ribs and three rows of tubercles. The primary ribs are coarse, begin near the umbilical wall from the lower row of tubercles and slightly lowered between the ventral tubercles. The intercalary ribs are visible on young whorls up to 35 mm in diameter, extending from the primary ribs (MZ MGU, no. 1/85). The

Plate 28



intercalary ribs begin from near the lateral tubercles and lie anterior to the primaries.

S u t u r e. The suture is typical of the genus *Eodouvilleiceras*; the ventral lobe (V) is narrow, deep; the external branch of the umbilical lobe is separated in the asymmetrical first umbilical U_1 lobe, and the inner branch is separated into the shorter second umbilical U_2 lobe. The inner lateral lobe is also subdivided; the branch I_2 lies on the external surface of the shell. The external saddle V/U is hypertrophic.

C o m p a r i s o n. This species is distinguished from the similar species *E. clansayense* by the presence in adult whorls of three-peaked ventral tubercles and also by the smooth intercalary ribs. It differs from *E. aphanasievi* and *E. extenuatum* established by Egoian (1965) by the presence of three-peaked ventral tubercles.

R e m a r k s. Sakharova established *E. trituberculatum* based on the presence of three-peaked ventral tubercles in two specimens from the Upper Aptian beds exposed near the village of Akusha (*Acanthohoplites nolani* Zone), housed in the monographic section of the Museum of Earth Sciences of Moscow State University (holotype MZ MGU, no. 1/85 and paratype MZ MGU, no. 2 /85). Sakharova described the ornamentation in detail noting the asymmetry of ribs on the flank (Sakharova, 1985, p. 175). To compare her material with ours we reproduce her specimens in Pl. 28. fig. 2.

O c c u r r e n c e: Russia (Dagestan); Kazakhstan (Mangyshlak); Upper Aptian, *Acanthohoplites nolani* Zone.

M a t e r i a l. Three complete specimens and two fragments. Dagestan, village of Akusha (PIN, nos. 5265/101, PIN, no. 5265/102, MZ MGU, nos. 2/85, 1/85); Mangyshlak, Kugusem well (PIN, no. 5265/114); Upper Aptian, *Acanthohoplites nolani* Zone.

S u p e r f a m i l y Ancyloceratoidea Gill, 1871

Ancylocerataceae Meek, 1876: Casey, 1960, part I, p. 16.
Ancyloceratoidea Meek, 1876: Kakabadze, 1981, p. 83.
Ancylocerataceae: Mikhailova, 1983, p. 93.
Ancyloceratoidea: Kakabadze and Hoedemaeker, 2004, p. 39.
Ancylocerataceae: Wright et al., 1996, part L, vol. 4, p. 206.

D i a g n o s i s. Shell heteromorphic: baculitid (straight), hamuliconic, ancyloceratid, cryoceratids, or heteroceratids. In many taxa, secondary coiling apparently resulting in umbilical perforation. Ornamentation diverse, composed of ribs, sometimes in combination with tubercles, less commonly, very weak.

The suture is with a few saddles and lobes, which in large specimens can be strongly dissected. The primary suture is unstable five-lobed (VUU^1ID) and the number of lobes is soon reduced to four (VUID). The umbilical lobe is the largest, trifid; the dorsal lobe is acuminate.

C o m p o s i t i o n. Five families: Bochianitidae Spath, 1922; Ancyloceratidae Gill, 1871; Crioceratitidae Gill, 1871; Heteroceratidae Spath, 1922; and Hemihoplitidae Spath, 1924. Upper Jurassic (Tithonian)–Lower Cretaceous; Russia, Europe, Asia, Africa, North and South America, Australia.

Wright et al. (1996) also recognized the families Hamulinidae Gill, 1871, Labeceratidae Spath, 1925, Ptychoceratidae Gill, 1871, and possibly Macroscaphitidae Hyatt, 1900. The last two should be assigned to the superfamily Turrilitoidea Gill, 1871. In the representatives of the family Ptychoceratidae, the morphogenesis of the suture was studied, which reflects characteristic features of the order Lytoceratida (Mikhailova, 1983). The lowering of the rank of Heteroceratidae to a subfamily seems unjustified

R e m a r k s. The superfamily Ancyloceratoidea descends from Perisphinctoidea, which is discussed above. It is possible that the original family Bochianitidae, which appeared in the Tithonian was ancestral to several families which later gave rise to Deshayesitoidea, Douvilleiceratoidea, and Parahoplitoidea.

Family Ancyloceratidae Gill, 1871

Ancyloceratidae Meek, 1876: Casey, 1960, part I, p. 16; Kakabadze, 1981, p. 83; Wright et al., 1996, part L, vol. 4, p. 210.
Ancyloceratidae: Kakabadze and Hoedemaeker, 2004, p. 39.

D i a g n o s i s. Shell ancyloceratid, composed of three parts: planispiral, straight shaft, and hook.

The morphogenesis of the shell and suture was studied in *Luppovia* Bogdanova, Kakabadze et I. Michailova (Kakabadze et al., 1978a), *Caspianites* Casey (Bogdanova and Mikhailova, 1975), and *Audouliceras* Thomel (Mikhailova and Baraboshkin, 2007). Features discussed above in the description of the superfamily are established.

The ornamentation is diverse, strong, composed of ribs and tubercles.

C o m p o s i t i o n. Wright et al. (1996) subdivided the family into four subfamilies, including the type subfamily and also Heteroceratinae, as mentioned

E x p l a n a t i o n o f P l a t e 28

Fig. 1 and 2. *Eudouvilleiceras trituberculatum* Sacharova, 1985; (1) specimen MZ MGU, no. 2/85; (2) holotype MZ MGU, no. 1/85: (2a) lateral view (2b) ventral view at the diameter 28 mm, (2c) ventral view at the diameter 34 mm, (2d) ventral view at the diameter 60 mm, (2e) ventral view at the diameter 70 mm; Dagestan, village of Akusha; Upper Aptian; *Acanthoplites nolani* Zone.

Fig. 3. *Caspianites wassiliewskyi* (Renngarten, 1926); specimen PIN, no. 5265/279; Tuarkyr, Babashi well; Middle Aptian, *Epicheloniceras subnodosocostatum* Zone.

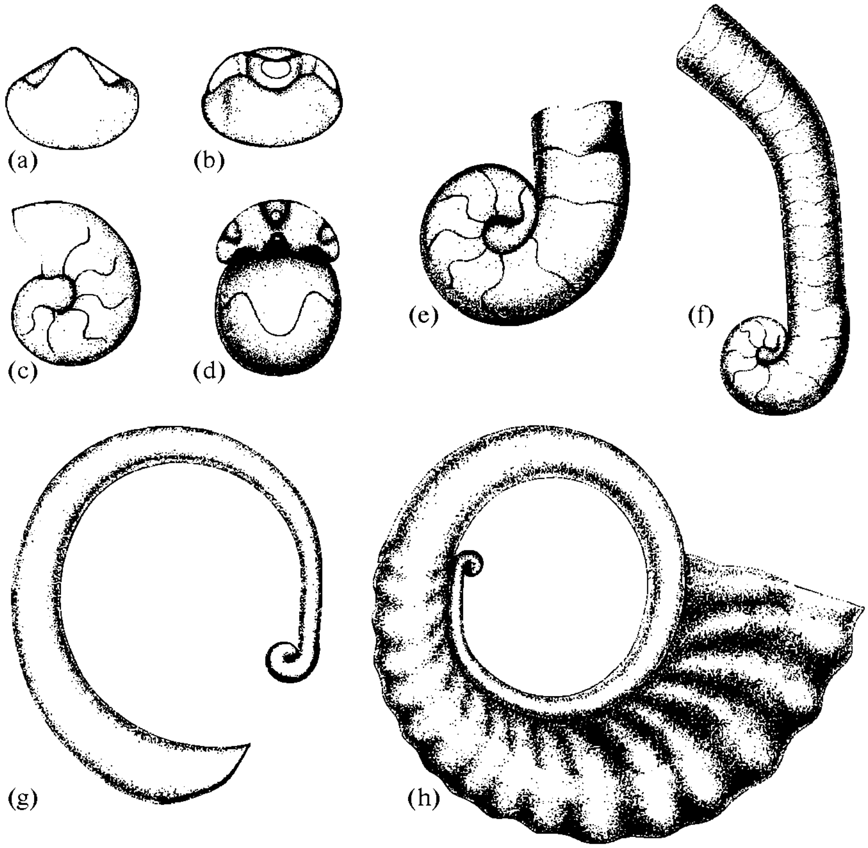


Fig. 83. Morphogenesis of the shell shape in *Caspianites wassiliewskyi* (Renngarten), specimen TsNIGR Museum, no. 1/11288: (a, b) protoconch, (c, d) first whorl, (e) beginning of the shaft, (f) transition of shaft to broach arch, (g) first and second whorls, (h) two and a half whorls, umbilical perforation in the center, incipient ornamentation.

above. In addition, it is proposed to recognize based on the small size Helicancyloceratinae Hyatt, 1894 and Leptoceratinae Thieuloy, 1966. The recognition of these subfamilies is provisional. Hauterivian–Lower Albian; Russia, Europe, Asia, Africa, North and South America, Australia.

C o m p a r i s o n. Ancyloceratidae is distinguished from the planispiral family Crioceratitidae Gill, 1871 by the presence of the straight shaft; at the later stages, in heteroceratids, the shaft becomes curved and the initial part of the shell is planispiral or turretelliform.

Genus *Caspianites* Casey, 1961

Crioceras (Ammonitoceras): Renngarten, 1926, p. 30.

Caspianites: Casey, 1961a, p. 56; Casey, 1980, p. 646; Kakabadze, 1981, p. 120; Wright et al., 1996, p. 221.

Ammonitoceras (Caspianites): Bogdanova and Kakabadze, 1976, p. 125.

T y p e s p e c i e s. *Crioceras (Ammonitoceras) wassiliewskyi* Renngarten (Renngarten, 1926, p. 30) [(=*Crioceras Ridzewskyi* Sinzow (1907, p. 507, pl. 6, figs. 13–18), non *Acanthoceras Ridzewskyi* Karakasch (Karakash, 1897, p. 28, pl. 4, figs. 9, 10)]; Middle Aptian; Mangyshlak. Designated by Casey (1961a, p. 56).

S h e l l s h a p e. The protoconch is elongated, with a high median saddle (Fig. 83). Its diameter reaches 0.50 mm, and the width is 0.60 mm. The first whorl is embracing, at the end with a well-developed constriction. A short straight shaft begins immediately after that constriction. The shaft is later curved in a broad arch, extending far from the first whorl. The contact of an archlike shaft with the first whorl coincides with the constriction, i.e., with the end of the embryonic shell. This part of the shell is referred to as the second uncontacting whorl (straight shaft and broad arch). Inside the whorl, the umbilical perforation is present. The succeeding whorls (up to 20 cm in diameter) are in contact and, later, more or less noticeably depart from one another.

The cross section varies from a crescentic in the first whorl to rounded in the second, oval and rounded, and, later, trapezoid, elongated in height at the last stages (Fig. 84).

Thus we observed (1) embryonic shell (Dm = 0.9 mm), including the protoconch similar in morphology to that of monomorphic ammonoids; (2) short straight shaft up to 1–1.5 mm long, similar to that at the early stages of the genus *Baculites* (Smith, 1901); (3) uncontacting second whorl with an umbilical perforation, 4.5–5 times exceeding in diameter the embryonic shell; (4) contacting, slightly overlapping succeeding whorls.

O r n a m e n t a t i o n. Singular elongated ribs appear at the beginning of the third whorl, on which lower lateral tubercles are observed from the third–fourth rib, while umbilical tubercles appear from the second half of the third whorl. Tubercles on the ventrolateral shoulder emerge later. Thus, at the end of the third whorl, the shell is covered by singular primary ribs with three rows of tubercles. Later, the lateral, ventrolateral, and, shortly after, the umbilical tubercles disappear. From that stage, the ornamentation is represented by thin and densely spaced ribs, which cross the venter.

S u t u r e (Fig. 85). The prosuture is with high ventral and lower dorsal saddle (see Fig. 33). The primary suture and the next, third, suture are composed of five lobes: VUU^1ID. The first umbilical lobe (U^1) in the primary suture is dissected by the seam. Shortly after, the U^1 lobe disappears, and the sixth suture is composed of only four lobes. This outline remains up to the 31st suture and, with reference to the shell shape, to the end of the second uncontacting whorl. Almost at the same time, the incipient trifid division of the wide umbilical lobe (U) is observed, while the saddles become bifid, and the dorsal and inner lateral lobes become more complex. A digit on the lateral sides of the ventral lobe appears relatively late in ontogeny.

The following is of particular importance: (1) the primary suture is composed of five lobes (VUU^1ID) rather than four (VUID); (2) after the third suture, the first umbilical lobe disappears; (3) new elements do not appear in ontogeny and the first umbilical lobe is not restored; (4) the increased complexity of the existing elements begins relatively late, approximately from the 33rd suture.

S p e c i e s c o m p o s i t i o n. *C. wassiliewskyi* (Renngarten, 1926), *C. cadoceriformis* (Sinzow, 1905), *C. tuarkyriensis* Kakabadze, 1981. Kazakhstan (Mangyshlak), Turkmenistan; Middle Aptian, *Epicheloniceras subnodosocostatum* Zone.

C o m p a r i s o n. The genus in question is distinguished from *Ammonitoceras* by the branching of ribs mostly from the umbilical bullae and only initial and short-term branching is associated with the lateral tubercles, and by the earlier disappearance of the ventrolateral tubercles and thinner ribbing of the last whorls.

R e m a r k s. Renngarten (1926, p. 30) established that the species identified by Sinzow as *Crioceras ridzewskyi* Karakasch (Sinzow, 1907, p. 507, pl. 6, figs. 13–18) is in fact a different species. Renngarten carefully analyzed the morphological characters of Sinzow's specimen and recognized essential difference from Karakash's species (*Acanthoceras Ridzewskyi* Karakasch, 1897, p. 28, pl. 4, figs. 9, 10) and proposed to give this form a new name, *Crioceras*

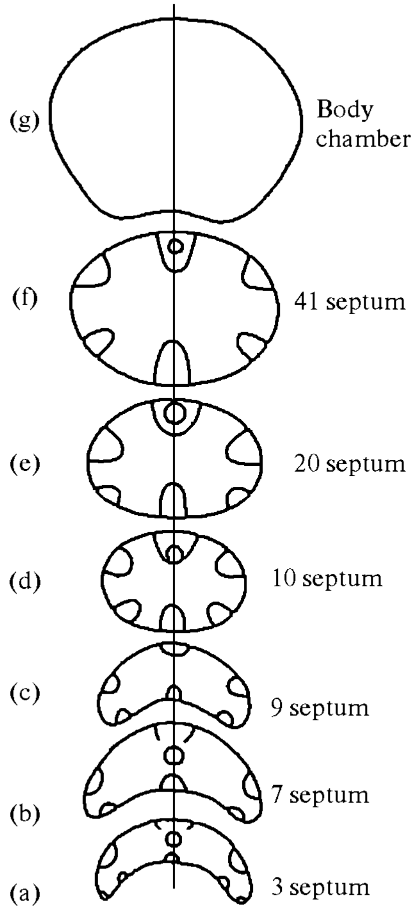


Fig. 84. Morphogenesis of the whorl cross section of *Caspianites wassiliewskyi* (Renngarten), specimen TsNIGR Museum, no. 1/11288: (a–e) ×28, (f) ×5, (g) ×2.2.

(Ammonitoceras) wassiliewskyi. Later, Casey (1961a, p. 56) established the new genus *Caspianites* and designated *Crioceras* (*Ammonitoceras) wassiliewskyi* Renngarten as the type species.

Caspianites wassiliewskyi **(Renngarten, 1926)**

Plate 28, fig. 3; Plate 29, figs. 1–5

Crioceras Ridzewskyi: Sinzow, 1907, p. 507, pl. 6, figs. 13–14.

Crioceras (Ammonitoceras) wassiliewskyi: Renngarten, 1926, p. 30.

Caspionites wassiliewskyi: Casey, 1961a, p. 56; Bogdanova and Mikhailova, 1975, p. 97.

Ammonitoceras (Caspianites) wassiliewskyi: Bogdanova and Kakabadze, 1976, p. 126, fig. 1.

L e c t o t y p e. TsNIGR Museum, no. 51/11068; specimen figured by Sinzow (1907, pl. 6, fig. 13); Middle Aptian, *Epicheloniceras subnodosocostatum* Zone; Kazakhstan, Mangyshlak, vicinity of Doshchan cemetery. Designated by Casey (1961a, p. 56).

S h e l l s h a p e. The protoconch is ridgelike (see Fig. 83). The shell is mostly large, weakly inflated, heteromorphic, with an umbilical perforation. The cross section varies from crescentic in the first whorl to trap-

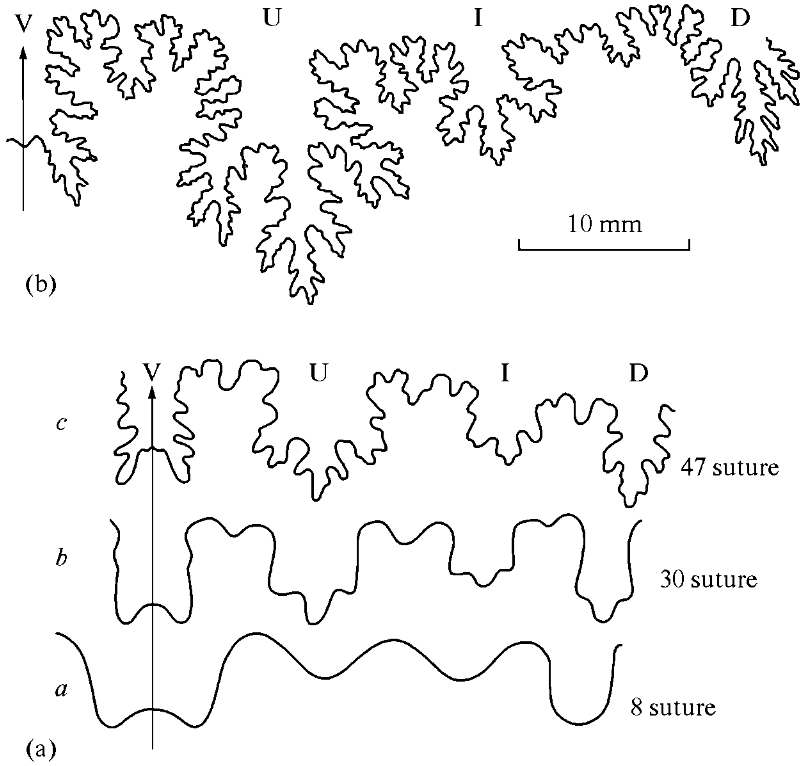


Fig. 85. *Caspianites wassiliewskyi* (Renngarten): (a) specimen TsNIGR Museum, no. 3/11288, scheme of suture morphogenesis; (b) specimen TsNIGR Museum, no. 1/11276, suture; Tuarkyr, Babashi well, Middle Aptian, *Epicheloniceras subnodosocostatum* Zone.

ezoid (see above). The venter and flanks are flat or very weakly convex. The inner side in the last whorls is weakly concave. The umbilicus is wide, stepped, with high and steep umbilical wall in the first whorls and with a lower wall in the later whorls.

Dimensions in mm and ratios:

Specimen no.	Dm	WH	WW	UW	WH/ Dm	WW/ Dm	UW/ Dm
TsNIGR Museum 4/11288	12.6	4.5	5.8	5.2	0.36	0.46	0.41
TsNIGR Museum 3/11288	21.4	7.8	9.5	8.3	0.36	0.44	0.39
TsNIGR Museum 2/11276	23.7	8.6	10.8	8.9	0.36	0.45	0.38
TsNIGR Museum 2/11288	35.1	14.7	15.2	11.5	0.40	0.43	0.33
TsNIGR Museum 3/11276	40.4	17.2	17.2	15.2	0.42	0.42	0.38
PIN 5265/272	67.3	30.0	23.7	24.6	0.45	0.35	0.36
TsNIGR Museum 1/11276*	103.4	46.9	48.9	37.0	0.45	0.47	0.36
TsNIGR Museum 4/11276	126.0	51.7	52.0	39.4	0.41	0.41	0.31
TsNIGR Museum 1/11276		84.7	75.7				

* Only the phragmocone is measured, see the photograph.

O r n a m e n t a t i o n. At the beginning of the third whorl, singular primary ribs appear, associated with the lateral, further on, umbilical, and, finally, ventrolateral tubercles. Thin intercalary ribs only appear on the fourth whorl at the same time with the ventrolateral tubercles. The primary ribs sometimes branch off the umbilical and lateral tubercles, but after the disappearance of the lateral tubercles (Dm > 45–60 mm), the ribs bifurcate from the umbilical bullae. Ventrolateral tubercles become weaker, but place of their appearance is designated by the bend of the ribs, which are effaced at Dm = 100 mm. After the umbilical tubercles are effaced, the primary and intercalary ribs in the upper half of the flank become identical.

S u t u r e. The suture is typical of the genus *Caspianites* (see Fig. 33). The main elements for the species are additionally shown in Fig. 85.

C o m p a r i s o n. This species is distinguished from *C. cadoceriformis* (Sinzow, 1905) by the more strongly convex and lower whorls and by the arrangement of the first umbilical lobe on the flank rather than on the umbilical wall. It is distinguished from *C. tuarkyriensis* Kakabadze, 1981 by the less pronounced ornamentation, the presence of intercalary ribs at adult stage, and the presence of ventrolateral tubercles.

O c c u r r e n c e. Kazakhstan (Mangyshlak, Aktyubinsk Region), Turkmenistan (Tuarkyr, Great

Balkhan); Middle Aptian, *Epicheloniceras subnodosocostatum* Zone.

Material. Eight variously preserved specimens. Tuarkyr, Umokdere gorge (TsNIGR Museum, no. 1/11276); Babashi well (PIN, no. 5265/279, TsNIGR Museum, nos. 1/11288, 2/11288, 3/11288); Great Balkhan, Utuludzha well (TsNIGR Museum, nos. 3/11276, 4/11288); Aktyubinsk Region, village of Turtkul' (PIN, no. 5265/272); Middle Aptian, *Epicheloniceras subnodosocostatum* Zone.

Genus *Luppovia* Bogdanova, Kakabadze et I. Michailova, 1978

Luppovia: Kakabadze et al., 1978a, p. 83; Kakabadze, 1981, p. 122; Wright et al., 1996, p. 225.

Type species. *Luppovia dostshanensis* Bogdanova, Kakabadze et I. Michailova, 1978 (Kakabadze et al., 1978a, p. 83); Middle Aptian, *Epicheloniceras subnodosocostatum* Zone; Kazakhstan, Mangyshlak, vicinity of the Doshchan cemetery. Designated by the authors of the genus.

Shell shape. The shell is relatively small, heteromorphic, composed of a few planispiral whorls, with an umbilical perforation and straightened body chamber. The protoconch is elongated, angustisellate. The first whorl (=embryonic shell) is coiled, after the primary constriction followed by a short straight shaft, becoming a broad arch. The latter approaches the first whorl, touching it or remaining very near. Therefore, an umbilical perforation appears inside the uncontacting "second whorl." Later, whorls are in contact.

The width of the cross section of the initial whorls somewhat exceeds their height. After the whorls become in contact, a depression appears on their inner side, which disappears in the last whorls. The shaft extending from the coiled portion is straight or slightly curved. The whorl cross section is wide and subtrapezoid. A hook was possibly present.

Ornamentation. The ornamentation is composed of singular, widely spaced, radial ribs with three pairs of tubercles: ventrolateral, lateral and umbilical. The ventrolateral tubercles in the adult whorls are stronger, than the others. At the end of the last whorl and on the shaft, apart from singular ribs, there are strong intercalary or bifid ribs. Branching begins from the umbilical or lateral tubercles. The ornamentation appears at the end of the third whorl.

Suture. The suture is of the ancyloceratid type and develops following the formula: $VUU^1ID \rightarrow (V_1V_1UID) \rightarrow (V_1V_1)(U_2U_1U_2)ID$. The prosuture is bilobed, with high ventral and lower dorsal saddles. The primary suture is five-lobed, composed of the ventral, umbilical, first umbilical, inner lateral, and dorsal lobes. At the end of the first whorl, the first umbilical lobe disappears and further changes are associated with the increasing complexity of the existing saddles and lobes without appearance of new elements.

Species composition. *L. dostshanensis* Bogdanova, Kakabadze et I. Michailova, 1978; *L. adjiderensis* Bogdanova, Kakabadze et I. Michailova, 1978. Kazakhstan (Mangyshlak); Turkmenistan; Middle Aptian, *Epicheloniceras subnodosocostatum* Zone.

Comparison and remarks. The general shell shape and ornamentation, composed of coarse straight singular ribs, make the genus *Luppovia* similar to the Late Barremian genus *Parancyloceras* Spath, 1924. They differ in the presence of the third pair (umbilical) tubercles and wider contacting whorls in *Luppovia*.

Apart from *Luppovia,* shell and sutural morphogenesis was studied in *Caspianites* (Bogdanova and Mikhailova, 1975) and *Hemihoplites* (Matheronites) (Sharikadze et al., 1989).

These genera were shown to have similar initial stages. Similar characters include the size and shape of the embryonic shell, presence of uncontacting second whorl with an umbilical perforation (Pl. 38, fig. 1). A small difference is the fact that, in *Luppovia,* the umbilical perforation is smaller and the tube of the shell after the constriction straightens more rapidly (Pl. 30, fig. 7). The change in the suture in ontogeny is uniform: the prosuture is bilobed, the primary suture is five-lobed (VUU^1ID), reduction of the first umbilical lobe and transition to the fourth suture (YUID), a trifid umbilical lobe is developed.

The morphogenesis of the initial parts of the shell conforms to what is observed in *Caspianites* (second whorl with an umbilical perforation), but in the third suture (the primary suture not observed), only four lobes are present.

The similarity of *Luppovia* to some representatives of *Hemihoplites (Matheronites)* ex gr. *ridzewskyi* Renngarten is observed in the same type of ornamentation, including the presence of three pairs of tubercles, but in *H. (M.)* ex gr. *ridzewskyi* the terminal stage of an open shell has not been established.

Luppovia dostshanensis Bogdanova, Kakabadze et I. Michailova, 1978

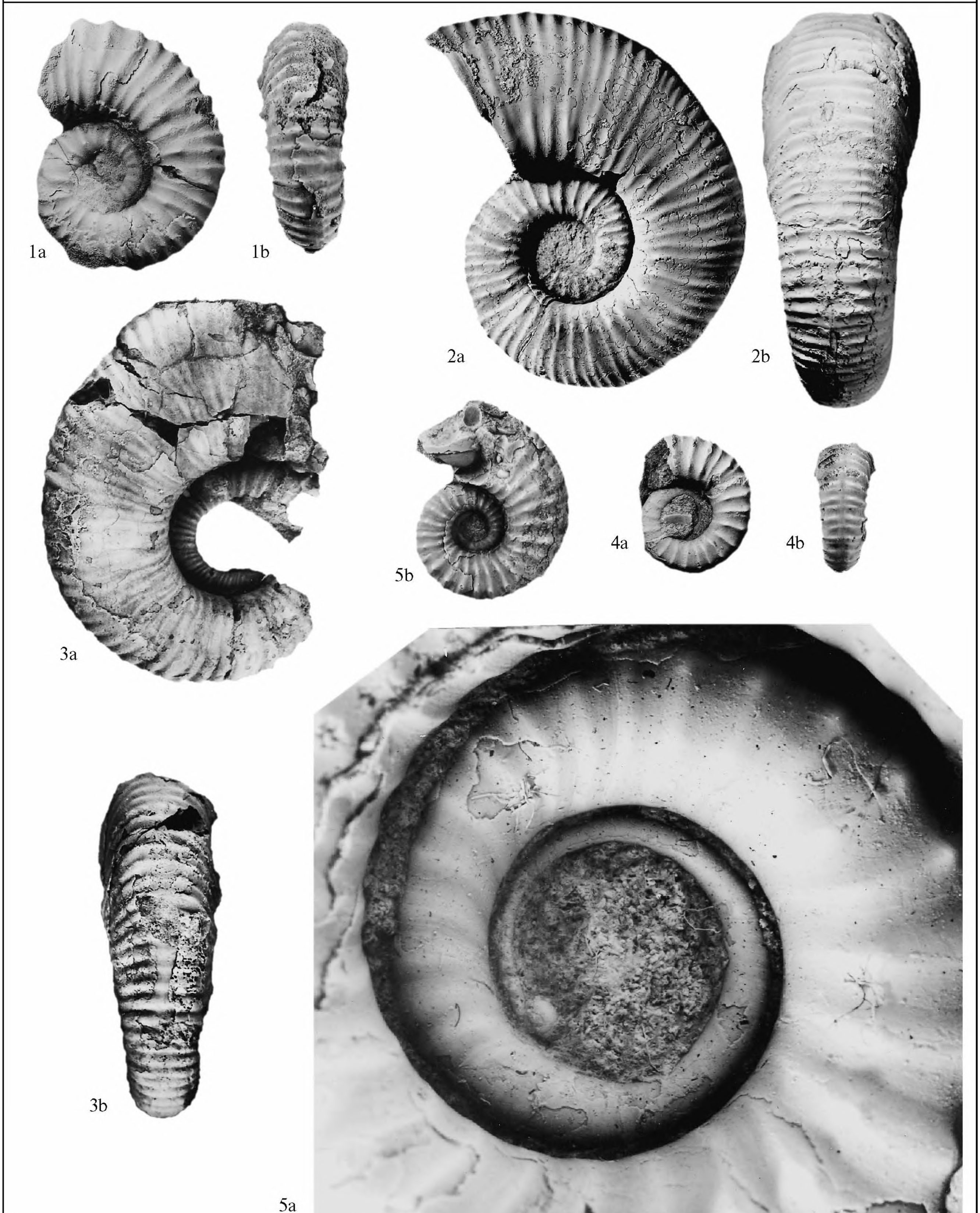
Plate 30, figs. 1–5

Luppovia dostshanensis: Kakabadze et al., 1978a, p. 84, p. 86, figs. 1–5.

Holotype. Museum of the Geological Institute of the National Academy of Sciences of Georgia (GIN Georgia), no. 1/97. Mangyshlak, East Karatau, vicinity of the Doshchan cemetery; Middle Aptian, *Epicheloniceras subnodosocostatum* Zone. Designated by the authors of the species.

Shell shape. The protoconch (Figs. 86a, 86b) is 0.53 mm wide and 0.46 mm in diameter, has a high median saddle. The primary constriction at the end of the first whorl delineates the embryonic shell, which reaches 0.8 mm in diameter. The short straight (baculitiform) tube (Fig. 86c, Pl. 30, fig. 1a) immediately follows the constriction. The second whorl with an umbilical perforation is in contact with the first whorl

Plate 29



or approaches it very closely (Fig. 86d). The following two–three weakly contacting whorls terminate in the shaft. In these whorls, the venter and flanks become flattened and a concave zone appears on the inner side because of the developing whorl overlap. The shoulder is steep. The umbilical wall is high and almost vertical.

The cross section of the shell clearly shows the caecum and a long prosiphon (Fig. 87). The siphuncle is originally almost central.

The cross section noticeably narrows within the first whorl and, at the transition to the straight shaft, is fundamentally changed from a low crescentic to oval and rounded (Fig. 88). The whorl cross section of the planispiral part is broadly trapezoid, becoming subquadrate in the straight part.

The shell is heteromorphic. An umbilical perforation is present between the first and second whorls; subsequent whorls are weakly contacting. The terminal part of the shell uncoils to form a shaft.

D i m e n s i o n s i n m m a n d r a t i o s:

Specimen GIN Georgia, no.	Dm	WH	WW	UW	WH/Dm	WW/Dm	UW/Dm
4/97	25.4	9.8	10.3	11.0	0.34	0.40	0.43
1/97 holotype	28.0	10.8	12.2	11.0	0.38	0.43	0.39
3/97	32.3	11.3	13.2	12.5	0.34	0.40	0.39
2/97	30.0	12.0		12.5	0.40		0.41
10/97	29.0	12.3	15.0	11.5	0.42	0.51	0.39

O r n a m e n t a t i o n. The third whorl possesses thin singular ribs, with very rapidly appearing three pairs of tubercles: originally ventrolateral and lateral, later umbilical. The ornamentation gradually increases, including the straight part of the whorl. All three pairs of tubercles are well developed. The ventrolateral tubercles are better developed. Closer to the shaft, some ribs branch off the lateral tubercles. The ventrolateral tubercles are present on both branches of the ribs. On the shaft, some ribs lack umbilical tubercles. On the flanks and venter, the ribs pass straight and, on the inner side, they are thin and form a sinusoidal forward bend.

S u t u r e (Fig. 89). The suture is studied in detail in specimen GIN Georgia, no. 7/97. The prosuture is bilobed, the primary suture is five-lobed; the smallest first umbilical lobe (U^1) disappears at the end of the first whorl. Further complication of the suture occurs through the dissection of the existing elements. The last suture is given for specimen GIN Georgia, no. 1/97. It is also relatively simple. The umbilical and

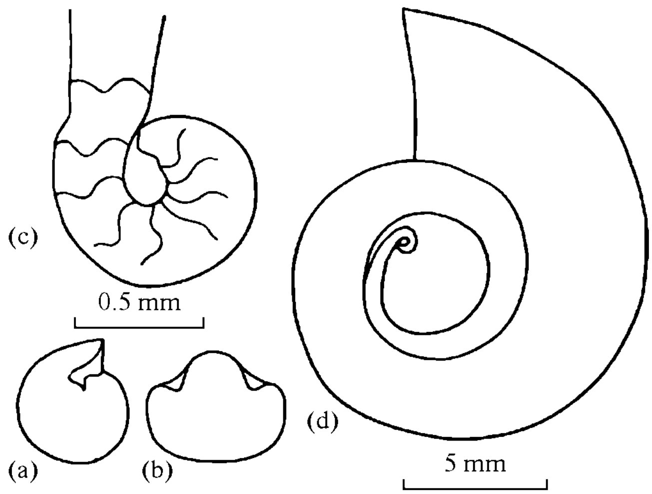


Fig. 86. Morphogenesis of the shell of *Luppovia dostshanensis* Bogdanova, Kakabadze et I. Michailova: (a–c) specimen no. GIN Georgia, no. 7/97: (a, b) protoconch; (c) first whorl and beginning of the shaft; (d) specimen no. GIN Georgia no. 5/97, arrangement of the whorls; Great Balkhan, Bordzhakly well; Middle Aptian, *Epicheloniceras subnodosocostatum* Zone.

inner lateral lobes are trifid; relatively deep dorsal lobe and bifid ventral lobe are separated from each other by the bifid saddles of equal height.

C o m p a r i s o n. A comparison with *L. adjiderensis* is given in the description of this species.

O c c u r r e n c e. Kazakhstan (Mangyshlak), Turkmenistan (Tuarkyr, Great Balkhan); Middle Aptian, *Epicheloniceras subnodosocostatum* Zone.

M a t e r i a l. Seven well-preserved specimens, with the initial whorls in three specimens remained. Mangyshlak, Karatau Range, vicinity of the Doshchan cemetery (GIN Georgia, no. 1/97); Great Balkhan, Utuludzha well (GIN Georgia, nos. 2/97, 3/97, 5/97, 10/97), Bordzhakly well (GIN Georgia, nos. 6/97, 7/97, PIN, no. 5265/271); Middle Aptian, *Epicheloniceras subnodosocostatum* Zone.

***Luppovia adjiderensis* Bogdanova, Kakabadze et I. Michailova, 1978**

Plate 30, figs. 6 and 7

Luppovia adjiderensis Kakabadze et al., 1978a, p. 87, p. 86, figs. 6 and 7.

H o l o t y p e. GIN Georgia, no. 9/97, western Kopet Dagh, Adzhidere River; Middle Aptian, *Epicheloniceras subnodosocostatum* Zone. Designated by the authors of the species. Unfortunately, the provenance

E x p l a n a t i o n o f P l a t e 29

Figs. 1–5. *Caspianites wassiliewskyi* (Renngarten, 1926); specimens: (1) TsNIGR Museum no. 3/11276; Great Balkhan, Utuludzha well; Middle Aptian, *Epicheloniceras subnodosocostatum* Zone; (2) TsNIGR Museum, no. 1/11276; Tuarkyr, Umokdere gorge; the same age; (3) PIN, no. 5265/272; Aktyubinsk Region, village of Turtkul'; the same age; (4) TsNIGR Museum, no. 2/11276; Great Balkhan, Bordzhakly well; the same age; (5) TsNIGR Museum, no. 2/11288: (5a) lateral view, ×8, (5b) lateral view (four-fifths of natural size); Tuarkyr, Babashi well; the same age.

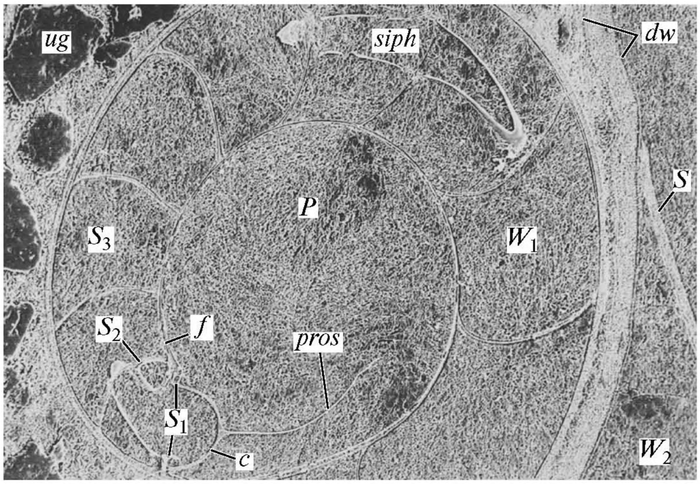


Fig. 87. *Luppovia* sp., MZ MGU, no. 12153, protoconch and first whorl with prosiphon, caecum and siphuncle, ×20. Designations: (*P*) protoconch; (W_1) first whorl; (W_2) second whorl; (*ug*) umbilical gap; (*siph*) siphon; (*dw*) dorsal wall; (*S*) septum; (S_1) proseptum; (S_2) primary septum; (S_3) third septum; (*f*) flange; (*pros*) prosiphon; (*c*) caecum (after Doguzhaeva and Mikchailova, 1982).

of the holotype in the explanation to the plates in the paper published in 1978 (Tuarkyr, Mansu well) is indicated incorrectly.

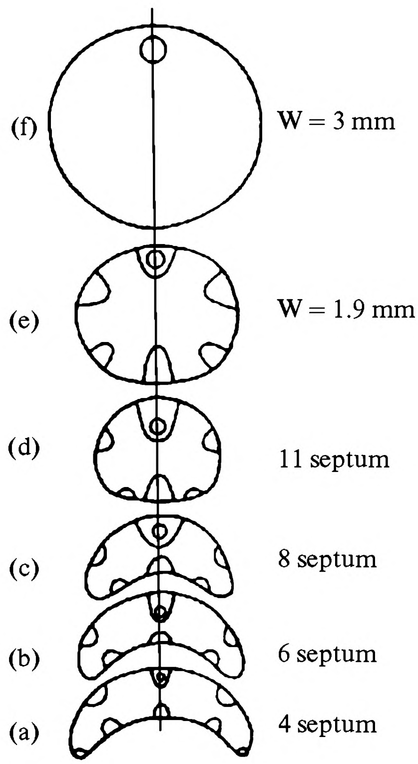


Fig. 88. Morphogenesis of the shell cross section in *Luppovia dostshanensis* Bogdanova, Kakabadze et I. Michailova: (a–c) specimen GIN Georgia, no. 7/97: (a–d), ×24, (e) ×8, (f) ×6; Great Balkhan, Bordzhakly well; Middle Aptian, *Epicheloniceras subnodosocostatum* Zone.

S h e l l s h a p e. The shell is planispiral; the second whorl is not contacting. The whorls are low, slowly expanding in height. The cross section of the second whorl is broadly ellipsoidal and, in succeeding whorls, it becomes suboctogonal; the whorl width exceeds the height. The umbilicus is wide, stepped. The umbilical wall is steep.

D i m e n s i o n s i n m m a n d r a t i o s:

Specimen GIN Georgia, no.	Dm	WH	WW	UW	WH/Dm	WW/Dm	UW/Dm
9/97 holotype	31.0	11.0	12.6	13.2	0.35	0.40	0.42

O r n a m e n t a t i o n. Up to 2.5–3.0 mm of height, the shell is smooth. Singular ribs appear in the third whorl. Further on, at the whorl height of about 4.5 mm, the ventrolateral tubercles appear and, slightly later, umbilical tubercles appear as well. As the shell grows, the tubercles, especially ventrolateral ones, become stronger. The ribs are mostly singular; from early to later whorls, they become more widely spaced. On the venter, ribs are weaker between the ventrolateral tubercles. The ribs branch very rarely. The holotype has only one bifid rib. The ribs branch from the lateral tubercles; the anterior branch is strong, with ventrolateral tubercles, and the posterior branch is thinner and has no tubercles.

S u t u r e. The suture is traced from the second uncontacting whorl; therefore, Fig. 90 shows four rather than five lobes. Further changes generally conform to those observed in *L. dostshanensis*. The saddles at the same time become bifid and, after that, the umbilical lobe acquires two lateral digits. The trifid umbilical lobe remains later in ontogeny. The inner lateral lobe flattens at the base and is subdivided by the

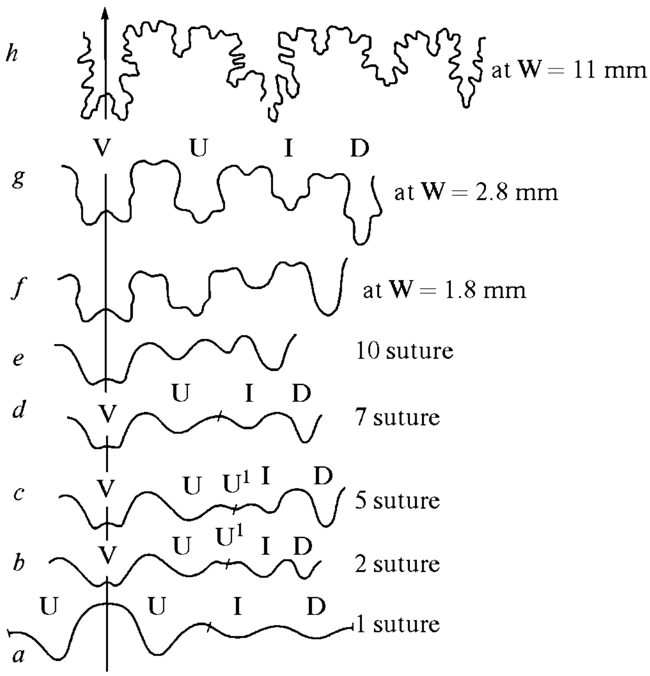


Fig. 89. Morphogenesis of the suture of *Luppovia dostshanensis* Bogdanova, Kakabadze et I. Michailova: (*a–g*) specimen GIN Georgia, no. 7/97, (*h*) holotype GIN Georgia, no. 1/97,: (*a–e*) ×77, (*f*, *g*) ×29, (*h*) ×17; Great Balkhan, Bordzhakly well; Mangyshlak, vicinity of the Doshchan cemetry; Middle Aptian, *Epicheloniceras subnodosocostatum* Zone.

secondary saddle into two relatively equal parts. The dorsal lobe is acuminate and relatively deep.

C o m p a r i s o n. This species considered is distinguished from *L. dostshanensis* by the lower whorls, ellipsoidal rather than subtrapezoid outline of the cross sections, the more widely spaced singular ribs, almost complete absence of rib branching, and the bifid inner lateral lobe.

O c c u r r e n c e. Turkmenistan (Tuarkyr, Kopet Dagh); Middle Aptian, *Epicheloniceras subnodosocostatum* Zone.

M a t e r i a l. Two well-preserved planispiral specimen. Kopet Dagh, Adzhidere River (GIN Georgia, no. 9/97), Tuarkyr, Umokdere gorge (PIN, no. 5265/281); Middle Aptian, *Epicheloniceras subnodosocostatum* Zone.

Genus *Pseudoaustraliceras* Kakabadze, 1981

Pseudoaustraliceras: Kakabadze, 1981, p. 114; Wright et al., 1996, p. 216; Etayo-Serna, 1983, p. 7; Kakabadze and Hoedemaeker, 2004, p. 72.

T y p e s p e c i e s. *Crioceras ramososeptatum* Anthula, 1899 [(Anthula, 1899, p. 127 (73)]; Dagestan, village of Ashilta, Middle Aptian. Designated by the author of the genus.

S h e l l s h a p e. The shell is medium-sized and large, planispiral, with uncontacting whorls in early whorls and weakly contacting in the later whorls (Pl. 36, fig. 1; Pl. 37, fig. 1).

O r n a m e n t a t i o n. The ornamentation is represented by primary ribs, possessing up to three rows of tubercles (umbilical, ventrolateral, and ventral) and thin intercalary ribs, one rib between two primaries.

S u t u r e. The suture is ancyloceratid (Fig. 91). The ventral lobe (V) is deep, bifid; the umbilical (U), inner lateral (I), and dorsal (D) lobes are trifid, relatively symmetrical. The umbilical lobe is the largest and deepest and the inner lateral lobe is shallowest.

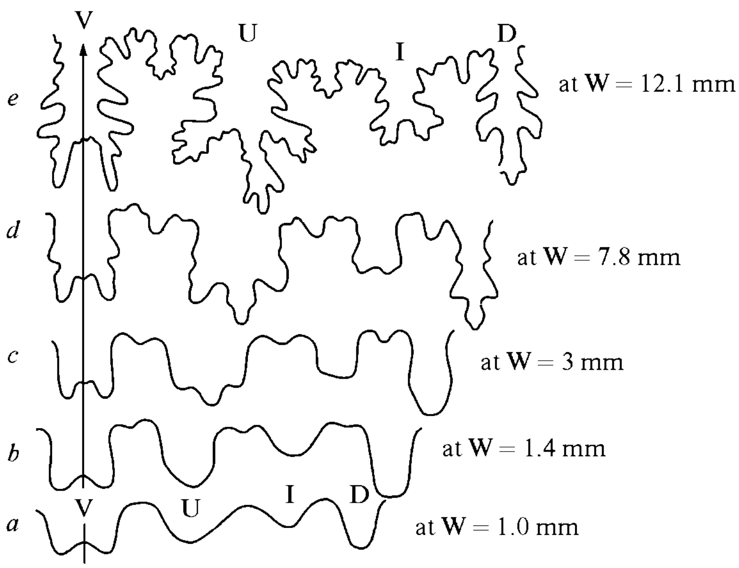


Fig. 90. Morphogenesis of the suture of *Luppovia adjiderensis* Bogdanova, Kakabadze et I. Michailova; specimen GIN Georgia, no. 9/97, holotype: (*a*) ×50; (*b*) ×40; (*c*) ×22; (*d*) ×16; (*e*) ×8; western Kopet Dagh, Adzhidere River, Middle Aptian, *Epicheloniceras subnodosocostatum* Zone.

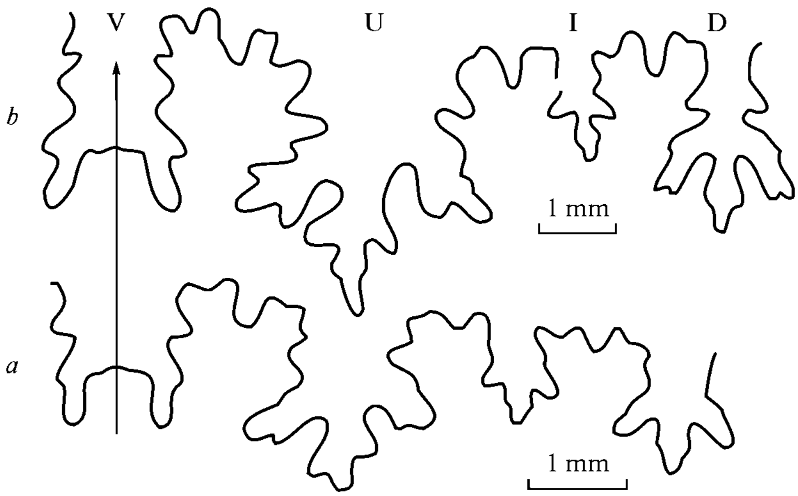


Fig. 91. Suture of *Pseudoaustraliceras pavlowi* (Wassiliewskyi, 1908); specimen PIN, no. 5265/280; Great Balkhan, Bordzhakly well.

The saddles are bifid, the external saddle (V/U) is highest and widest and the inner saddle (I/D) is lowest and narrowest.

S p e c i e s c o m p o s i t i o n. This genus includes *P. ramososeptatum* (Anthula, 1899), *P. pavlowi* (Wassiliewsky, 1908), *P. tshaltubense* (Rouchadze, 1932), *P. caucasicum* Kakabadze, 1981, *P. austral* (Waagen, 1873), *P. ramboulai* (Collignon, 1962), *P. hirtzi* (Collignon, 1962), *P. columbiae* (Basse, 1928). Russia (northern Caucasus, Dagestan), Turkmenistan, Georgia, Bulgaria, Hungary, Madagascar, India, and others.

C o m p a r i s o n. This genus differs from the similar genus *Australiceras* in the larger ventrolateral tubercles, which appear earlier than the umbilical and ventral tubercles.

R e m a r k s. Rouchadze (1933) described and figured a few specimens of Aptian *Ancyloceras* cf. *pavlowi* Wass., *A. ramososeptatum* Anthula and the new species *A. tshaltubense*. Later, Eristavi (1955, p. 113) published data on these species, retaining the generic name *Ancyloceras* and placing them into a separate group (p. 133) *Ancyloceras pavlowi* Wass., which, apart from the above species, included *A. ramososeptatum* Anth. and *A. tshaltubense*. At the same time, he noted that this group is intermediate between the genus *Ammonitoceras* and the *Ancyloceras abichi* group Anth. The stratigraphic position of this group in Georgia was indicated as the Lower Aptian.

Casey (1960, p. 44) included *"Crioceras" ramososeptatum* Anthula and *"Crioceras" austral* Waagen (described from India) in the genus *Australiceras,* proposed by Whitehouse in 1926.

***Pseudoaustraliceras pavlowi* (Wassiliewskyi, 1908)**

Plate 19, figs. 3 and 4; Plate 32, figs. 1–5; Plate 33, fig. 1; Plate 34, fig. 1; Plate 35, fig. 1

Crioceras Pavlowi: Wassiliewskyi, 1908a, p. 46, pl. 3, figs. 1a, 1b, and 1c, text-fig. 5.

Ammonitoceras pavlowi: Luppov et al., 1949, p. 251, pl. 74, figs. 4a, 4b, and 4c, text-fig. 81 (reproduced Wassiliewskyi's illustrations); Drushchits, 1960b, p. 294, pl. 38, figs. 2a and 2b; pl. 39, fig. 2.

Pseudoaustraliceras pavlowi: Kakabadze, 1981, pl. 18, fig. 4; Kakabadze and Hoedemaeker, 1997, p. 69, pl. 9, figs. 2a–2c; 2004, pl. 66, fig. 1; Bogdanova and Mikhailova, 2005, pl. 7, figs. 3a and 3b.

Pseudoaustraliceras ramososeptatum: Kakabadze, 1981, pl. 16, figs. 2 and 3.

H o l o t y p e. TsNIGR Museum, no. 12/11320, specimen figured by Wassiliewskyi (1908a, pl. 3, fig. 1); Middle Aptian; vicinity if Saratov, Guselka River.

S h e l l s h a p e. The shell is medium-sized with slightly touching whorls at the medium and later stages. The cross section is low, oval between the tubercles and rounded angular, cutting through the tubercles.

E x p l a n a t i o n o f P l a t e 30

Figs. 1–5. *Luppovia dostshanensis* Bogdanova, Kakabadze et I. Michailova, 1978; specimens: (1) PIN, no. 5265/271; Great Balkhan, Bordzhakly well, Middle Aptian, *Epicheloniceras subnodosocostatum* Zone; (2) GIN Georgia, no. 10/97; Great Balkhan, Utuludzha well; the same age; (3) holotype GIN Georgia, no. 1/97; Mangyshlak, vicinity of the Doshchan cemetery; the same age; (4) GIN Georgia, no. 3/97; (5) GIN Georgia, no. 2/97; Great Balkhan, Utuludzha well, the same age.

Figs. 6 and 7. *Luppovia adjiderensis* Bogdanova, Kakabadze et I. Michailova, 1978; (6) holotype GIN Georgia, no. 9/97; Kopet Dagh, Adzhidere; Middle Aptian, *Epicheloniceras subnodosocostatum* Zone; (7) specimen GIN Georgia, no. 8/97, second and third whorls, ×10; Great Balkhan, Kirov collective farm; the same age.

Plate 30

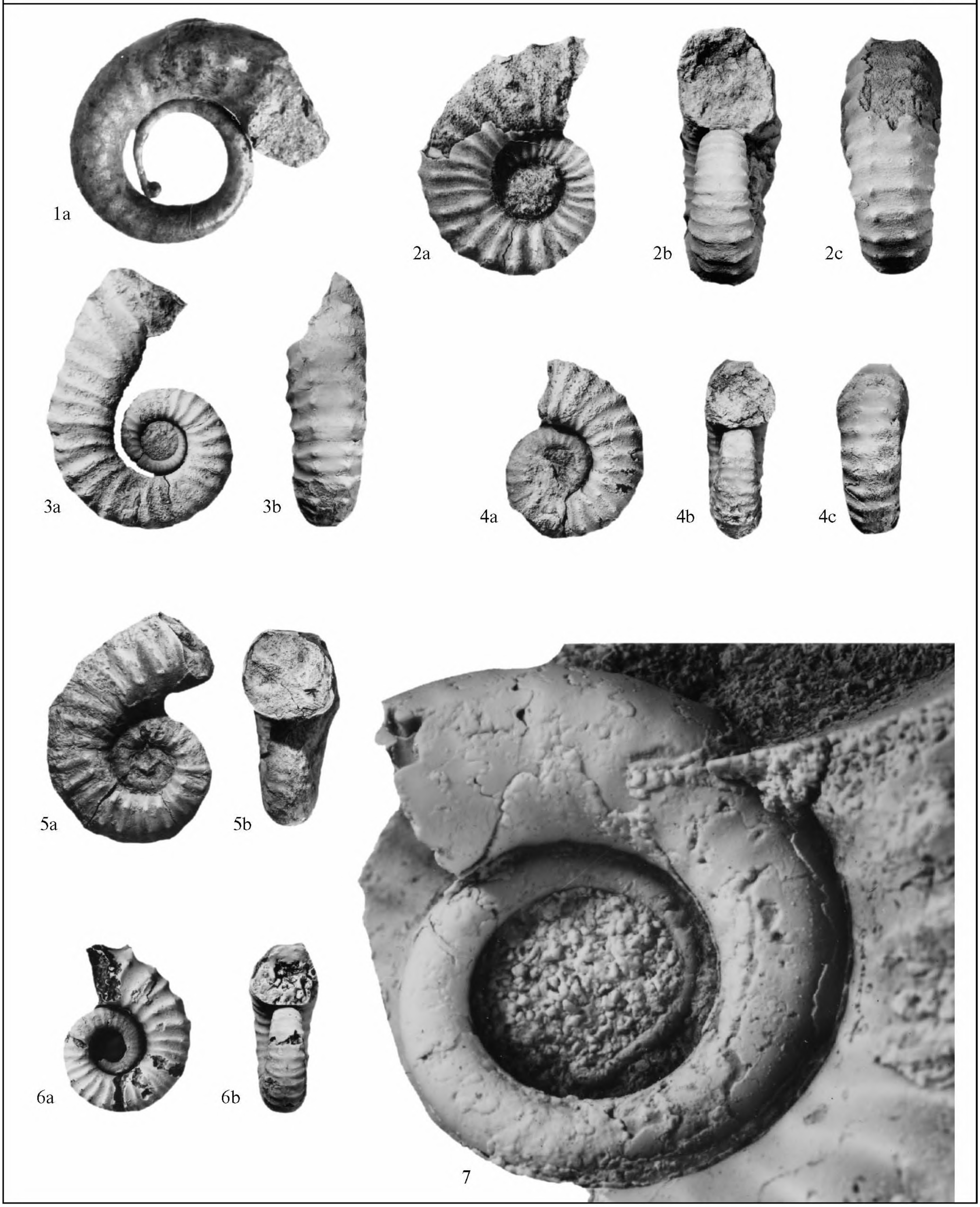
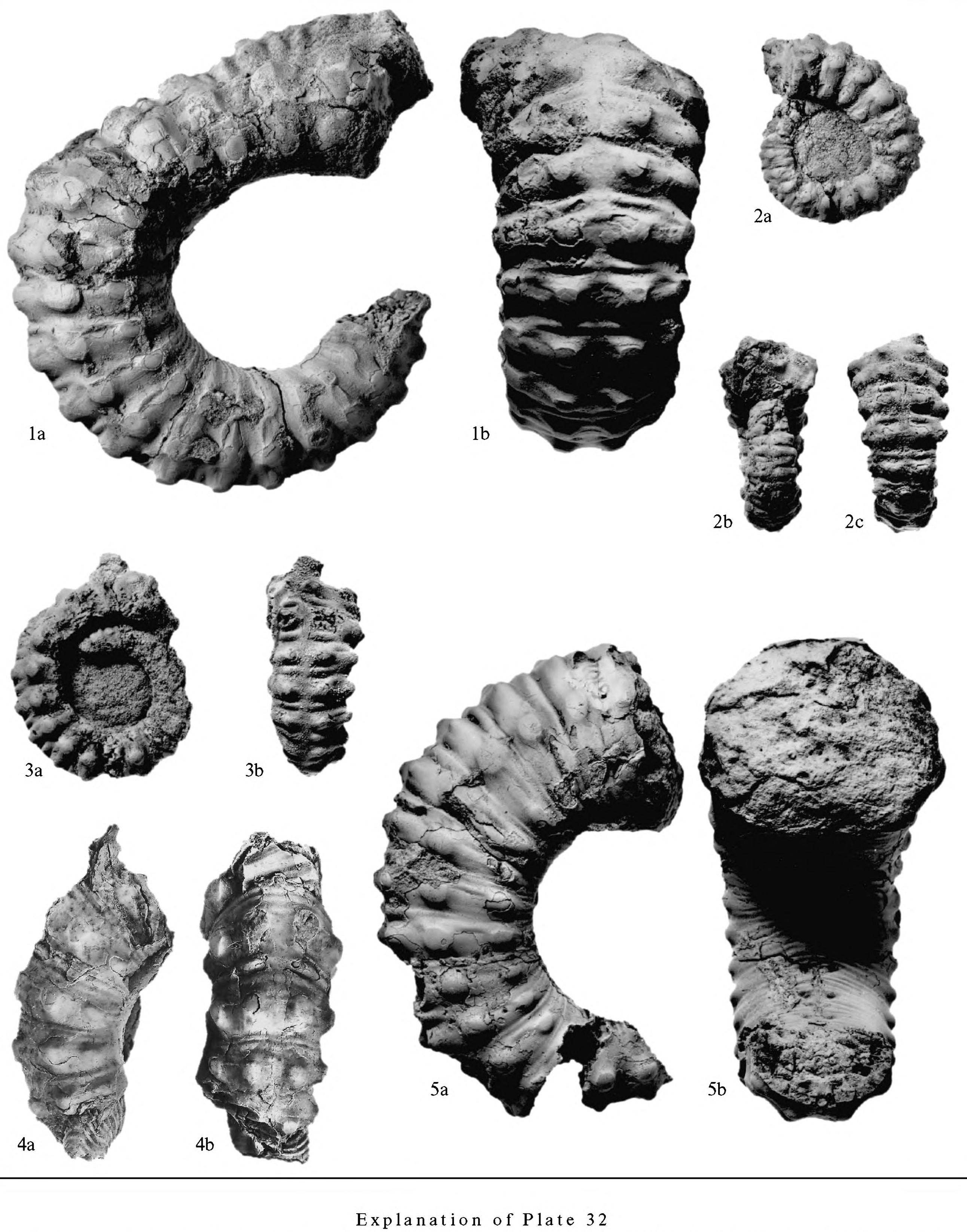


Plate 31

Explanation of Plate 31

Fig. 1. *Parahoplites sjogreni* (Anthula, 1899); specimen MZ MGU, no. 1/101; Dagestan, village of Butri, Middle Aptian, *Parahoplites melchioris* Zone.

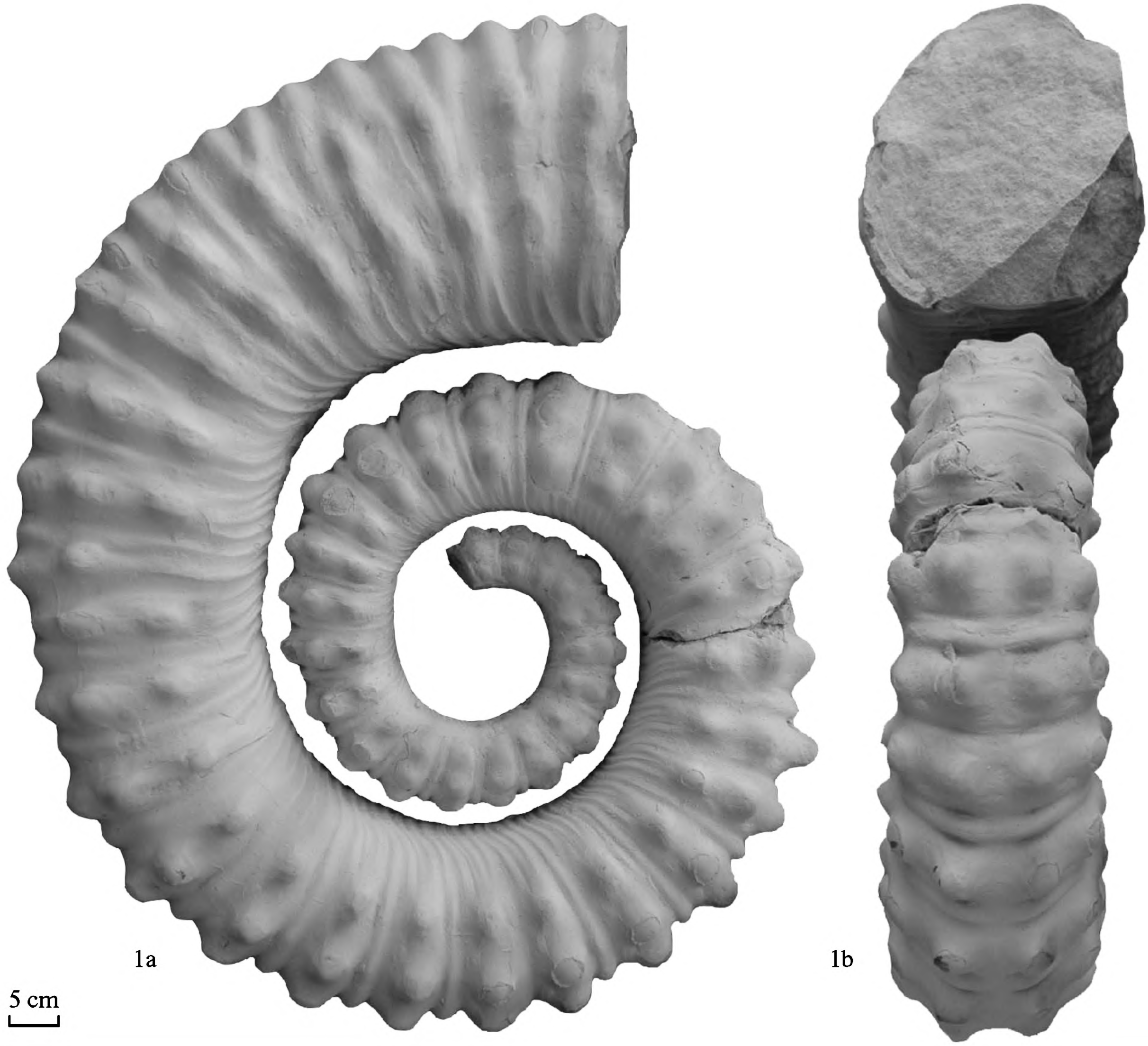
Plate 32



Explanation of Plate 32

Figs. 1–5. *Pseudoaustraliceras pavlowi* (Wassiliewsky, 1908); specimens: (1) PIN, no. 5265/266; (2) PIN, no. 5265/267; (3) PIN, no. 5265/268; Great Balkhan, Bordzhakly well; Middle Aptian; (4) MZ MGU, no. 40/96; Ulyanovsk, Solov'ev gully, Lower Aptian; (5) PIN, no. 5265/265; Kuba Dagh, Yangadzha Station, Middle Aptian.

Plate 33



Explanation of Plate 33

Fig. 1. *Pseudoaustraliceras pavlowi* (Wassiliewsky, 1908); specimen PIN, no. 5265/287; northwestern Caucasus, Belaya River; Middle Aptian.

Dimensions in mm and ratios:

Specimen PIN, no.	Dm	WH	WW	UW	WH/Dm	WW/Dm	UW/Dm
5265/270	26.2	8.7	13.7	15.3	0.33	0.52	0.58
5265/267	33.1	12.7			0.38		
5265/268	33.4						
5265/269		20.9	22.3				
5265/266	75.2	30.0	37.4	33.1	0.40	0.50	0.44
5265/265	87.1	34.7	41.2	36.5	0.40	0.47	0.41

Ornamentation. The primary ribs have three rows of tubercles. The largest ventrolateral tubercles are rounded and blunt, but when intact, they are acuminate (this is observed when the shell is enclosed in the matrix). The ventral tubercles become elongated to the end of the last whorl. The tubercles occurring near the umbilical shoulder are the smallest and also somewhat elongated.

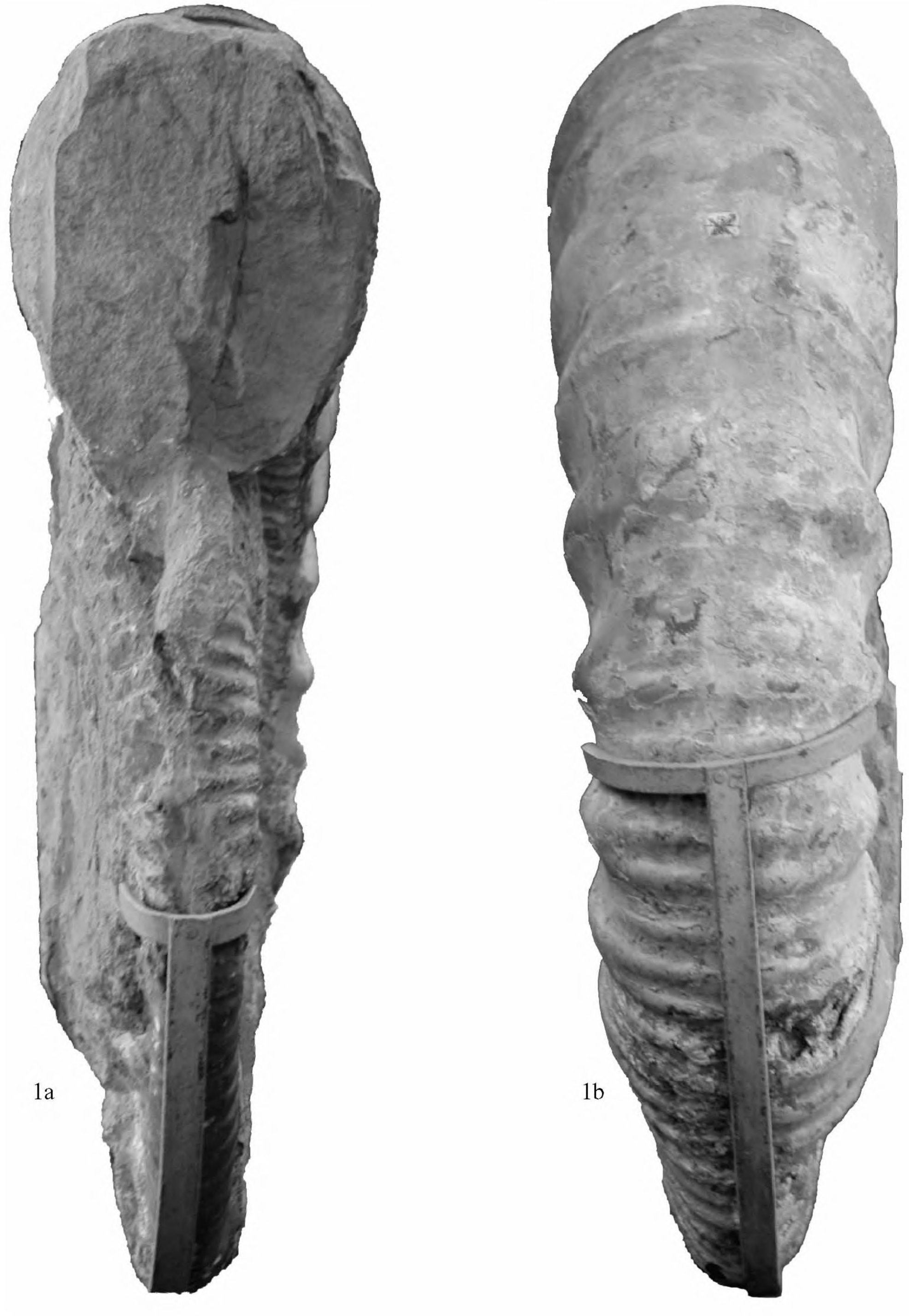
Thin intercalary ribs are located anterior to the primaries, extending from the lateral tubercles. In specimen PIN, no. 5265/265, they are weak but observed to the lower row of tubercles. On the inner side, all ribs are thin, uniform, and numerous. The space equal to the distance between the primary ribs on the venter has 5–7 auxiliary ribs. In the preceding whorl (specimen PIN, no. 5265/267, Dm = 33.1 mm), the ornamenta-

Plate 34

Explanation of Plate 34

Fig. 1. *Pseudoaustraliceras pavlowi* (Wassiliewsky, 1908); specimen TsNIGR Museum no. 8/632; northwestern Caucasus, Belaya River; Middle Aptian.

Plate 35



Explanation of Plate 35

Fig. 1. *Pseudoaustraliceras pavlowi* (Wassiliewsky, 1908); specimen TsNIGR Museum no. 8/632; northwestern Caucasus, Belaya River; Middle Aptian.

tion remains the same. At the shell diameter less than 24.0 mm, the ventral tubercles decrease and disappear (specimen no. 9302).

Suture. See the description of the genus above.

Comparison. The species considered is distinguished from *P. caucasicum* Kakabadze, 1981 by the presence of only one intercalary rib instead of three or four intercalary ribs. It differs from the more similar *P. ramososeptatum* (Anthula, 1899) at the late stages in the retaining the described type of ornamentation in *P. pavlowi* and in the transition to the smooth and closely spaced ribs in *P. ramososeptatum* (Pl. 36, fig. 1; Pl. 37, fig. 1).

Remarks. The type species *P. ramososeptatum* is found in Russia and adjacent countries considerably less frequently than *P. pavlowi*. Apart from Anthula's specimen from Ashilty (Dagestan), there is only one specimen figured and described by Drushchits (1960b, p. 294, pl. 31, fig. 1) from the northern Caucasus (Belaya River).

Occurrence. Russia (northern Caucasus, Dagestan, Volga Region near Ulyanovsk), Kazakhstan (Mangyshlak), Turkmenistan (Great Balkhan, Kuba Dagh, Kopet Dagh), Colombia.

Material. Seven moderately and well-preserved specimens. Volga Region near Ulyanovsk: Ulyanovsk, Solov'ev gully (MZ MGU, no. 40/96, collected by G.K. Kabanov), upper part of the Lower Aptian; northern Caucasus, Urukh River (PIN, no. 5265/270); Great Balkhan: Bordzhakly well (PIN, nos. 5265/266, 5265/267, 5265/268); Kuba Dagh: Yangadzha (PIN, no. 5265/265); Kopet Dagh, Temen Spring (PIN, no. 5265/269); Middle Aptian.

Suborder Haploceratina Besnossov et Michailova, 1983

Shell monomorphic, from smooth to strongly ornamented. Primary suture five-lobed (VUU^1ID). Suture becoming more complex through development of new umbilical lobes. Sometimes, inner lateral lobe divided, which in general not characteristic of this suborder. Dorsal lobe trifid, rarely bifid. Distinguished from suborder Ammonitina by trifid umbilical lobe (Fig. 92). Four superfamilies: Sonniniaceae Buckman, 1892, Oppeliaceae Douville, 1890, Haplocerataceae Zittel, 1884, and Acanthocerataceae Hyatt, 1900 (Fig. 93). Middle Jurassic–Cretaceous (Bajocian–Maastrichtian).

Superfamily Haploceratoidea Zittel, 1884

Haplocerataceae: Arkell et al., 1957, p. L271; Luppov and Drushchits, 1958, p. 82; Wright et al., 1996, p. 9.

Diagnosis. Shell from discoidal to weakly inflated. Whorl cross section oval, varying in width. Venter narrowly rounded with sharp keels (one–three). Ribs sickle-shaped or almost sickle-shaped, sometimes absent. Often with spiral grooves or ridges. Ornamentation decreasing or absent on body chamber.

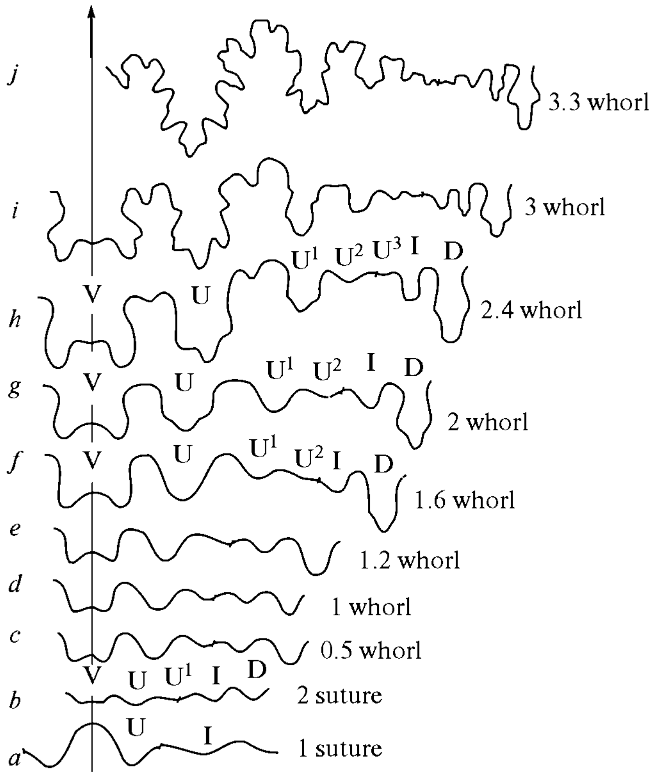


Fig. 92. Morphogenesis of the suture of *Aconeceras (Aconeceras) trautscholdi* Sinzow; specimen PIN, no. 5265/ 1479: (*a–f*) ×42, (*g, h*) ×32, (*i, j*) ×12; Dagestan, village of Tsudakhar, Lower Aptian (after Mikhailova, 1983).

Remarks. Luppov and Drushchits (1958) included in this superfamily five families: Strigoceratidae Buckmann, 1924, Haploceratidae Zittel, 1884, Oppeliidae H. Douville, 1890, Phlycticeratidae Spath, 1928, and Mazapilitidae Spath, 1928. Aconecarids were assigned at that time to the superfamily Desmocerataceae, as was initially proposed by Spath (1923). Wright et al. (1996) assigned three families, Haploceratidae Zittel, 1884, Oppeliidae H. Douvillé, 1890, and Binneytidae Reeside, to this superfamily. The subfamily Aconeceratinae was assigned to the family Oppeliidae. From the Middle Jurassic (Aalen) to Late Cretaceous (Early Santonian); globally, but mostly in the basins of the Tethyan Paleobiogeographical Realm.

The origin of the superfamily is uncertain (Wright et al., 1996, p. 9).

Family Aconeceratidae Spath, 1923

Aconeceratidae: Luppov and Drushchits, 1958, p. 109; Casey, 1961a, p. 119; Riccardi et al., 1987, p. 122.

Diagnosis. Narrow, often oxyconic shells. Whorls high, almost completely overlapping, with narrow venter; keel acute or slightly rounded, smooth or serrated. Ornamentation composed of weak sickle-

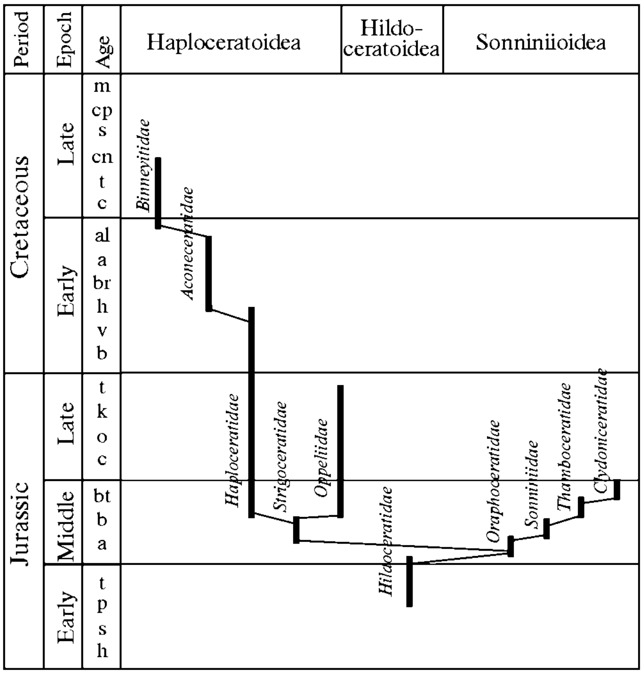


Fig. 93. Phylogenetic reconstruction of the suborder Haploceratina (after Beznossov and Mikhailova, 1991).

shaped ribs, sometimes almost indiscernible. Saddles broad, bifid; several auxiliary lobes present.

C o m p o s i t i o n. The family includes the following genera: *Protaconeceras* Casey, 1954 from the Upper Hauterivian, France, England, Argentina; *Aconeceras* Hyatt, 1903 from the Upper Barremian–Lower Albian, Europe, Central Asia, Greenland, Madagascar, South Africa, Australia; *Doridiscus* Casey, 1961 from the Lower Aptian, England; *Nothodiscus* Casey in Collignon, 1962 from the Upper Aptian, Madagascar; *Falciferella* Casey, 1954 from the Middle and Upper Albian, England; *Naramoceras* McNamara, 1985 from the Middle and Upper Albian, Australia; *Koloceras* Riccardi, Aguirre Urreta, Medina, 1987 from the Upper Albian, Argentina, Angola.

C o m p a r i s o n a n d r e m a r k s. Appearance, composition, similarity, and differences of aconeceratids from members of the closely related families or higher taxa, taxonomy, and distribution were discussed in detail by Casey (1961a, pp. 119–122) and, later, by Argentinian authors (Riccardi et al., 1987, pp. 122–123). In this work, we accept the separate family Aconeceratidae.

Genus *Aconeceras* Hyatt, 1903

Aconeceras: Arkell et al., 1957, p. L286; Luppov and Drushchits, 1958, p. 109; Casey, 1964, p. 123; Wright et al., 1996, p. 14; Riccardi et al., 1987, p. 130.

T y p e s p e c i e s. *Ammonites nisus* d'Orbigny, 1841 (d'Orbigny, 1840–1842, p. 184); Upper Aptian (Gargasian), France. Designated by Casey (1961a, p. 123).

D i a g n o s i s. Involute, oxyconic shells with smooth or serrated keel, entire or perforated; flanks flattened or weakly convex, with sharp umbilical shoulder; smooth or with radial sickle-shaped thin or wide ribs. Suture: $VUU^1U^2:U^3ID$ (Fig. 92). Ventral lobe wide, short (higher than adjacent umbilical U lobe). Succeeding umbilical lobes distinctly serrated and, near umbilical shoulder, with many additional lobes. According to Mikhailova (1983, p. 156), sutural morphogenesis in representatives of subgenus *Sanmartinoceras* clearly distinguished from that of Desmoceratoidea and different from that of Haploceratoidea, hence, we included aconeceratitids in the Haploceratidae (Fig. 94).

C o m p o s i t i o n. Subgenera: *Aconeceras:* Aptian, France, England, Russia, Turkmenistan; *Sanmartinoceras* Bonarelli, 1921, Upper Aptian–Lower Albian, Europe, Greenland, Madagascar, South Africa, South America, Australia; *Sinzovia* Sazonova, 1958, Lower Aptian–Lower Albian, Europe, Russia, Turkmenistan, Madagascar, Africa, South America, Australia; *Theganoceras* Whitehouse, 1926, Aptian, England, Germany, South Africa, Antarctica; *Gyaloceras* Whitehouse, 1927, Upper Aptian–?Lower Albian, England.

C o m p a r i s o n. The genus is distinguished from *Protaconeceras* Casey, 1954 by the acute and, hence, triangular whorl cross section, the less convex flanks and more strongly dissected suture. It differs from *Doridiscus* Casey, 1961 in the triangular whorl cross section, the sharp umbilical shoulder turned to the vertical umbilical wall, and the more complexly dissected suture.

Subgenus *Aconeceras* Hyatt, 1903

Aconeceras (Aconeceras): Wright et al., 1996, p. 14.

T y p e s p e c i e s. As in the genus.

D i a g n o s i s. Shell small, almost involute; flanks flattened; venter acute; keel low, not clearly delineated, serrated; ribs very thin, sickle-shaped, appearing late in ontogeny. Middle and Late Aptian.

S p e c i e s c o m p o s i t i o n. *Aconeceras (A.) nisus* (d'Orbigny, 1841), Aptian, France, England, Russia (Dagestan), Turkmenistan; *A. (A.) haugi* (Sarasin, 1893), Aptian, England, Germany, Russia (northern Caucasus), Turkmenistan; *A. (A.)* nov. sp. 1, Aptian (Gargasian), France.

C o m p a r i s o n. Characters distinguishing this genus from the most closely similar genus *Sinzowia* are given in the description of the latter.

Aconeceras (Aconeceras) nisus (d'Orbigny, 1841)

Plate 38, fig. 3

Ammonites nisus: d'Orbigny, 1840–1842, p. 184, pl. 55, figs. 7–9.

Oppelia nisus: Sarasin, 1893, p. 152, pl. 4, fig. 9a, pl. 5, fig. 9b, pl. 6, fig. 9c.

Aconeceras nisum: Hyatt, 1903, p. 100, pl. 12, figs. 4–6.

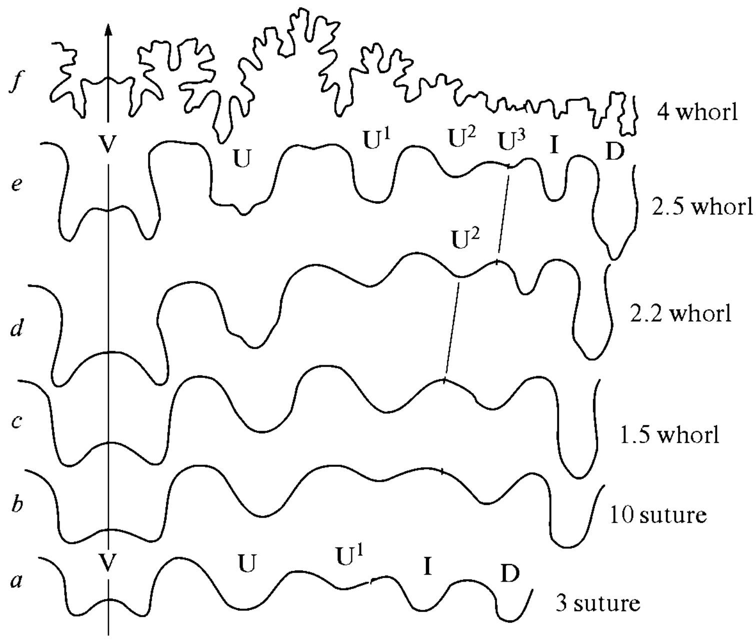


Fig. 94. Morphogenesis of the suture of *Sanmartinoceras clansayens* Egoian; northern Caucasus, Khokodz River; Late Aptian (after Mikhailova, 1978).

Aconeceras cf. *nisus:* Casey, 1961a, p. 128, text-fig. 40; Collignon, 1962, p. 31, pl. 229, fig. 973.

Aconeceras nisus: Thomel, 1980, p. 87, fig. 174.

H o l o t y p e. Specimen figured by d'Orbigny (1940–1842, p. 184, pl. 55, figs. 7–9); France, Department of Aube; Upper Neocomian.

S h e l l s h a p e. The shell is small, flattened, with rapidly expanding whorls. The venter is narrow, coronatiform; the flanks are very weakly convex. The maximum whorl width is up to the shell diameter 10 mm is in the upper region of the whorl and, then, the flanks become parallel and, at the diameter of 25 mm and more, the greatest width is nearer the umbilicus. The umbilical wall is low and vertical. The cross section is rectangular–oval, strongly elongated in height (Fig. 95). The umbilicus is moderately narrow to Dm = 10 mm and narrow and stepped at larger diameters.

D i m e n s i o n s i n m m a n d r a t i o s:

Specimen TsNIGR Museum, no.	Dm	WH	WW	UW	WH/Dm	WW/Dm	UW/Dm	WW/WH
195/10367	20.0	11.0	4.8	2.2	55	0.24	0.11	0.44
197/10367	16.7	8.8	4.1	2.8	52	0.24	0.17	0.44
199/10367	10.3	4.8	2.8	2.5	46	0.27	0.24	0.60
200/10367	10.0	4.7	2.8	2.5	47	0.28	0.25	0.60

O r n a m e n t a t i o n. The shell surface almost lacks radial ornamentation, except for in some specimens with very thin sickle-shaped striae, invisible with the naked eye. An acute, finely serrated keel appears in the middle of the venter at Dm = 5–7 mm.

C o m p a r i s o n. Our specimens are distinguished from the specimen figured by d'Orbigny by the presence of a very thin sickle-shaped striation and by that they are very similar to the specimen figured by Sarasin

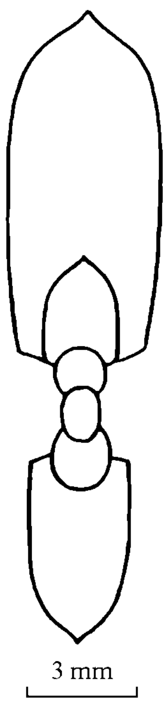
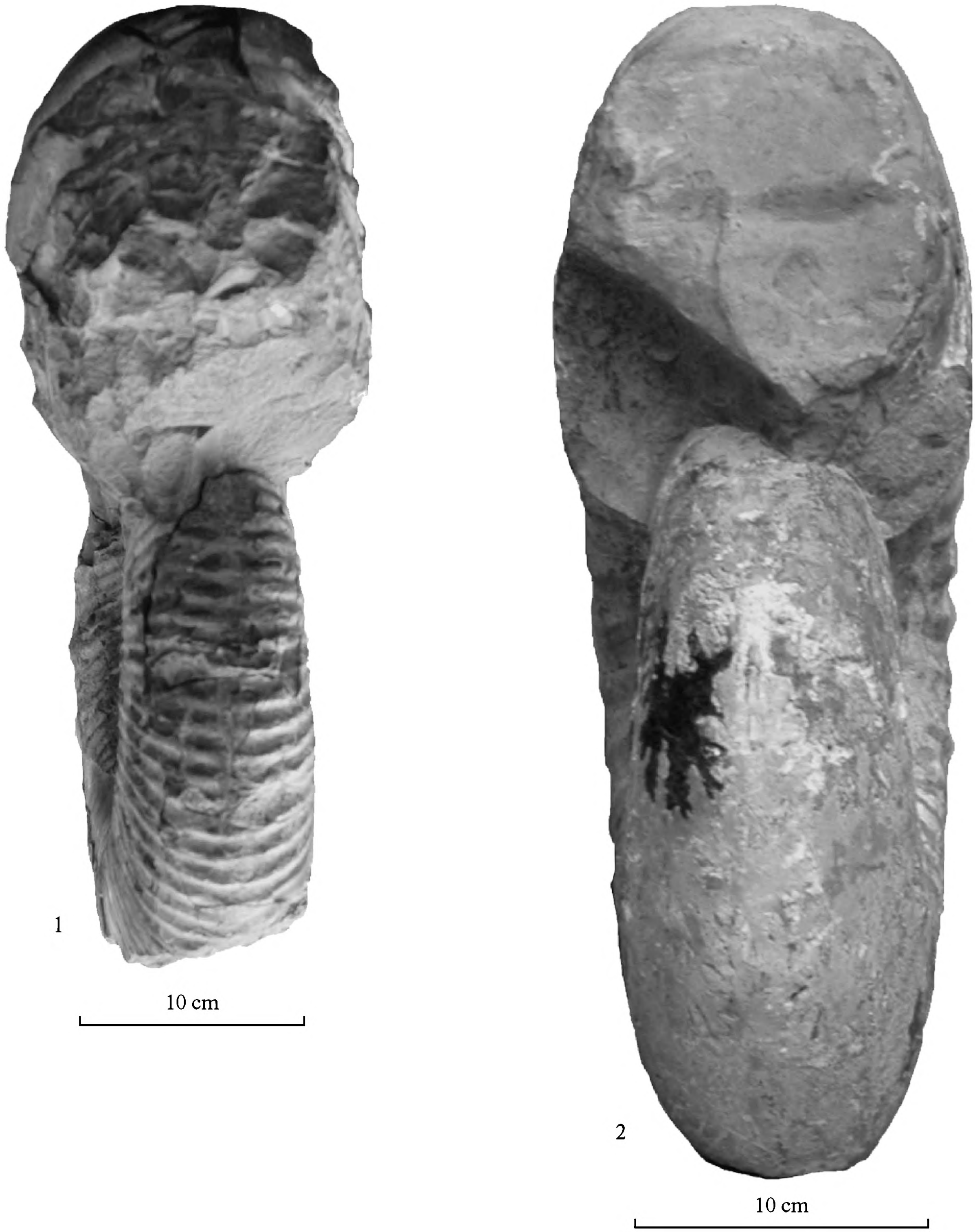


Fig. 95. Cross section of *Aconeceras (Aconeceras) nisum* (d'Orbigny); specimen TsNIGR Museum, no. 198/10367; Lesser Balkhan , Middle Aptian.

Plate 36



Explanation of Plate 36

Fig. 1. *Pseudoaustraliceras* aff. *ramososeptatum* (Anthula, 1899); specimen MZ MGU, no. 2/101; northwestern Caucasus, Belaya River, Upper Aptian.

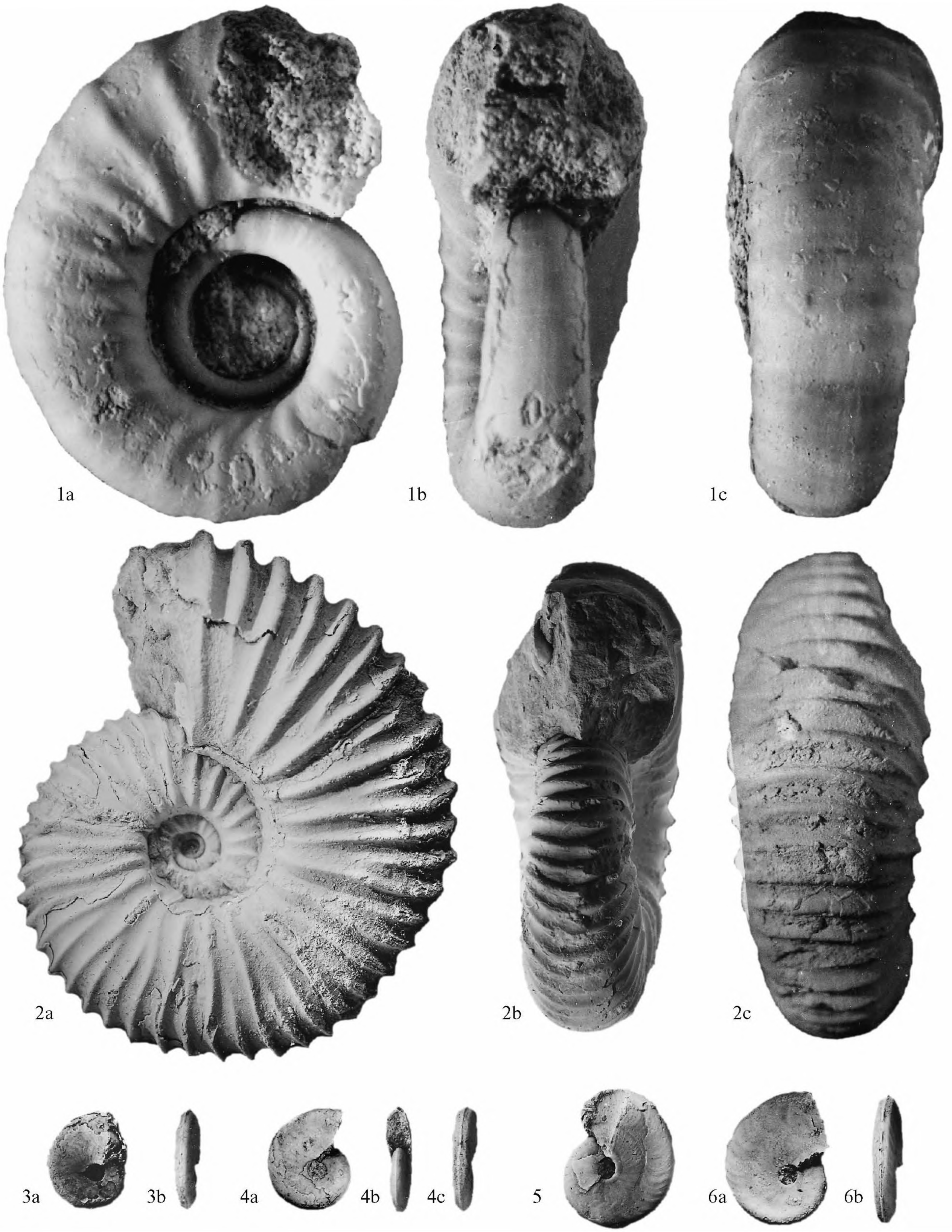
Fig. 2. *Parahoplites sjogreni* (Anthula, 1899); specimen MZ MGU, no. 1/101; Dagestan, village of Butri, Middle Aptian, *Parahoplites melchioris* Zone.

Plate 37

Explanation of Plate 37

Fig. 1. *Pseudoaustraliceras* aff. *ramososeptatum* (Anthula, 1899); specimen MZ MGU, no. 2/10; northwestern Caucasus, Belaya River, Upper Aptian.

Plate 38



(1893, pls. IV–VI, figs. 9a, 9b, 9c). Both figured French specimens are distinguished from the Turkmenistan specimens by the triangular whorl cross section. The shells of this species are distinguished from most species of *Aconeceras* by the almost complete absence of ornamentation on the flanks.

Occurrence. Turkmenistan (Great and Lesser Balkhan, Kuba Dagh), Middle Aptian, *E. subnodosocostatum* and *P. melchioris* zones, Upper Aptian, *A. prodromus* Zone; southeastern France and southern England, Upper Aptian.

Material. Seventeen variously preserved shells and molds. The suture is indistinct. Great Balkhan [Oglanly well (TsNIGR Museum, nos. 199/10367, 495-498/10367, 97/12133), Utuludzha well (TsNIGR Museum, nos. 196/10367, 499/10367, 84/12133)], Kuba Dagh Range [Kubasengir Range (TsNIGR Museum, nos. 195/10367, 74/12133), Yangadzha station (TsNIGR Museum, nos. 500–502/10367)], Lesser Balkhan [Torengly well (TsNIGR Museum, nos. 197, 198/10367, 200/10367)] Middle Aptian, *Epicheloniceras subnodosocostatum* and *Parahoplites melchioris* zones, Upper Aptian, *Acanthohoplites prodromus* Zone.

Aconeceras (Aconeceras) haugi (Sarasin, 1893)

Plate 38, figs. 4 and 5

Oppelia haugi: Sarasin, 1893, p. 156, pl. 4, fig. 11a, pl. 5, fig. 11b, pl. 6, fig. 11c; Koenen, 1902, p. 53, pl. 45, fig. 5.

Aconeceras cf. *haugi:* Casey, 1961a, p. 123, pl. 123, text-fig. 40i.

Holotype. Specimen figured by Sarasin (1893, pl. 4, fig. 11a, pl. 5, fig. 11b, pl. 6, fig. 11c); Aptian; southeastern France, St.-Dizier. Designated herein by monotypy.

Shell shape. The shell is small, flattened, with rapidly expanding slightly overlapping whorls. The venter is narrow, coronatiform. The ventrolateral shoulder is rounded, but distinct. The flanks are weakly convex; the maximum shell width is in the middle of the whorl height. The umbilical wall is low and vertical. The whorl cross section is rectangular–oval, strongly elongated. The umbilicus is narrow and stepped.

Dimensions in mm and ratios:

Specimen TsNIGR Museum, no.	Dm	WH	WW	UW	WH/Dm	WW/Dm	UW/Dm	WW/WH
201/10367	20.5	10.8	4.5	3.2	50	0.21	0.15	0.42
203/10367	18.1	9.5	4.2	2.6	44	0.23	0.14	0.44
202/10367	17.5	8.8	4.2	3.3	50	0.24	0.19	0.48
205/10367	15.6	8.1	3.8	2.8	52	0.24	0.18	0.47
206/10367	13.5	7.4	3.3	2.3	55	0.24	0.17	0.45
204/10367	12.9	5.7	3.1	2.4	52	0.24	0.19	0.46
207/10367	11.6	5.8	3.2	2.1	50	0.28	0.18	0.56
208/10367	11.2	5.4	3.0	2.0	48	0.27	0.18	0.56

Ornamentation. The shell is covered flattened sickle-shaped ribs, narrow near the umbilical shoulder and widening toward the mid-flank. In the umbilical half of the lateral sides, the ribs lean forward and, in the upper half, form a relatively steep ribs arched backward. The ribs have uneven sides: the anterior side is gently sloping, while the posterior side is steep. At the point of curvature, the ribs are raised, forming triangular folds. A shallow concentric groove sometimes runs in this place. On the ventrolateral shoulder, the ribs are very prominent in relief and approach the keel at an angle of about 30°–40°. The spaces are narrower than the ribs. All ribs are covered by thin sickle-shaped striation, usually not more than three striae per rib. The striae vary in width and height. A finely serrated keel runs on the mid-venter from the diameter of 10 mm. A shallow furrow is sometimes observed along the keel on the venter.

Comparison. *A. (A.) haugi* is most similar to *A. nisus* d'Orbigny and *A. nisoides* Sarasin and differs from the first in the distinct ornamentation, rectangular whorl cross section, and more conspicuously delineated keel. It is distinguished from *A. nisoides* by the smaller size and more clearly delineated wide flat ribs. The surface of the ribs of the described species bear thin striation parallel to the ribs, whereas, in *A. nisoides,* the ribs are indistinct and the striae are relatively prominent.

Occurrence. Turkmenistan (Tuarkyr, Great and Lesser Balkhan, Kuba Dagh), Middle Aptian;

Explanation of Plate 38

Fig. 1. *Luppovia* sp.; specimen PIN, no. 5265/281 (strongly magnified); Tuarkyr, Umokdere gorge; Middle Aptian, *Epicheloniceras subnodosocostatum* Zone.

Fig. 2. *Parahoplites melchioris* Anthula, 1899; specimen PIN, no. 5265/34; Dagestan, village of Aya-Makhi, Middle Aptian, *Parahoplites melchioris* Zone.

Fig. 3. *Aconeceras (Aconeceras) nisus* (d'Orbigny, 1842); specimen TsNIGR Museum, no. 197/10367; Lesser Balkhan, Torengly well; Middle Aptian, *Parahoplites melchioris* Zone.

Figs. 4 and 5. *Aconeceras (Aconeceras) haugi* (Sarasin, 1893); (4) specimen TsNIGR Museum, no. 202/10367; Great Balkhan, Utuludzha well; Middle Aptian, *Epicheloniceras subnodosocostatum* Zone; (5) specimen no. TsNIGR Museum no. 201/10367; Tuarkyr, Babashi well; the same age.

Fig. 6. *Aconeceras (Sinzowia) aptianum* (Sarasin, 1893); (6) specimen TsNIGR Museum, no. 192/10367; Lesser Balkhan, Torengly well; Middle Aptian, *Parahoplites melchioris* Zone.

southeastern France, Aptian; southern England and northern Germany, Lower Aptian.

Material. Sixteen variously preserved specimens, represented by complete shells and mold fragments. Tuarkyr [Babashi well (TsNIGR Museum, no. 201/10367)], Great Balkhan [Oglanly well (TsNIGR Museum, nos. 205/10367, 208/10367, 503, 504/10367, 98/12133)], [Utuludzha well (TsNIGR Museum, no. 202/10367)], [Bordzhakly well (TsNIGR Museum, no. 207/10367)], Kuba Dagh [Yangadzha (TsNIGR Museum, nos. 203, 204/10367, 206/10367, 66/12133)], Kuba Dagh [Kubasengir (TsNIGR Museum, no. 506/10367)], Lesser Balkhan [Torengly well (TsNIGR Museum, nos. 98/12133, 118, 119/12133)], Middle Aptian, *Epicheloniceras subnodosocostatum* and *Parahoplites melchioris* zones.

Subgenus *Sinzovia* I. Sazonova, 1958

Aconeceras (Sinzovia): Wright et al., 1996, p. 14; Riccardi et al., 1987, p. 157.

Type species. *Ammonites trautscholdi* Sinzow, 1870 (=*Ammonites bicurvatus* Trautschold, 1865 non Michelin, 1838); Lower Aptian; Russia, Simbirsk (now Ulyanovsk). Designated by Sazonova (1958, p. 126).

Diagnosis. Shell discoidal, relatively large for aconeceratids, almost involute; at early stages smooth; at late stages, with sickle-shaped ribs; ventral keel low, with small tubercles.

Composition. *A. (Sinzowia) nisoides* (Sarasin, 1893), Lower and Middle Aptian, France, England, Germany, Madagascar, Turkmenistan; *A. (S.) aptianum* (Sarasin, 1893), Middle and Upper Aptian, France, Russia (northern Caucasus), Turkmenistan; *A. (S.) trautscholdi* (Sinzow, 1870), Aptian, Germany, England, Russia, Morocco; *A.(S.) stollei* Casey, 1961, Aptian, Germany; *A. (S.) sazonovae* Wright, 2011, Aptian, Russia; *A. (S.) leanzai* Riccardi, Aguirre-Urreta, Medina, 1987, Albian, Argentina; *A. (S.) piatnitzkyi* Riccardi, Aguirre-Urreta, Medina, 1987, Upper Aptian, Argentina.

Comparison. This subgenus is distinguished from the subgenus *Aconeceras (Aconeceras)* by the presence in the ventral half of the flanks of relatively prominent sickle-shaped ribs, which appear earlier in ontogeny than in the ribbed representatives of the subgenus *Aconeceras (Sanmartinoceras)*.

Aconeceras (Sinzovia) aptianum **(Sarasin, 1893)**

Plate 38, fig. 6

Oppelia aptiana: Sarasin, 1893, p. 155, pl. 4, fig. 12a, pl. 5, fig. 12b, pl. 6, fig. 12c.

Sanmartinoceras aptianum: Casey, 1961a, p. 134, pl. 26, figs. 6a and 6b; text-figs. 43d and 43e.

Holotype. Specimen figured by Sarasin (1893, pl. 4, fig. 12a, pl. 5, fig. 12b, pl. 6, fig. 12c); Aptian; southeastern France, Basses-Alpes, Cheiron. Designated by Casey (1961a, p. 134).

Shell shape. The shell is small, flattened, with rapidly expanding whorls. The venter is relatively wide, coronatiform, with slightly divergent sides. The ventrolateral shoulder is rounded. The flanks are flattened, joining the low vertical umbilical wall at 90[deg]. The general whorl outline is rectangular, strongly compressed. The umbilicus is narrow and stepped.

Dimensions in mm and ratios:

Specimen TsNIGR Museum, no.	Dm	WH	WW	UW	WH/Dm	WW/Dm	UW/Dm	WW/WH	No. of ribs per half whorl
191/10367	25.0	11.7	6.0	4.4	0.47	0.24	0.18	0.51	14
192/10367	22.7	12.0	5.8	3.6	0.53	0.26	0.16	0.48	16
193/10367	19.9	10.7	5.1	3.0	0.54	0.26	0.15	0.48	15
194/10367	14.0	7.1	3.8	2.5	0.51	0.27	0.18	0.53	–

Ornamentation. The shell is covered by wide, flat, sickle-shaped striated ribs; striation repeats the course of the ribs. The ribs begin at the umbilical shoulder and, in the umbilical half of the flanks, they are very weakly discernible. In the ventral half, above the curvature of the "sickle," they rapidly increase forming prominent semicircular folds, most distinct near the ventrolateral shoulder. There are 14–16 ribs per half whorl, separated by equally wide or narrower spaces. A distinct finely serrated ventral keel appears on the shells over 8–10 mm in diameter.

Suture (Fig. 96). Apart from the ventral and umbilical lobes, four lobes lie on the external side of the whorl. The ventral lobe has ventral prongs set widely apart and located somewhat below the umbilical lobe. The umbilical lobe is narrow, weakly asymmetrical. The saddle V/U is considerably lower than the saddle U/U_1.

Variability. The variability is observed in the degree of rib development in the ventral half of the flanks, in their width and the width of spaces between the ribs.

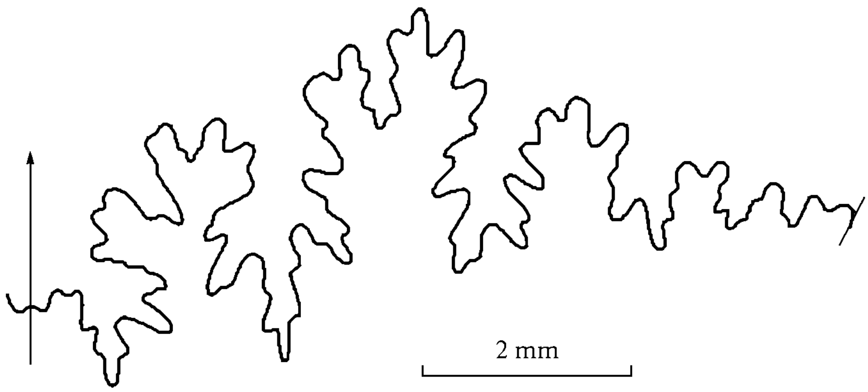


Fig. 96. Suture of *Aconeceras (Sinzovia) aptianum* (Sarasin); specimen TsNIGR Museum, no. 191/10367; Kopet Dagh, Yailak gorge; Middle Aptian, *Parahoplites melchioris* Zone.

Comparison and remarks. This species is most closely similar to *A. (Sinzovia) trautscholdi* Sinzow (Sinzow, 1899, p. 27, pl. A, figs. 1, la, lb), although the ribbing in the species described is weaker than in *A. (Sinzovia) trautscholdi,* except in the ventral area of the flanks, where ribs are most prominent. The ribs in *A. (S.) aptianum* are narrower and relatively higher than in *A. (S.) trautscholdi.* In addition, all figured specimens of the latter species from different localities are larger than those described. The specimens of *A. (S). aptianum,* which have the weakest ribbing, resemble specimens of the species *Aconeceras (A.) haugi* Sarasin (Sarasin, 1893, pl. 4, fig. 11a, pl. 5, fig. 11b, pl. 6, fig. 11c), but are distinguished from these by the wider ribs with narrow spaces in between, and in the absence of prominent folds at the point of rib curvature that are characteristic of *A. (A.) haugi.*

Occurrence. Turkmenistan (Great and Lesser Balkhan, Kopet Dagh), Middle Aptian; southeastern France, Upper Aptian; southern England, Lower Aptian.

Material. Ten specimens varying in preservation. Great Balkhan: Oglanly well (TsNIGR Museum, no. 507/10367), Utuludzha well (TsNIGR Museum, nos. 508-510/10367, 511/10367), Bordzhakly well (TsNIGR Museum, no. 194/10367); Lesser Balkhan: Torengly well (TsNIGR Museum, nos. 192, 193/10367, 512/10367); Kopet Dagh: Yailak gorge (TsNIGR Museum, no. 191/10367), Middle Aptian, *Epicheloniceras subnodosocostatum* and *Parahoplites melchioris* zones.

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